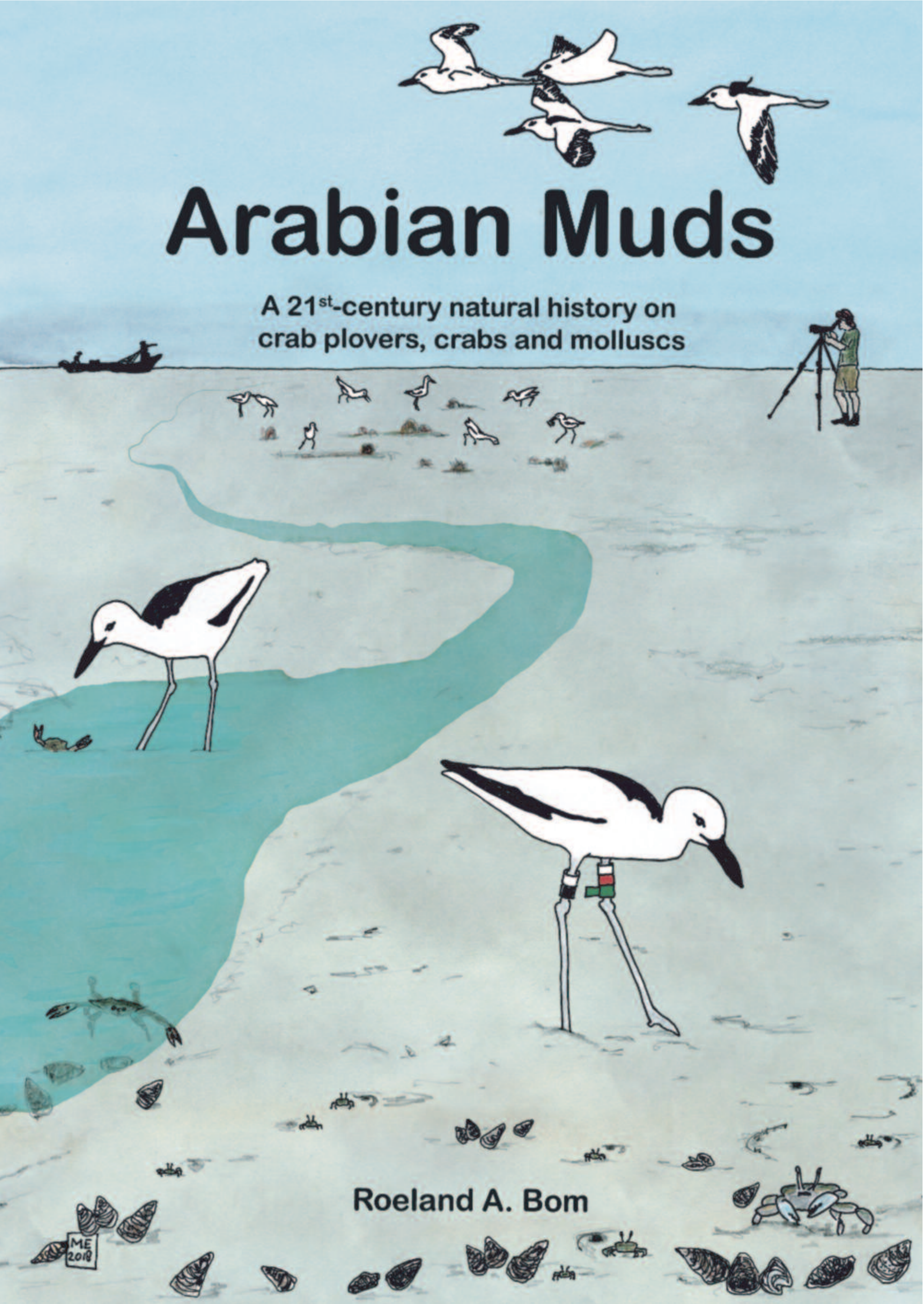
Arabian Muds

A 21st-century natural history on crab plovers, crabs and molluscs



Roeland A. Bom

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A 21st-century natural history on crab plovers, crabs and molluscs

The research presented in this thesis was conducted at the Department of Coastal Systems at the NIOZ Royal Netherlands Institute for Sea Research, ‘t Horntje, (Texel), The Netherlands, according to the requirements of the Graduate School of Science (Faculty of Mathematics and Natural Sciences, University of Groningen).

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A 21st-century natural history on crab plovers, crabs and molluscs

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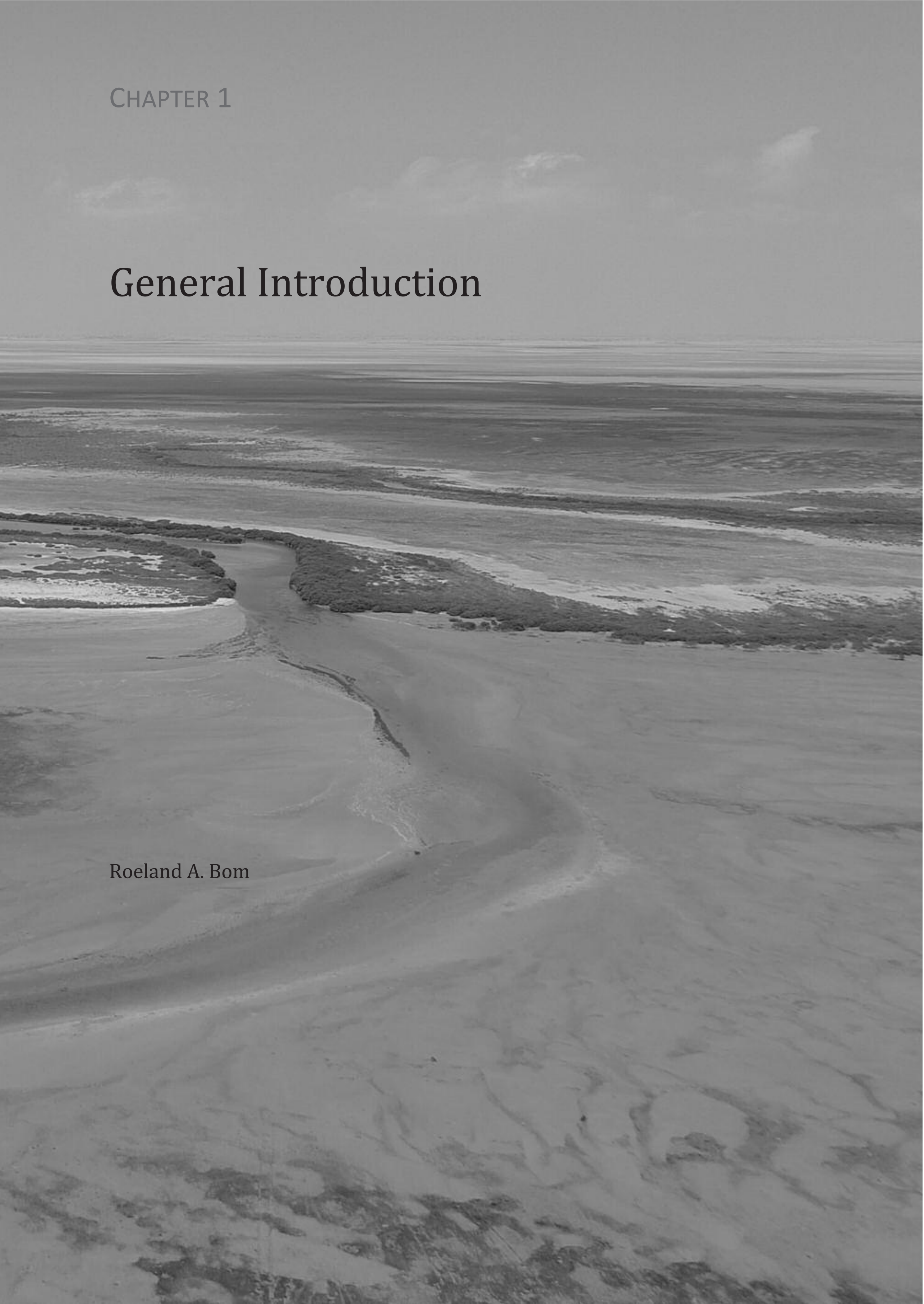
Contents



CHAPTER 1

General Introduction

Roeland A. Bom

"In considering the distribution of organic beings over the face of the globe, the first great fact which strikes us is that neither the similarity nor the dissimilarity of the inhabitants of various regions can be wholly accounted for by climatal and other physical conditions." (Darwin 1859)

Across the globe, organisms appear to be strikingly different with respect to their morphology, physiology and behaviour, even in climatically similar areas. This observation inspired Darwin (1859) to be one of the first to understand that many characteristics of organisms reflect the way in which individuals and groups of organisms interact with each other, in their attempts to acquire shelter, food and mates. Thus, interactions within and between species are a major evolutionary force in the history of life (Dietl & Kelly 2002) and "The relation of organism to organism is the most important of all relations" (Darwin 1859).

The marine tropics provide a classical example of an environment with climatically similar conditions in which species show distinct patterns in diversity and characteristics. Currently, there are four tropical marine areas distinguished with assemblies of animals with shared characteristics (Fig. 1.1) (Vermeij 1993; Briggs 2006). By far the largest of these 'biogeographical areas' is the Indo-West Pacific. Coastal ecosystems in this area are renowned for their large biodiversity, and for its animals having remarkably well-developed traits that relate to defence against predators. Most of what is currently known about the animals in the Indo-West Pacific stems from work on rocky shores and shallow waters and is based on work on marine invertebrates and fishes (Vermeij 1993; Briggs 2006). Intertidal mudflats, soft bottom areas that are exposed during low tide and covered with high tide, have received relatively little published attention from ecologists.

This thesis concerns the little studied intertidal mudflats of Barr Al Hikman in the Sultanate of Oman. More specifically, I studied whether the physical and behavioural defence mechanisms of crabs and molluscs against predation are as well-developed in Barr Al Hikman as in other coastal areas in the Indo-West Pacific, and how that affects the ecology of shorebirds that use these invertebrate species as a resource. In this first chapter I present a synopsis of the Indo-West Pacific biogeographical area, intertidal mudflat ecosystems in general and Barr Al Hikman in particular. Next I will introduce shorebirds and the crab plover *Dromas ardeola*, the species that plays the leading part in this thesis.

Indo-West Pacific

The coastal region of the Indo-West Pacific is recognized as a separate biogeographical area on the basis of its distinct array of marine invertebrate (e.g. molluscs, crabs) and fish species. The marine species that live in the Indo-West Pacific became isolated from the other tropical regions around 3 to 3.5 million years ago. Before that time, there was a more or less unbroken connection between all tropical oceans. After its isolation, barriers prevented species to move between areas. The barriers of the Indo-West Pacific as we known them today are represented

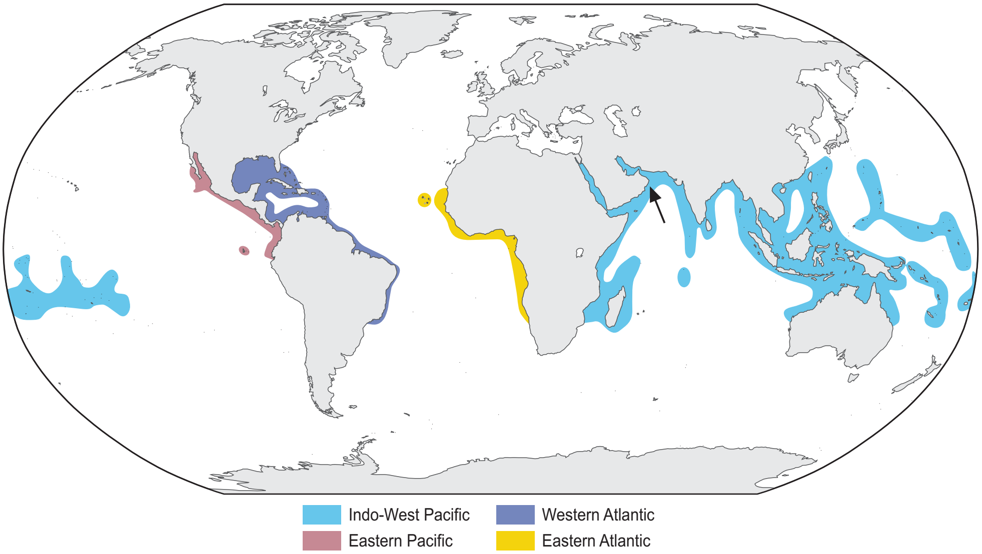


Figure 1.1. Major tropical marine biogeographical regions. Adapted from Vermeij (1993). Barr Al Hikman is indicated by the arrow.

by a deep stretch of ocean in the east, and the African continent in the west, where the land extends just far enough south to keep warm-water molluscs, crabs and benthic fish species from dispersing around Kaap de Goede Hoop (Briggs 2007). During its isolation, species have undergone a remarkable history compared with the other biogeographical areas. Marine animals became distinctly diverse (Vermeij 1993; Briggs 2006; Ng *et al.* 2008) and evolved anti-predation traits that are extremely well-developed when compared to species in other biogeographical regions (Vermeij 1978; Palmer 1979).

There are several explanations for the remarkable history of the marine fauna in the Indo-West Pacific. Geerat Vermeij has hypothesized that the high diversity results from low extinction rates and high environmental stability whereas the powerful armature are a result of a long-lasting arms races which could prosper in the Indo-West Pacific because it is a large and nutrient rich area (Vermeij 1976, 1978; Kosloski & Allmon 2015, and see the subsequent chapters in this thesis).

Intertidal mudflats

Intertidal mudflats can be found in estuaries with a (large) tidal range. Around the world about 30 large (>80.000 ha) and many more smaller areas can be found, covering all climatic zones and biogeographical areas (Deppe 1999). Intertidal mudflats are attractive areas to do research, not only because of their many natural values, but also because the spatiotemporal distribution of marine benthic food sources are often relatively easy to quantify and some of the secondary consumers (mainly shorebirds) can be observed with relative ease.

Within the Indo-West Pacific large intertidal mudflats are found north of Australia, around Indonesia, at the coastal areas of Bangladesh, India, Pakistan, Iran and several areas around the Arabian Peninsula and the east coast of Africa (Butler *et al.* 2001; van de Kam *et al.* 2004; Delany *et al.* 2009). The intertidal mudflats of Australia have received extensive attention from ecologists. For the other areas, at best, basic information exists on the occurrence of some of the organisms present (e.g. Piersma *et al.* 1993b; Delany *et al.* 2009; Conklin *et al.* 2014). Within the Indo-West Pacific, our study system in Oman is situated in a particularly interesting area as the area falls within the Somali current, an upwelling system that brings cold and nutrient rich water to the coasts of Oman and Yemen (Sheppard *et al.* 1992; Izumo *et al.* 2008). Due to the excessive nutrient input, upwelling systems are generally characterised by high biological productivity of unicellular algae (such as diatoms), seagrasses and mangroves.

Primary producers are the food source for a larger number of primary consumers such as molluscs, polychaetes and crustaceans. Then, the primary consumers are the main resource for a large number of secondary consumers including fish, crabs and shorebirds (Swennen 1976; van de Kam *et al.* 2004). These secondary consumers depend on intertidal mudflats for their survival, despite that many of them spend only part of their lives on intertidal mudflats. For instance, a large number of shorebird species spend the complete non-breeding season at intertidal mudflats areas (van de Kam *et al.* 2004). Furthermore, intertidal mudflats act as nursery grounds for many marine species, including fish, crabs and shrimps (Potter *et al.* 1983; Kuipers & Dapper 1984; van der Veer *et al.* 2001).

Barr Al Hikman

Barr Al Hikman is a mainland peninsula located within the Sultanate of Oman (20.6° N, 58.4° E, Fig. 1.1). The hinterland of the peninsula consists of about 1400 km^2 sabkha (salt areas) where only bacterial and archaeal communities can persist (Vogt *et al.* 2018). Coastal dunes along with scattered mangrove stands of Avicennia marina form a narrow 5–20 fringe between the sabkhas and the intertidal mudflats (Fouda & Al-Muharrami 1995). The intertidal area consists of about 190 km^2 mudflats and some scattered reefs. Basic ecological research has shown that the intertidal and sublittoral area of Barr Al Hikman is an important (nursery) area for marine animals including turtles (Ross 1985), whales (Salm *et al.* 1993), shorebirds (Green *et al.* 1992) and shrimps (Mohan & Siddeek 1996).

Over the last 50 years, Oman and most other countries in the Arabian Peninsula abruptly changed from a closed and traditional society (vividly described by Thesiger (1959) in his deservedly appraised book ‘Arabian Sands’) into a modern economy. Many of the intertidal mudflats in the area suffered from land reclamation, pollution and overfishing (Sheppard *et al.* 2010; Burt 2014). Yet, Barr Al Hikman still features many characteristics of a pristine coastal area (Reise 2005). The area lacks extensive dike constructions that characterize many of the ‘modern’ intertidal areas (Fig. 1.2) (Reise 2005), so hydrodynamic and sedimentary processes are merely undisturbed. Extensive seagrass beds still exist, which have disappeared from other intertidal areas (in the Dutch Wadden Sea after a wasting disease during the 1930s, Swennen 1976). The variety of shark and ray species caught in the shallow waters of Oman is similar to what is reported about the coastal areas in Europe a century ago (Lotze 2005, 2007). The density of shorebirds are also similar to the densities in other intertidal areas before they decreased in recent decades.

Shorebirds

Shorebirds are often regarded as sentinel species of intertidal mudflats, because their morphological characteristics, their habitat use and their foraging behaviour may reflect current and past conditions of the mudflats (Piersma & Lindström 2004). It is beyond the scope of this thesis to review the many inspiring publications and PhD theses on shorebirds (see for instance the last three theses of the NIOZ Royal Netherlands Institute for Sea Research and references therein (Bijleveld 2015; de Fouw 2016; Oudman 2017). Work which was of incredible help to develop the ideas presented in this thesis. Particularly, I benefited from this previous work that showed how to study the intrinsic relation between shorebirds and the benthic community; that is, how morphological and behavioural anti-predation traits in benthic invertebrate may affect prey choice in shorebirds and how we can use optimal foraging behaviour to understand prey choice 'decisions' (see work by Piersma 1994; Zwarts 1997; van Gils 2004).

Most shorebirds in the Indo-West Pacific, including Barr Al Hikman, breed in temperate or high Artic regions. A few can be marked as local breeders; they migrate for breeding, but stay within the same biogeographical area. These local species are of particular interest if we are to understand which parts of the ecology of shorebirds serve best as sentinels for current ecological pressures that threaten the future of coastal marine ecology of the Indo-West Pacific. Among them is the crab plover *Dromas ardeola*, the focal bird of this thesis.

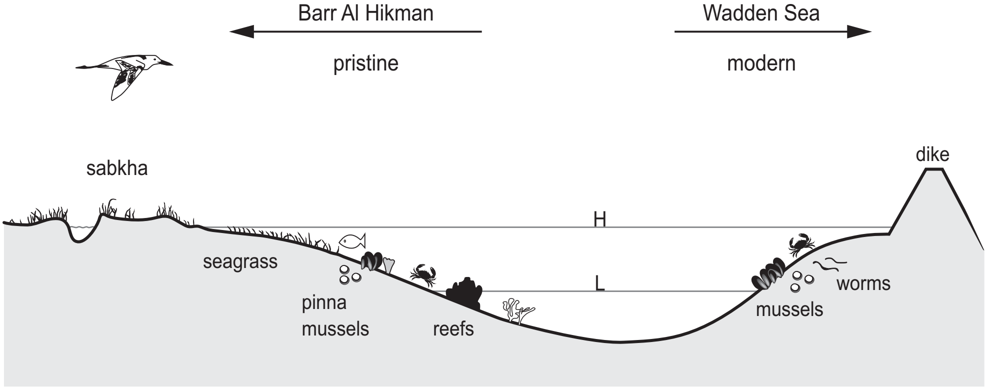


Figure 1.2. Barr Al Hikman still features many characteristics of a pristine coastal area. The area lacks dike constructions and harbours seagrass beds, intact fish populations and large reef constructions. In many aspects this contrasts with the situation of other intertidal mudflat areas, such as the Wadden Sea in the Netherlands. Adapted from Reise (2005).

Crab plovers

Crab plovers are shorebirds extraordinaire, with their long legs, black-and-white plumage and massive bill (Fig. 1.3). They are in the order Charadriiformes (shorebirds), and comprise the only member of the family Dromadidae. Their closest relatives are the probably only distantly related pratincoles and coursers (Pereira & Baker 2010). The world population of crab plovers is estimated at 60.000 – 80.000 birds (Delany *et al.* 2009). They are endemic to the shores of the Indo-West Pacific, and breed exclusively on islands around the Arabian Peninsula (Rands 1996). Here, they breed in colonies on sandy islands and generally lay a single egg in self-excavated burrows (Tayefeh *et al.* 2013b). Temperature inside the burrows is close to optimal for embryo development, and probably allow crab plovers to spend a large amount of time off the nest (De Marchi *et al.* 2008; De Marchi *et al.* 2015a). After hatching, chicks remain within the breeding area until the end of the breeding season, where they are provisioned by both of the parents (Almalki *et al.* 2015). In autumn, they join one of their parents in migration to the non-breeding area, where parental care continues (De Sanctis *et al.* 2005). The heavy bill and the

Figure 1.3. Crab plovers are shorebirds extraordinaire. This picture shows a crab plover with a young. Crab plovers are generally provisioned by one of their parents throughout their entire first year.

frontally positioned eyes indicate that crab plovers forage on well-defended prey which they detect by visual hunting. Indeed, some literature and a large number of pictures on the internet show that the diet of crab plovers include massive crabs that strongly defend themselves (Swennen *et al.* 1987). The environment to which crab plovers are endemic is relatively poorly studied by biologists, and much of the life-history of the species remains unknown.

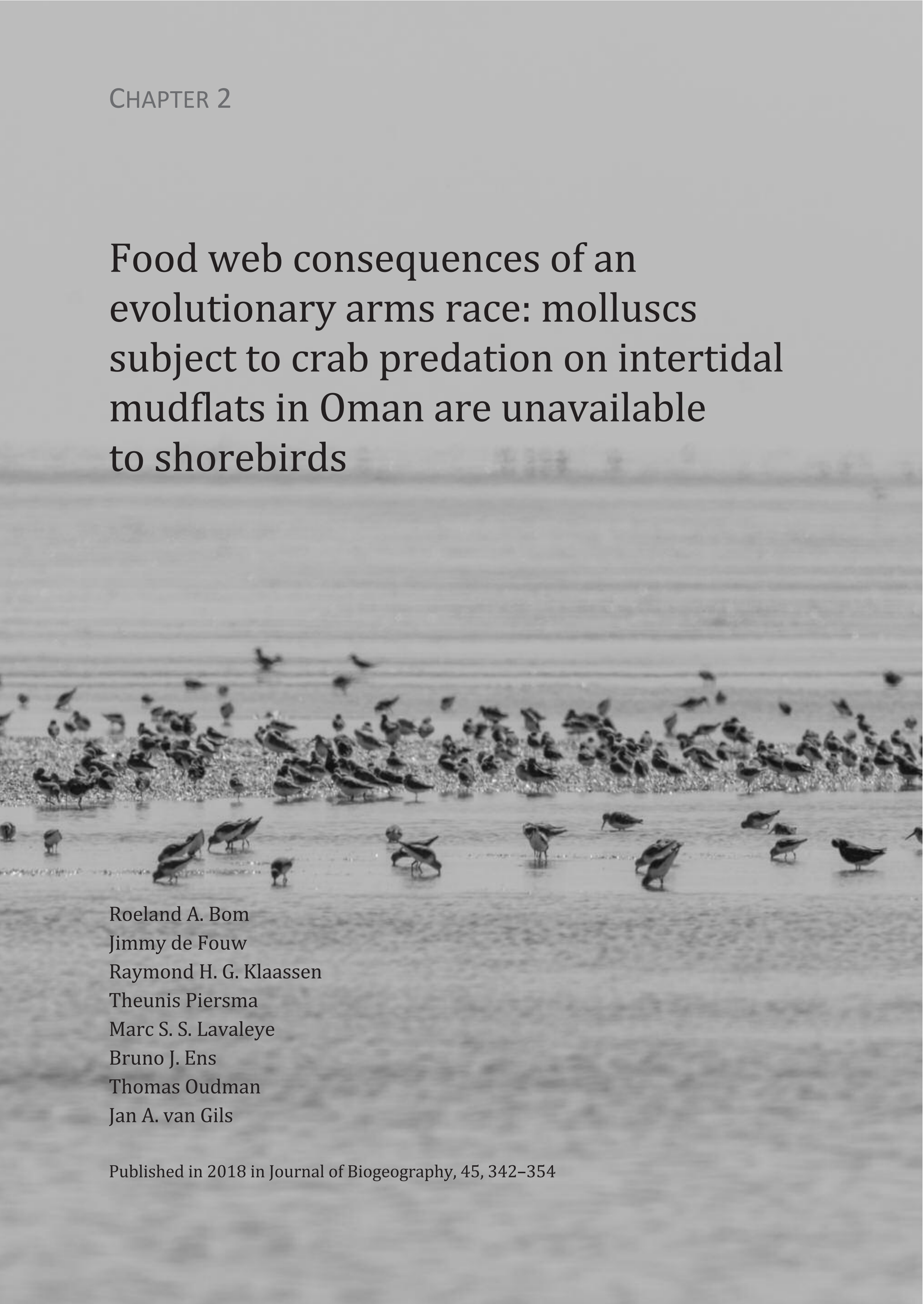
Thesis outline

The fundaments of this thesis are laid in **Chapter 2** which describes the macrozoobenthic community in terms of species abundances but also with respect to their morphological and behavioural anti-predation characteristics. The main conclusion of this chapter is that crabs have a profound role in shaping the ecosystem. **Chapter 3** describes the spatiotemporal dynamics of crab in relation to the intertidal environment in more detail. **Chapter 4** concerns the burrow architecture of some of the crabs that can be found at Barr Al Hikman. Then we move on to the shorebirds, which starts in **Chapter 5** with a general description of the shorebird community on the basis of three winter surveys. In the next chapter, **Chapter 6**, the crab plover is introduced in more detail when we put the survey results to the test by matching them with demography (survival and reproduction) estimates based on colour ring observations. **Chapter 7** and **Chapter 8** focus on the processes that shape the foraging behaviour of crab plovers, highlighting that crab plovers prefer swimming crabs with well-developed armature. To study the (foraging) behaviour of crab plovers in more detail, a method to classify crab plover behaviour from state-of-the-art GPS and accelerometer tracking technology is developed in **Chapter 9**. In **Chapter 10** we used this method to study the whereabouts of the crab plovers in relation to the tidal cycle and link them to the behaviour of their preferred prey. **Chapter 11** takes a brief excursion to Kuwait, the breeding grounds of the crab plovers wintering at Barr Al Hikman. It describes some basic aspects of breeding ecology. It also provides an estimate of the total breeding population size at Kuwait, and update the list of currently known breeding areas. In **Chapter 12** I aim put the results in a wider context by discussing the evolutionary processes that have shaped the crab plover, crabs and molluscs, and their intimate relation with the environment they live in. Finally, I will expand on how these findings may contribute to our general understanding of the processes that shaped the Barr Al Hikman ecosystem, and discuss its importance for the management of its natural resources.

The results here presented here are based on over eight years of observations that, to cite the great naturalist Gilbert White, ‘are, I trust, true in the whole, though I do not pretend to say that they are perfectly void of mistake, or that a more nice observer might not make many additions, since subjects of this kind are inexhaustible.’ (White 1789)

Acknowledgements

I thank Thomas Oudman, Theunis Piersma and Jan van Gils for constructive comments on an earlier version of this chapter and Maaike Ebbinge for preparing figure 1.1 and 1.2.



Chapter 2

Food web consequences of an evolutionary arms race: molluscs subject to crab predation on intertidal mudflats in Oman are unavailable to shorebirds

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Abstract

Molluscivorous shorebirds supposedly developed their present wintering distribution after the last ice age. Currently, molluscivorous shorebirds are abundant on almost all shores of the world, except for those in the Indo-West Pacific (IWP). Long before shorebirds arrived on the scene, molluscan prey in the IWP evolved strong anti-predation traits in a prolonged evolutionary arms race with durophagous predators including brachyuran crabs. Here, we investigate whether the absence of molluscivorous shorebirds from the intertidal mudflats of Barr Al Hikman, Oman can be explained by the molluscan community being too well defended. Based on samples from 282 locations across the intertidal area the standing stock of the macrozoobenthic community was investigated. By measuring anti-predation traits (burrowing depth, size and strength of armour), the fraction of molluscs available to molluscivorous shorebirds was calculated. Molluscs dominated the macrozoobenthic community at Barr Al Hikman. However, less than 17% of the total molluscan biomass was available to shorebirds. Most molluscs were unavailable either because of their hard-to-crush shells, or because they lived too deeply in the sediment. Repair scars and direct observations confirmed crab predation on molluscs. Although standing stock densities of the Barr Al Hikman molluscs were of the same order of magnitude as at intertidal mudflat areas where molluscivorous shorebirds are abundant, the molluscan biomass available to shorebirds was distinctly lower at Barr Al Hikman. The established strong molluscan anti-predation traits against crabs precludes molluscan exploitation by shorebirds at Barr Al Hikman. This study exemplifies that dispersal of 'novel' predators is hampered in areas where native predators and prey exhibit strongly developed attack and defence mechanisms, and highlights that evolutionary arms races can have consequences for the global distribution of species.

Introduction

Marine molluscs have evolved their defence mechanisms under the selective pressure imposed by durophagous (shell-destroying) predators (Vermeij 1977a). Fossil records show the long evolutionary time over which this took place. During this period, molluscs strengthened their shell armour by increasing their shell thickness, and by the development of spines, ribs and/or nodules. At the same time, durophagous predators became better shell crushers, peelers, drillers and/or splitters (Vermeij 1976, 1977b, 1978, 1987, 2013). These observations led to the seminal idea that molluscan prey and durophagous predators have been, and currently are, engaged in an evolutionary arms race in which molluscs continuously evolve their defence mechanisms to adapt to their durophagous predators, which (in turn) continuously evolve their attack mechanisms (Vermeij 1994; Dietl & Kelley 2002).

Evolutionary arms races between molluscs and durophagous predators are most notable in tropical oceans, probably because higher ambient temperatures enabled higher calcification rates in molluscs, and more metabolic activity in durophagous predators (Vermeij 1977b; Zipser & Vermeij 1978). Within the tropical oceans, the Indo-West Pacific (IWP) has been recognized as an area where evolutionary arms races have been especially intense. Specifically, in the IWP molluscs have the hardest to crush shells, and durophagous crabs and fishes have the strongest claws and the strongest shell-crushing abilities (Vermeij 1976, 1977b, 1987, 1989; Palmer 1979; Vermeij 1987, 1989). It has been hypothesized that the evolutionary arms race between molluscs and predators in the IWP has benefitted from a long history of co-evolution and escalation, low extinction rates, high nutrient availability, and high environmental stability (Vermeij 1974, 1978, 1987; Roff & Zacharias 2011; Kosloski & Allmon 2015).

Although molluscs dominate many of the intertidal macrozoobenthic communities in the IWP (Piersma *et al.* 1993a; Keijl *et al.* 1998; Purwoko & Wolff 2008); Fig. 2.1), these same intertidal mudflats lack a substantial number of molluscivorous shorebirds (Piersma 2006; Fig. 2.1). Many of world’s molluscivorous shorebirds are long-distance migrants, travelling between arctic and boreal breeding areas and temperate and tropical wintering grounds. The IWP is well within the flight range of the breeding areas of several molluscivorous shorebirds, including Eurasian oystercatcher (*Haematopus ostralegus*, hereafter: oystercatcher), great knot (*Calidris tenuirostris*) and red knot (*Calidris canutus*). However, most oystercatchers and great knots migrate to areas outside the IWP (Delany *et al.* 2009; Conklin *et al.* 2014), while red knots are absent from the IWP (Piersma 2007), except for one area in north-west Australia (Tulp & de Goeij 1994; Conklin *et al.* 2014).

The fossil record shows that molluscs and the first durophagous predators, including crabs and fishes, developed their defence and attack mechanisms during the Mesozoic Marine Revolution in the Jurassic or earliest Cretaceous (Vermeij 1977a, 1987; Walker & Brett 2002; Harper 2003; Dietl & Vega 2008). Shorebirds (Charadriiformes) appeared during the late Cretaceous between 79 and 102 Mya. Lineages of the currently known molluscivorous shorebirds diverged from other Charadriiformes lineages around 20 Mya (Paton *et al.* 2003; Baker *et al.* 2007), whereas the current migratory flyways (Fig. 2.1) were established after the Last Glacial Maximum, about 20 kyr (Buehler & Baker 2005; Buehler *et al.* 2006). With the molluscan anti-predation traits evolving before the appearance of molluscivorous shorebirds,

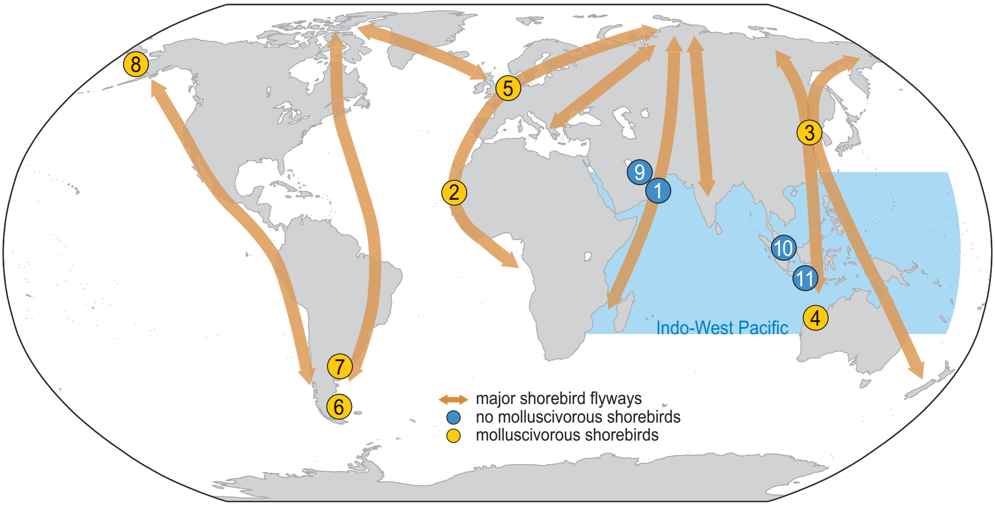

Figure 2.1. World map (Robinson projection) showing the IWP biogeographical area and the major shorebird flyways. The numbers refer to sites that are mentioned in the text: 1) Barr Al Hikman, Oman, our study site, 2) Banc d'Arguin, Mauritania, 3) Bohai Bay, China, 4) Roebuck Bay, Australia, 5) Wadden Sea, the Netherlands, 6) Río Grande, Argentina, 7) San Antonio Oeste, Argentina, 8) Alaska, United States of America, 9) Khor Dubai, United Arabian Emirates, 10) Java, Indonesia, 11) Sumatra, Indonesia.

it could be that the relative scarcity of molluscivorous shorebirds within the IWP is a consequence of relatively intense and long-lasting evolutionary arms races in the IWP – arms races that have rendered the heavily defended molluscs unavailable to shorebirds.

Here, we investigate whether the absence of molluscivorous shorebirds from the intertidal mudflats of Barr Al Hikman in the Sultanate of Oman (Fig. 2.1, site 1) can be explained by molluscs being too well defended, because they have been, and remain, subject to durophagous predation. We compare our results with molluscan communities on intertidal sites where molluscivorous shorebirds are abundant, and use these results to make inferences about the IWP as a whole.

Materials and Methods

Study area

Barr Al Hikman (20.6° N, 58.4° E) is a peninsula of approximately 900 km^2, located in the centraleastern Sultanate of Oman (Fig. 2.2A) and bordering the Arabian Sea. Seaward of the coastline an area of about 190 km^2 of intertidal mudflats is divided into three subareas: Shannah, Khawr Barr Al Hikman and Filim (Fig. 2.2B–D). Over 400,000 nonbreeding shorebirds visit the area in winter (Chapter 5), making it one of the most important wintering sites for shorebirds in the IWP (Delany *et al.* 2009; Conklin *et al.* 2014). The oystercatcher and the great knot are the only molluscivorous shorebirds in the area. In 2008 their midwinter numbers were estimated at 3,900 and 360 respectively (Chapter 5, Appendix A2.1), thus comprising about 1% of the shorebird population at Barr Al Hikman. The area is relatively pristine, with only a few local industries, including salt mining and some, mainly offshore, fisheries. There is no harvesting of shellfish in the area.

Macrozoobenthos standing stock assessment

The standing stock of the macrozoobenthic community, the potential food source for shorebirds, was sampled in January 2008 at 282 sampling stations (Fig. 2.2C, D). These stations were arranged in nine 250-m grids across the three subareas (Fig. 2.2C, D). Each grid comprised four rows perpendicular to the coastline. On the mudflat at Filim, one grid was limited to one row

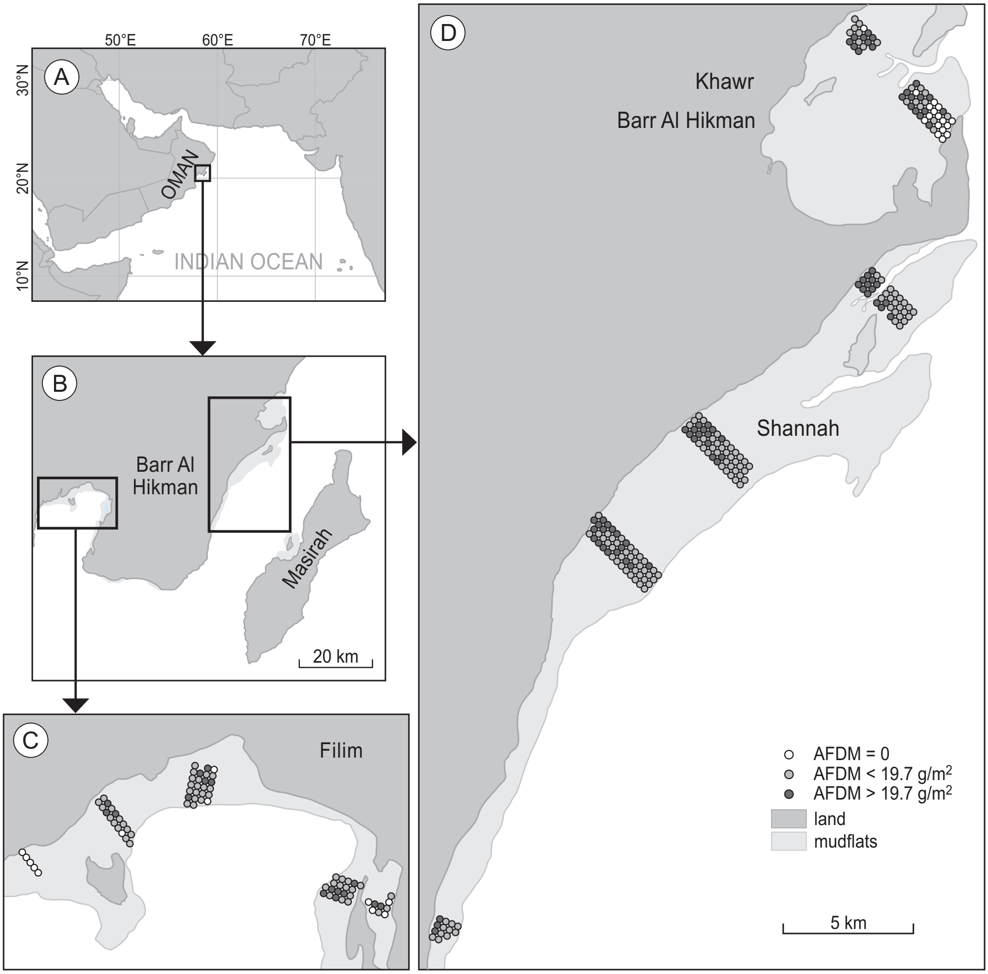

Figure 2.2. (A) Oman with Barr Al Hikman highlighted. (B) Barr Al Hikman. (C) Subsection Filim with macrozoobenthic biomass densities (g AFDM/m^{-2}) at each sampling station. (D) Sampling stations in subsections Khawr and Shannah. Maps c and d are on the same scale. Open points indicate sampling stations where no living benthos was found. Blue points indicate biomass density lower than the mean biomass density, and orange points indicate biomass density higher than the mean.

and another to two rows (Fig. 2.2C). Grids were aligned perpendicular to the coastline because variation within macrozoobenthic communities is often related to tidal height (Honkoop *et al.* 2006). The chosen inter-sampling distance of 250 m reflects the trade-off between spatial resolution and logistic feasibility. No additionally randomly located stations were sampled (as suggested by Bijleveld *et al.* (2012) and applied by Compton *et al.* (2013), because the aim of the study was not to extrapolate density estimates to unsampled locations. The chosen design of a fixed inter-sampling distance would give a biased estimation of the macrozoobenthic densities if the macrozoobenthic distributions were to show patterns at a regular distance as well (250 m in this case). However, earlier work at intertidal mudflats shows that such a pattern is unlikely to exist (Kraan *et al.* 2009).

All 282 sampling points were visited on foot during low tide. A sample consisted of a single sediment core with a diameter of 12.7 cm. The core was divided into an upper (0 – 4 cm) and a lower layer (4 – 20 cm, see below for explanation). These layers were separately sieved through a 1-mm mesh. Samples were brought to a field laboratory, where they were stored at relatively low temperatures. Next, within two days after collection, macrozoobenthic animals (i.e. all benthic animals larger than 1 mm in size) were sorted out and stored in a 6% borax-buffered formaldehyde solution. Later, at NIOZ, each organism was identified to taxonomic levels ranging from phylum to species. Taxonomic names are in accordance with those listed in the World Register of Marine Species (WoRMS, http://www.marinespecies.org/, accessed: 2016-12-20).

Each organism was measured to the nearest 0.1 mm. From a subsample, biomass expressed as ash-free dry mass (AFDM) was obtained by drying the samples at 55°C for a minimum of 72 hours, followed by incineration at 560°C for 5 hours. Prior to incineration, the bivalves' shells were separated from their soft tissue to make sure only flesh and no calcium carbonate was burned. Gastropods and crustaceans were incinerated without separating soft tissue from shell or exoskeleton. As applied by (van Gils *et al.* 2005b), it is assumed that 12.5% of organic matter resided in the hard parts of gastropods and hermit crabs (living in the shells of gastropods), and 30% in crustaceans other than hermit crabs. The relation between AFDM and shell length was fitted with non-linear regression models using the software program R (R Development Core Team 2013) with the package 'nlme' (Pinheiro *et al.* 2011). The *varPower* function was used to correct for the variance in biomass that increased with size. Significant regression models were derived for 18 species (see Table 2.1 for molluscs) which were used to predict AFDM for 4,885 specimen. For species for which no significant regression model could be derived (due to low sample size), a direct measure of AFDM was used if available (864 individuals), and species-specific average AFDM values otherwise (198 individuals).

The average overall (i.e. for the entire intertidal area) numerical density (# m^{-2}) and biomass density (g AFDM m^{-2}) was calculated by statistically weighting the contribution of each grid to the average according to the size of the area that it represents. The standard deviations of these means were also calculated by statistically weighting each grid according to its size. The size of the area that each grid represents was calculated with Voronoi polygons using QGIS (Quantum GIS Development Team 2012).

Anti-predation traits

Predation opportunities for shorebirds on molluscs are hampered by anti-predation traits in molluscs. Such anti-predation traits include: (1) burrowing depth (Zwarts & Wanink 1993), (2) size (Zwarts & Wanink 1993), and (3) shell armour (Piersma *et al.* 1993b). The extent to which anti-predation traits actually affect predation opportunities for shorebirds depends on the size and foraging method of a given shorebird species. In this study, the oystercatcher, the great knot and the red knot were taken as reference species as these are well-studied species, and which are abundant on intertidal mudflats outside of the IWP. The available biomass was calculated for each species separately as the fraction of the molluscan biomass that is accessible, ingestible and breakable.

BURROWING DEPTH

When probing the mud, shorebirds can only access molluscs that are buried within the reach of their bill. Oystercatchers can probe to a depth of 9 cm (Sarychev & Mischenko 2014), great knots to 4.5 cm (Tulp & de Goeij 1994), and red knots to 4 cm (Zwarts & Blomert 1992). Burrowing depth of bivalves was measured in two ways. During the sampling campaign in 2008 the core was divided into two layers (0 – 4 cm and 4 – 20 cm) to distinguish the accessible from inaccessible food for red knots (Zwarts & Wanink 1993). To quantify the accessible and inaccessible part for great knots and oystercatchers, five sampling stations at the east coast of Shannah were visited again in April 2010. At each sampling point, a sediment sample was taken and then cut into transverse slices of 1 cm. From these samples, the exact burrowing depth of each encountered bivalve was measured to the nearest cm (Piersma *et al.* 1993a). The average percentage biomass density of bivalves found per 1 cm slice was then calculated. Gastropods were always found in the top 4 cm of the sediment.

SIZE

Great knots and red knots swallow their molluscan (bivalves and gastropods) prey whole. A mollusc can only be ingested up to a certain size, as indicated by its circumference (Zwarts & Blomert 1992). By and large, great knots can ingest roundly-shaped bivalves up to 28 mm across and more elongated bivalves with a shell length up to 36 mm (Tulp & de Goeij 1994). Red knots can ingest roundly-shaped bivalves up to 16 mm across and more elongated bivalves with a shell length up to 29 mm (Zwarts & Blomert 1992; Tulp & de Goeij 1994). At Barr Al Hikman all bivalves above 16 mm appeared to be roundly-shaped venerids to which the ingestible limits of respectively 28 mm and 16 mm for great knots and red knots can be applied. Whether a gastropod can be ingested by great knots and red knots depends both on the size and shape of the gastropod. Most likely, elongated gastropods can be swallowed more easily than rounded ones. Oystercatchers do not face constraints on size as they open the molluscs (they eat only bivalves) with their bill (Swennen 1990).

The length of each sampled organism was measured to the nearest 0.1 mm. From these measurements, the percentages of molluscs were calculated that are within the above mentioned ingestion thresholds for great knots and red knots, respectively.

BREAKING FORCE

After swallowing, great knots and red knots crush their molluscan prey in their gizzard. Red knots can generate forces up to 40 N in their gizzard (Piersma *et al.* 1993b), note that in this

Table 2.1. Information on the most abundant molluscs found at Barr Al Hikman.

Species with family	**biomass density** g AFDM/m^2 (±SD)	% < 16 mm	% < 28 mm	% in top 4 cm	% < 40 N	**Non-linear model** $Y = aX^b$ Y = AFDM (g) X = length (mm)		**Non-linear model** $Y = aX^b$ Y = breaking force (N) X = length (mm)		**Repair scars**	
						a	b	a	b	n	% scars
Bivalves											
Callista umbonella (Veneridae)	0.34 (±1.07)	0	0	0	0	0.012	2.81**	3.55	1.32**		
Jitlada arsinoensis (Tellinidae)	0.16 (±0.35)	100	100	24	100	0.034	2.23**			16	0
Marcia recens (Veneridae)	0.43 (±0.54)	0	2	98	1	0.016	2.74**	3.55	1.32**	6	0
Nitidotellina cf. *valtonis* (Tellinidae)	0.07 (±0.09)	100	100	87	100	0.011	2.63**	0.16	1.50*		
Pelecyora ceylonica (Veneridae)	0.29 (±0.42)	10	100	57	10	0.005	2.98**	0.07	2.33*	5	0
Pillucina fischeriana (Lucinidae)	3.62 (±3.88)	100	100	17	72	0.005	3.38**	1.72	1.40**	64	0
Gastropods											
Cerithium scabridum (Cerithiidae)[1]	3.22 (±2.55)	40	100	100	0	0.029	2.39**	378.58	0	39	21
Mitrella blanda (Columbellidae)[2]	0.09 (±0.11)	100	100	100	0	0.032	2.27**	0.02	17.90**	6	17
Nassarius persicus (Nassariidae)	0.47 (±0.24)	71	100	100	0	0.064	2.26**	0.15	1.13**	23	4
Pirenella arabica (Potamididae)	8.58 (±4.42)	13	100	100	1	0.002	3.55**	0.36	2.33**	68	11
Priotrochuss kotschyi (Trochidae)	0.14 (±0.14)	100	100	100	?	0.266	1.92**				
Salinator fragilis (Amphibolidae)[2]	0.04 (±0.07)	100	100	100	100	0.027	2.68**	–4.73	1.09*		

[1] break force - length model was not significant, average values used instead

[2] break force - length model was not significant, linear model ($Y = a + bX$) used instead

** $p < 0.001$ * $p < 0.05$

paper breaking force was erroneously expressed two orders of magnitude too low), which is taken as the border between breakable and non-breakable prey items (thereby ignoring the possibility that the slightly larger great knot can generate somewhat higher forces within their larger gizzards). To quantify the strength of the molluscan shell armour, the forces needed to break the shells of the abundant mollusc species were measured with an Instron-like breaking-force device described by Buschbaum *et al.* (2007). The breaking force device works by placing a mollusc between two plates on top of a weighing scale, after which the pressure on the upper plate is gently increased with a thread spindle until the shell crushes. Molluscivorous shorebirds crush shells in a similar way (Piersma *et al.* 1993b). The lower plate is connected to a balance which measures the maximum exerted weight to crush a shell. After calibration, this measure can be converted to a measure of force (to the nearest 0.1 N) (Buschbaum *et al.* 2007).

Breaking force was measured in alcohol-preserved molluscs, collected alive in March 2015 and crushed a month later. Alcohol-stored bivalves require the same forces to crush as freshly collected ones (Yang *et al.* 2013). Breaking force was measured for the 10 most abundant (in terms of biomass density) molluscs, except for the tellinid *Jitlada arsinoensis*, the trochid *Priotrochus kotschyi* and the venerid *Marcia recens*, for which the samples did not contain enough specimens. To predict the breaking force for each sampled mollusc, the relation between break force and shell length was fitted with non-linear regression models, similar to the biomass-length regression models. For the gastropods *Mitrella blanda* and *Salinator fragilis* the linear regression was not significant, but the non-linear model was (Table 2.1). Neither linear nor non-linear regressions were significant for *Cerithium scabridum*, and hence the species-specific mean was used. For *J. arsinoensis* the regression model of the similar *Nitidotellina* cf. *valtonis* was used, and for *M. recens* the regression model of the similar *Callista umbonella*.

REPAIR SCARS

A widely used way to assess if a molluscan community is subject to crab predation is to check molluscs for repair scars, which they form after unsuccessful peeling or crushing by crabs (Vermeij 1993; Cadée *et al.* 1997). Here, the eight most abundant molluscs found at Barr Al Hikman were checked for repair scars. Molluscs were collected alive in January 2009 and checked for repair scars under a microscope. The repair frequency was defined as the number of individuals having at least one repair divided by the total number of inspected molluscs (Cadée *et al.* 1997).

Results

Standing stock

A total of 5,947 macrozoobenthic specimens were collected, which yielded 64 distinct taxa of which 27 were identified to species level (Appendix A2.2). Table 2.2 presents the numerical density (individuals per m^2) and the biomass density (g AFDM m^{-2}) per taxonomic group for the entire sampled area (see Appendix A2.2 for AFDM measures per taxon and per sub-area). The average numerical density for the total area was 1,768 animals per m^2 and the biomass density was 19.7 g AFDM per m^2. More than 99% of the numerical and biomass densities were comprised of gastropods, bivalves, crustaceans, and polychaetes, with gastropods (64%) and bivalves (25%) dominating the biomass. Crustaceans (5%) and polychaetes (5%) were less abundant. At the species level, three species clearly stood out in terms of biomass density: the gastropods *Pirenella arabica* and *Cerithium scabridum* (Fig. 2.3A) and the bivalve *Pillucina fischeriana* contributed 44%, 16% and 18% to the total biomass density, respectively. Numerical density was dominated by *P. fischeriana* with 40% (Appendix A2.2). In 10% of the samples, no benthic organisms were found (Fig. 2.2C, D). Table 2.1 presents the biomass densities of the most abundant molluscs.

Figure 2.3. (A) A typical view on the intertidal mudflats of Barr Al Hikman with high abundance of the thick-shelled *Cerithidea* and *Pirenella* gastropods about 30 mm long. (B) Repair scars in three gastropods. From left to right: *P. arabica*, *C. scabridum*, *Nassarius persicus*.

Anti-predation traits and food availability for shorebirds

BURROWING DEPTH

In the samples taken in 2008, 75% of the bivalve biomass was found in the bottom layer (Table 2.1). Sampling in April 2010 confirmed this result. Fig. 2.4A shows the results of the 2010 sampling, with the average percentage of bivalve biomass density plotted against the burrowing depth. Lines show the maximum depth to which molluscivorous shorebirds have access. Based on the samples collected in 2010, oystercatchers, great knots and red knots can access 61%, 35% and 25% of the bivalve biomass, respectively.

SIZE

In total, 90% of the bivalve biomass was found in shells smaller than 28 mm and 65% of the biomass in shells smaller than 16 mm (Table 2.1, Fig. 2.4B). All gastropods were smaller than 30 mm (Fig. 2.5A, Table 2.1). All abundant gastropods (Table 2.1) were found to be elongated, meaning that most likely all gastropods were ingestible by great knots and red knots.

BREAKING FORCE

16% of the total molluscan biomass was breakable (< 40 N). 51% of the total bivalve biomass was breakable (Fig. 2.4C, Table 2.1) and less than 1% of the gastropod biomass (Fig. 2.5B, Table 2.1).

TOTAL AVAILABLE BIOMASS DENSITY

For oystercatchers, the available molluscan biomass density (all accessible bivalves) was 3.0 g AFDM/m^2 (63% of the total bivalve biomass density and 17% of the total molluscan biomass density). For great knots, the available molluscs are comprised of all bivalves and gastropods that are accessible, ingestible and breakable. As 1% of the total gastropod biomass (12.71 g AFDM m^{-2}) was breakable, and as all gastropods were accessible and ingestible to great knots, the available gastropod biomass density equals 0.1 g AFDM m^{-2}. For bivalves, out of the total

Table 2.2. Average numerical density and biomass density (±SD) for the taxonomical macrozoobenthic groups at Barr Al Hikman.

Group	Taxonomic level	Numerical density (#/m^2)	Biomass density (g AFDM/m^2)
All benthos		1767.79 (±975.81)	19.72 (±8.70)
Anthozoa	class	3.02 (±4.03)	0.01 (±0.02)
Bivalvia	class	787.20 (±701.77)	4.95 (±3.56)
Crustacea	subphylum	259.57 (±218.03)	0.99 (±0.79)
Echinodermata	phylum	0.81 (±1.62)	0.01 (±0.02)
Gastropoda	class	476.89 (±384.79)	12.71 (±7.14)
Insecta	class	8.43 (±21.54)	0 (±0)
Plathyhelminthes	phylum	2.97 (±1.91)	0.01 (±0.01)
Polychaeta	class	226.91 (±136.62)	1.00 (±0.66)
Priapulida	class	1.20 (±1.78)	0.03 (±0.09)
Scaphopoda	class	0.80 (±1.81)	0 (±0)

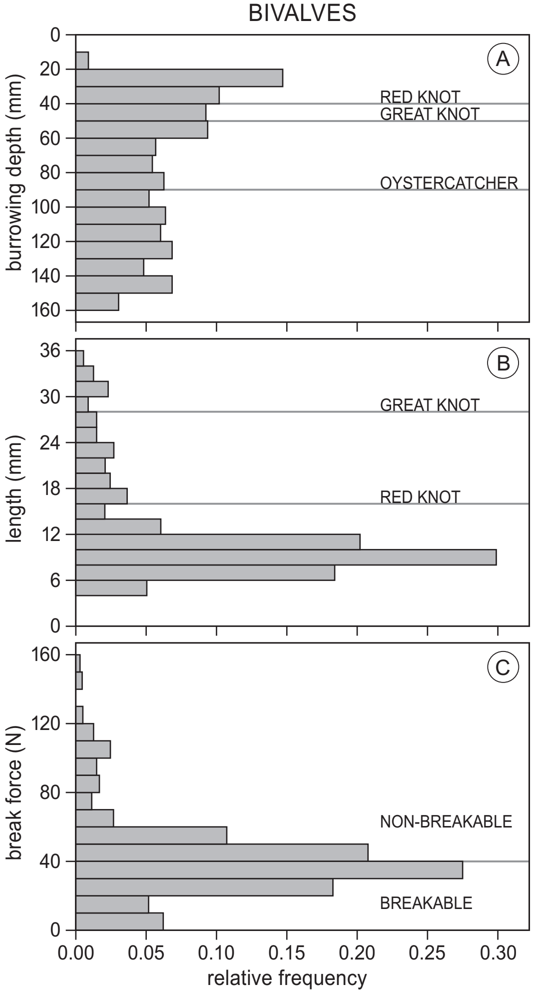

Figure 2.4. Frequency distributions of three anti-predation mechanisms in bivalves at Barr Al Hikman on the basis of biomass. (A) Frequency distribution of burrowing depth (note the reverse y-axis) with dashed lines indicating the maximum depth at which three molluscivorous shorebird species can probe. (B) Frequency distribution of lengths. Dashed lines shows which bivalves can be swallowed by red knots and great knots. (C) Frequency distribution of breaking force. The dashed line indicates the border between breakable and non-breakable bivalves.

bivalve biomass (4.95 g AFDM m^{-2}), 35% was accessible, 90% ingestible, and 51% breakable. This means that the available bivalve biomass density was 0.8 g AFDM m^{-2} (16% of the total bivalve biomass density, thereby ignoring a potential size-depth relation). Thus, the total available molluscan biomass density for great knots was 0.9 g AFDM m^{-2} (4% of the total molluscan biomass density). The same calculation for red knots arrives at an available gastropod biomass density of 0.1 g AFDM m^{-2}, and an available bivalve biomass density of 0.4 g AFDM m^{-2} (8% of the total bivalve biomass density). Thus, the total available molluscan biomass density for red knots was 0.5 g AFDM m^{-2} (3% of the total molluscan biomass density).

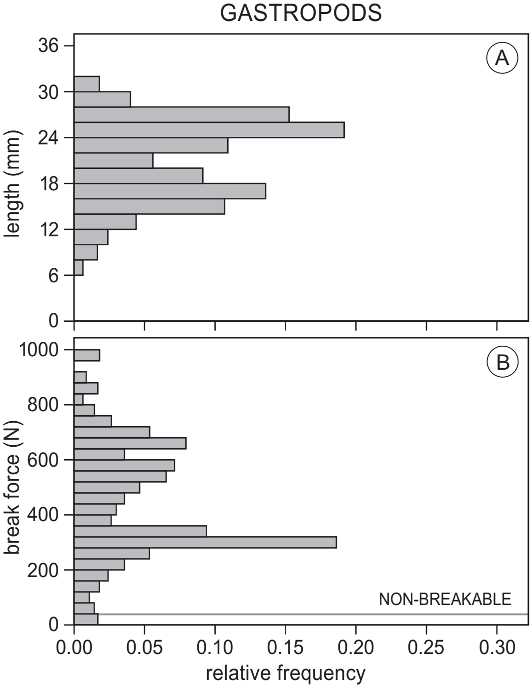

Figure 2.5. Frequency distributions of two anti-predation mechanisms in gastropods at Barr Al Hikman on the basis of biomass. (A) Frequency distribution of bivalve length. (B) Frequency distribution of breaking force. The dashed line indicates the border between breakable and non-breakable gastropods.

Repair scars

Repair scars were observed in all checked species of gastropods (Table 2.1, Fig. 2.3B). Between species, the repair frequency varied between 4 and 26%. All scars were interpreted as jagged "can-opener" breaks which crossed growth lines, and are most likely the result of predation attempts by crabs (Vermeij 1978, 1993; Cadée *et al.* 1997), except for one borehole scar in a specimen of *C. scabridum*. One specimen of *P. arabica* had two repair scars, all the others had either one or zero. No repair scars were observed in bivalves.

Discussion

Molluscan communities of intertidal mudflats compared

The macrozoobenthic community of Barr Al Hikman was dominated by molluscs, comprising 89 % of the total biomass density (64% gastropods, 25% bivalves). However, most of this potential food source was unavailable to molluscivorous shorebirds. Predation opportunities for shorebirds on gastropods were hampered by the shell armours of gastropods: only 1% of the total gastropod biomass was breakable (Fig. 2.5A). Also bivalves were largely unavailable to shorebirds, mainly because they were either too deeply burrowed or were too hard to break:

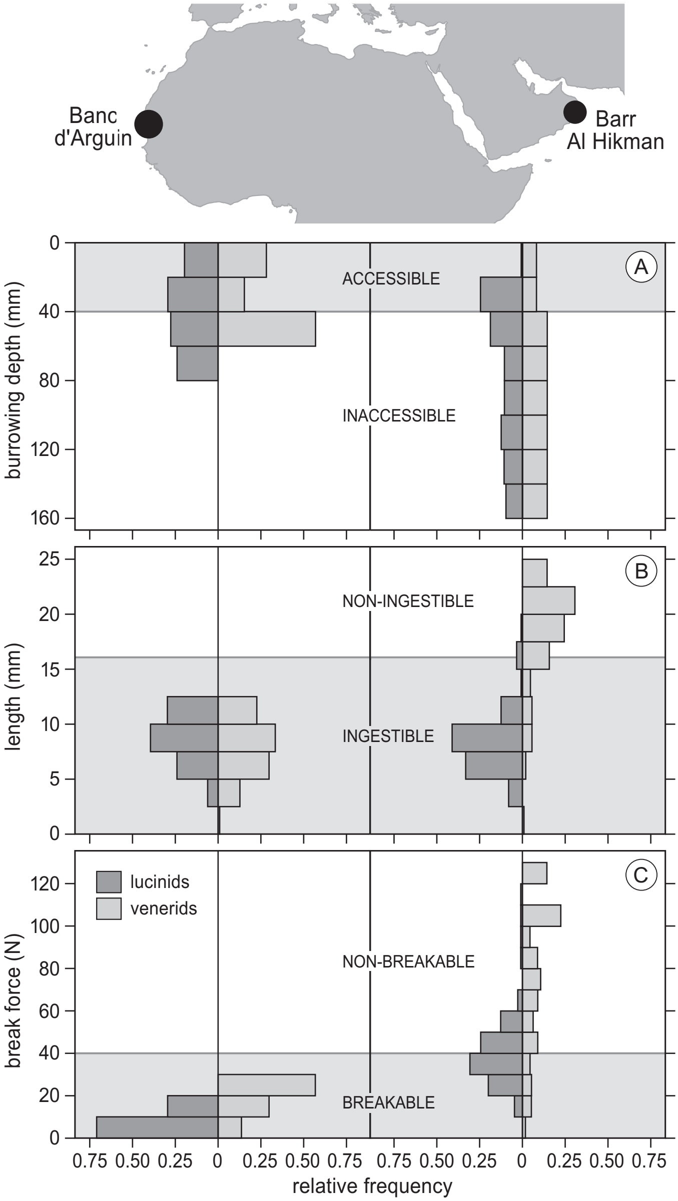

Figure 2.6. Histograms of three anti-predation traits measured in the venerid *Pelecyora isocardia* and lucinid Loripes orbiculatus at Banc d'Arguin and the venerid *P. ceylonica* and the lucinid *P. fischeriana* at Barr Al Hikman. (A) The average burrowing depth relative to the biomass density (note the reverse y-axis), with grey line indicating the depth to which red knots can probe. (B) Length relative to biomass with lines indicating which size is ingestible/non-ingestible by red knots. (C) Breaking force relative to the biomass density with a dashed line indicates which bivalves are breakable and non-breakable for red knots. Data for Banc d'Arguin was obtained by Piersma *et al.* 1993a and Yang *et al.*, 2013. Data for Barr Al Hikman was collected in this study. Depth distributions for *P. ceylonica* are based on samples collected in 2008 and for *P. fischeriana* based on samples collected in 2010 (see Methods).

for great knots and red knots 16% and 8% of the total bivalve biomass density was available, respectively. Conversely, for oystercatchers, which open bivalves before ingestion, 63 % of the total bivalve biomass density was available.

A comparison of the available molluscan biomass on intertidal areas around the world (at least for those for which detailed data were available) shows that Barr Al Hikman has the lowest average density of molluscs available to red knots (Figs. 2.1 & 2.6, Table 2.3, Appendix A2.3). Without discounting the unavailable prey, the average total density of molluscs at Barr Al Hikman was close to the average total density values of molluscs measured at other intertidal mudflats (Piersma *et al.* 1993a; Dittmann 2002; Table 2.3), meaning that there is little available molluscan biomass density because molluscs at Barr Al Hikman are relatively well defended. A direct comparison of the anti-predation traits in molluscs confirms this: the bivalves at Barr Al Hikman were among the hardest measured (Appendix A2.3) and the fraction of bivalves that was in the upper 4 cm of the sediment in Barr Al Hikman was among the lowest reported for any intertidal area (Table 2.3).

The data in Table 2.3 does not allow a comparison of intra-site variation, which is known to exist in biomass densities (Beukema 1976), prey sizes and burrowing depths (Zwarts & Wanink 1993), and may cause the actual average mollusc densities to differ slightly from our estimates (Table 2.3). Yet, the estimated differences are so large that they support the idea that molluscivorous shorebirds are nearly absent from Barr Al Hikman because molluscs at this site are relatively well defended.

It is of particular interest to further investigate the absence of red knots from Barr Al Hikman. Currently, red knots breed on the Taimyr Peninsula, Russia, due north of Barr Al Hikman. After breeding, these red knots do not migrate to Barr Al Hikman (6,000 km from the breeding areas), but fly much further, mainly to the Banc d'Arguin in Mauritania (more than 9000 km; see Fig. 2.1; Piersma 2007). The intertidal mudflats of Banc d'Arguin are at the same latitude as Barr Al Hikman, meaning that climatic conditions cannot explain why red knots skip Barr Al Hikman. At both sites, species of the venerid and lucinid families are the most abundant bivalves; at Banc d'Arguin these bivalves are the main prey for red knots (van Gils *et al.* 2016). A comparison of the anti-predation traits in both families shows that bivalves were better defended at Barr Al Hikman (Fig. 2.6, Table 2.3, Banc d'Arguin data from (Piersma *et al.* 1993a; Yang *et al.* 2013); see Appendix 2.4 for accompanying statistics). As a consequence, the available molluscan biomass density at Barr Al Hikman was only 15% of that at Banc d'Arguin (Table 2.3). This again points to food availability as the reason for red knots to skip Barr Al Hikman, and head to Banc d'Arguin instead.

Molluscs at Barr Al Hikman subject to durophagous predation

It can be expected that the molluscs at Barr Al Hikman have been and are subject to strong predation pressure, as molluscs will only show costly morphological and behavioural defences when they are exposed to strong predation pressure. This is the case both on an evolutionary timescale (Dietl & Kelley 2002; Bijleveld *et al.* 2015) and on the level of individual development (Appleton & Palmer 1988; Zaklan & Ydenberg 1997; Griffiths & Richardson 2006). Several durophagous predators occur in Oman, including crabs, fishes, lobsters, stomatopods, starfish, sea anemones, gastropods and birds (Randall 1995; Khorov 2012; Chapter 5). The established

Table 2.3. Total molluscan biomass and available molluscan biomass for red knots on a number of wintering and stopover sites and information on the most abundant (potential) prey items. In Alaska (USA), information was collected for the rock sandpiper (*Calidris ptilocnemis*), which is a similar-sized molluscivorous shorebird as the red knot. Based on their size and abundance, *Pillucina fischeriana* and *Pelecyora ceylonica* can be regarded as the most likely candidate prey for red knots at Barr Al Hikman.

#	**country**	**area**	**total molluscan biomass density** (g AFDM m^{-2})	**available biomass** (g AFDM m^{-2})	**most abundant (potential) molluscan prey items**	**% small molluscs in upper 4 cm**	**% breakable small molluscs**	**Reference**
1	Oman	Barr Al Hikman	17.7	0.5	*Pillucina fischeriana* *Pelecyora ceylonica*	17% 57%	58% 100%	this study
2	Mauritania	Banc d' Arguin	4.8	3.4	*Loripes orbiculatus* *Pelecyora isocardia*	44% 49%	100% 100%	Piersma *et al.* 1993a
3	China	Bohai Bay	4.5	>3.2	*Potamocorbula laevis*	100%	100%	Yang *et al.* 2013
4	Australia	Roebuck Bay	13.9	5.7	*Cavatidens omissa*, Tellina sp, *Serratina piratica*	all ~30%	*	Tulp & de Goeij 1994
5	Netherlands	Wadden Sea	19.7	3.0	*Limecola balthica* *Cerastoderma edule*	> 95% 100%	100% 100%	Piersma *et al.* 1993a
6	Argentina	Río Grande	>36	20.4	Darina solenoides, Mytilidae sp.	all 100%	*	Escudero *et al.* 2012
7	Argentina	San Antonio Oeste	23 – 117	10.9	*Brachidontes rodriguezi*	100%	*	González *et al.* 1996
8	United States	Alaska	11.4	11.4	*Limecola balthica*	100%	100%	Ruthrauff *et al.* 2017 & unpublished

*based on bivalve shell mass it can be expected that all these molluscs are breakable (van Gils *et al.* 2005a).

strong anti-predation traits could have evolved in response to either of them (Vermeij 1977a; Gregory *et al.* 1979; Gray *et al.* 1997). However, considering the usual trade-off with food intake, prey are not expected to evolve costly morphological or avoidance defences when predation risk is low (de Goeij & Luttikhuizen 1998; Dietl & Kelley 2002). Therefore, it is unlikely that the observed anti-predation mechanisms evolved in response to the few molluscivorous shorebirds that are around. It is more likely that they have evolved in response to predation pressure by brachyuran crabs and molluscivorous fish (sharks and rays), as both are abundant in the waters of Oman (Randall 1995; Khorov 2012). Repair scars were found in all gastropods species, providing evidence that molluscs at Barr Al Hikman are subject to crab predation (Table 2.1, Fig. 2.3B). Abundant crabs in Barr Al Hikman, including the giant mangrove crab (*Scylla serrata*) and the blue swimming crab (*Portunus segnis*), are known to feed on the heavily armoured *Cerithidea* and *Pirenella* gastropods (Wu & Shin 1997; pers. obs. RAB). As no repair scars were found in bivalves, it remains unknown whether bivalves are currently exposed to crab predation or whether they simply never survive predation attempts (Leighton 2002). Given that bivalves are easier to break than gastropods (Fig. 2.4 & Fig. 2.5), it is possible that crabs will always succeed in breaking their shell armour. Fish do not leave marks on the shells of neither bivalves nor gastropods after a failed breaking attempt (Vermeij 1993). Further study, perhaps on shattered shell remains, might show the potential extent of mollusc predation by fish at Barr Al Hikman.

Indo-West Pacific

Vermeij (1976, 1977b, 1978) exclusively used data collected from rocky shores to show that molluscs in the IWP are relatively well defended, apparently due to a prolonged and intense arms race with durophagous predators. Our study shows that these findings can now be extended to at least one intertidal mudflat area. It remains to be seen whether molluscs at other intertidal mudflat areas in the IWP are equally well-defended (for sites in the IWP where molluscs are abundant, see Piersma *et al.* 1993a; Keijl *et al.* 1998; Purwoko & Wolff 2008; Fig. 2.1, sites 4, 9, 10, 11). North-West Australia's mudflats are the only intertidal mudflat areas in the IWP where mollusc anti-predation traits have been measured (Fig 2.1, site 4, Table 2.3). These are also the only intertidal areas in the entire IWP where molluscivorous shorebirds are abundant (Tulp & de Goeij 1994; Conklin *et al.* 2014), perhaps because the bivalves found at these sites are an exception to the rule that molluscs in the IWP are difficult to break. Indeed, although bivalves were found relatively deeply burrowed (Tulp & de Goeij 1994), shell-mass data suggested that the bivalves in this area were relatively easy to break (van Gils *et al.* 2005a). Again this is in accordance with the idea that that the distribution of molluscivorous shorebirds in IWP can be explained by the strength of the defence mechanisms of the local molluscan communities.

Concluding remarks

Whether dispersing organisms can persist in regions beyond their native range largely depends on their attack and defence mechanisms relative to the traits found in their new communities (Vermeij 1978). Thus, it is unlikely that novel predators will successfully disperse to areas where predators and prey exhibit strongly developed attack and defence mechanisms due to an evolutionary arms race (Vermeij 1978). This explains why molluscivorous shorebirds are nearly absent from Barr Al Hikman: exploitation of molluscs by shorebirds at Barr Al Hikman may be precluded by molluscan anti-predation traits that were established long before the dispersal of modern shorebirds along the world's shorelines. We conclude that our study is a novel illustration of Vermeij's (1978, 1987) proposition that evolutionary arms races can have consequences for food-web structure and for the global distribution of species.

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Appendices

Appendix A2.1. Number of shorebirds present in Barr al Hikman in January 2008 (Chapter 5). The last 5 columns give the main diet as observed for each shorebirds species (unpublished data). A distinction is made between crabs and crustaceans other than crabs.

species	**number**			**diet**		
		Bivalves	Crustaceans	Crabs	Gastropods	Polychaetes
Bar-tailed godwit	65,300		+	+		+
Broad-billed sandpiper	200		+	+		+
Crab plover	6,900			+		
Curlew sandpiper	37,800		+	+		+
Dunlin	84,500		+			+
Eurasian curlew	7,100			+		+
Great knot	400	+		+		
Greater sandplover	2,800		+	+		+
Greenshank	500					
Grey plover	2,200			+		+
Kentish plover	2,100			+		
Lesser sandplover	35,700		+	+		+
Little stint	12,000		+			
Marsh sandpiper	100					
Eurasian oystercatcher	3,900	+		+		+
Redshank	34,500		+			
Ringed plover	100		+			+
Ruddy turnstone	5,700					
Sanderling	3,100		+	+		+
Terek sandpiper	700			+		
Whimbrel	700					
Total	**306,300**					

Appendix A2.2. Numerical density (#/m^2) and biomass density (g AFDM/m^2) for all identified species (or the level to which identification was possible). Averages values ± standard errors (between grid variance) are shown for the entire area and for the three sub-areas Filim, Khawr and Shannah. For Khawr no standard error is given as in this sub-area one grid was sampled.

Species	**taxonomic level**	**total**		**Filim**		**Khawr**		**Shannah**	
		numerical	biomass	numerical	biomass	numerical	biomass	numerical	biomass
ANTHOZOA									
Actiniaria spp.	order	3.02±4.03	0.01±0.02	1.21±1.66	0.01±0.02	1.44	0	4.96±4.96	0.02±0.03
BIVALVIA									
Arcuatula senhousia	species	0.53±0.94	0	0.58±1.45	0	1.44	0	0	0
Bivalvia sp.	class	0.11±0.52	0	0	0	0	0	0.38±0.76	0
Callista umbonella	species	1.26±3.10	0.34±1.07	3.10±0.92	0.92±2.06	1.44	0.31	0	0
Cardiolucina semperiana	species	0.18±0.52	0	0	0	0	0	0.38±76	0
Diplodonta crebristriata	species	0.42±0.74	0	0	0	0	0	0.90±0.88	0
Jitlada arsinoensis	species	36.01±88.74	0.16±0.35	92.51±163.37	0.38±0.64	1.44	0.02	21.87±25.82	0.12±0.13
Laternula anatine	species	0.37±0.68	0.03±0.05	0	0	1.44	0.11	0	0
Marcia recens	species	5.53±4.54	0.43±0.54	4.17±4.26	0.01±0.02	11.48	1.22	3.01±1.99	0.24±0.26
Nitidotellina cf *valtonis*	genus	16.75±30.54	0.07±0.09	42.08±51.61	0.09±0.14	0	0	11.1±5.69	0.09±0.08
Ostreidae sp.	family	0.75±1.36	0.01±0.01	0	0	2.87	0.03	0	0
Pelecyora ceylonica	species	17.59±22.23	0.29±0.42	10.19±22.85	0.32±0.81	47.36	0.49	5.36±3.42	0.15±0.07
Pillucina fischeriana	species	706.14±732.40	3.62±3.88	44.56±50.44	0.22±0.27	218.16	0.87	1370.06±450.85	7.17±2.29
Pinguitellina cf. *pinguis*	genus	0.32±1.46	0	0	0	0	0	0.68±2.25	0
Pinguitellina pinguis	species	0.24±0.62	0	0	0	0	0	0.52±0.87	0
Tivela mulawana	species	0.56±1.35	0	0.92±2.20	0	0	0	0.67±1.21	0
CRUSTACEA									
Amphipoda sp.	order	188.01±210.25	0.25±0.30	0	0	22.96	0.03	391.41±67.76	0.53±0.17
Anomura sp.	Infraorder	39.71±37.04	0.42±0.46	62.6±67.62	0.50±0.83	22.96	0.18	35.51±12.43	0.50±±0.29
Astacidea sp.	Infraorder	5.11±8.03	0.10±0.18	1.21±1.66	0	1.44	0	9.46±10.61	0.20±0.22
Brachyura sp.	Infraorder	1.43±3.28	0±0.01	1.16±2.91	0±0.01	0	0	2.39±4.40	0.01±0.01
Caridea sp.	Infraorder	0.31±0.84	0	0	0	0	0	0.67±1.21	0
Isopoda sp.	order	2.4±4.48	0	0	0	0	0	5.16±5.57	0
Leucosiidae sp.	family	4.94±4.58	0.03±0.02	6.68±7.44	0.04±0.03	1.44	0.01	5.86±2.83	0.03±0.02

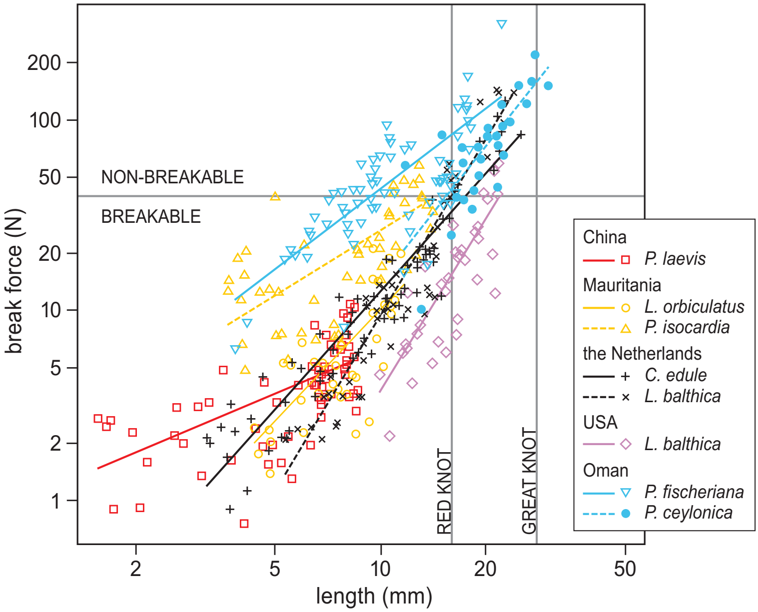
Appendix A2.2. Continued.

Species	**taxonomic level**	**total**		**Filim**		**Khawr**		**Shannah**	
		numerical	biomass	numerical	biomass	numerical	biomass	numerical	biomass
CRUSTACEA continued									
Macrophthalmus grandidieri	species	0.24±0.62	0	0	0	0	0	0.52±0.87	0
Macrophthalmus laevis	species	0.33±0.99	0	1.21±1.66	0.01±0.01	0	0	0	0
Macrophthalmus sulcatus	species	4.38±7.69	0.11±0.19	12.2±11.23	0.30±0.28	0	0	2.19±2.21	0.07±0.07
Maxillopoda sp.	class	0.37±0.68	0	0	0	1.44	0	0	0
Mysida sp.	order	4.54±6.99	0.01±0.01	2.43±3.32	0.02±0.02	0	0	8.33±8.82	0.1±0.01
Pinnotheridae sp.	family	1.16±3.00	0.01±0.04	4.22±4.58	0.05±0.05	0	0	0	0
Portunidae sp.	family	1.81±3.15	0.01±0.01	0.92±2.20	0.01±0.01	0	0	3.36±3.97	0.01±0.02
Scopimera sp.	genus	3.58±6.55	0.04±0.06	8.50±11.63	0.08±0.11	2.87	0.06	1.06±1.15	0.01±0.01
Xanthidae sp.	family	1.23±2.20	0.01±0.01	3.35±3.09	0.02±0.02	0	0	0.67±1.21	0
ECHINODERMATA									
Holothuroidea sp.	class	0.81±1.62	0.01±0.02	0	0	0	0	1.73±2.20	0.02±0.03
GASTROPODA									
Aticulastrum cylindricum	species	1.05±1.22	0.02±0.02	0.92±2.20	0.01±0.02	1.44	0.01	0.90±0.88	0.03±0.03
Bulla ampulla	species	0.42±0.74	0.02±0.06	0	0	0	0	0.9±0.88	0.05±0.08
Cerithium scabridum	species	194.78±177.56	3.22±2.56	40.05±49.12	0.81±0.92	361.69	5.13	193.24±193.00	3.58±2.89
Crepidula sp.	genus	1.25±3.38	0	0	0	0	0	2.68±4.85	0
Gastropoda sp.	class	1.37±1.88	0.05±0.08	0.58±1.45	0.02±0.05	0	0	2.61±1.91	0.10±0.09
Littoraria intermedia	species	1.48±1.78	0.03±0.05	0	0	1.44	0.02	2.38±2.25	0.06±0.08
Mitrella blanda	species	9.57±8.62	0.09±0.12	12.2±15.91	0.12±0.23	5.74	0.05	10.15±4.91	0.10±0.04
Nassarius persicus	species	25.95±12.82	0.47±0.24	15.77±16.15	0.26±0.28	35.88	0.54	26.43±10.17	0.55±0.21
Nerita textilis	species	1.06±1.42	0.02±0.02	0	0	2.87	0.05	0.67±1.21	0.01±0.02
Oliva bulbosa	species	0.66±1.26	0.04±0.08	0	0	0	0	1.42±1.59	0.10±0.10
Opisthobranchia sp.	infraclass	0.84±1.48	0	0	0	0	0	1.81±1.77	0
Pirenella Arabica	species	162.66±185.23	8.39±4.42	70.44±66.60	4.56±4.20	443.5	11.19	60.53±43.94	9.01±4.53
Pirenella / Cerithium	genus	66.06±73.88	0.19±0.22	23.1±24.12	0.03±0.03	147.83	0.38	45.86±78.95	0.18±0.27
Priotrochus kotschyi	species	6.30±9.75	0.14±0.14	1.21±1.66	0	7.18	0.17	8.83±14.43	0.20±0.17

Appendix A2.2. Continued.

Species	taxonomic level	total		Filim		Khawr		Shannah	
		numerical	biomass	numerical	biomass	numerical	biomass	numerical	biomass
GASTROPODA									
Salinator fragilis	species	3.08±4.14	0.04±0.07	0	0	1.44	0.01	5.82±4.81	0.08±0.09
Umbonium eloiseae	species	0.36±1.04	0	0	0	0	0	0.77±1.51	0
Umbonium vestiarium	species	0.32±1.46	0	0	0	0	0	0.68±2.25	0
INSECTA									
insect larvae	class	8.43±21.54	0	0	0	0	0	18.12±30.52	0
PLATYHELMINTHES									
Platyhelminthes	phylum	2.97±1.91	0.01±0.01	3.01±3.03	0.01±0.01	2.87	0	3.01±1.99	0.01±0.01
POLYCHAETA									
Chaetopteridae sp.	family	15.99±18.36	0.23±0.29	21.77±20.23	0.31±0.32	4.31	0.04	19.09±21.68	0.28±0.34
Polychaeta sp.[1]	phylum	210.92±129.36	0.77±0.50	106.02±68.76	0.51±0.33	132.05	0.38	317.02±101.03	1.15±0.43
PRIAPULIDA									
Priapulida sp.	class	1.2±1.78	0.03±0.09	1.21±1.66	0	0	0	1.86±2.17	0.07±0.13
SCAPHOPODA									
Dentalium octangulatum	species	0.80±1.81	0	0	0	0	0	1.71±2.48	0

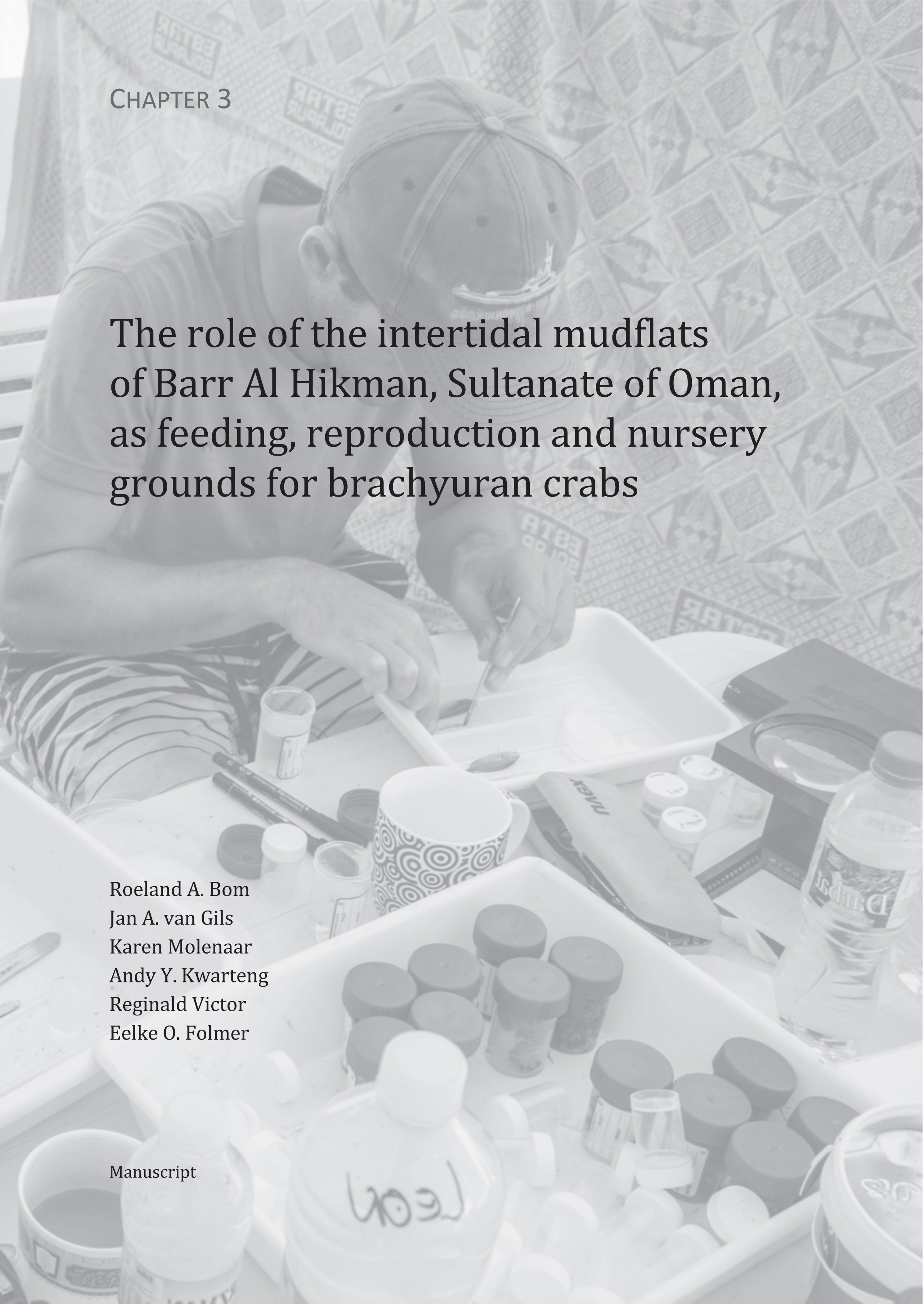
[1] Polychaetes of the families Capitellidae, Cirratulidae, Glyceridae, Maldanidae, Nereididae, Opheliidae, Orbiniidae, Palmyridae, Spionidae and Terebellidae were recognized in our samples, but not all polychaetes were identified to family level.



Appendix A2.3. Shell break force as a function of shell length in five bivalve species. Data on *Loripes orbiculatus*, *Pelecyora isocardia*, *Potamocorbula laevis*, *Limecola balthica* (Wadden Sea) and *Cerastoderma edule* was earlier published by Yang *et al.* 2013. Data on *Pillucina fischeriana* and *Pelecyora ceylonica* was collected for this study and data for *Limecola balthica* (Alaska) was unpublished. All data was collected by TO or RAB and obtained using the breakforce machine described in the methods. For further information on the species we refer to Table 2.3. Vertical lines indicate the maximum size that red knots and great knots can ingest and the horizontal line indicates the maximum break force red knots can generate in their gizzards.

Appendix A2.4. Results of the binomial proportions test comparing the proportion of biomass that is accessible and not accessible, ingestible and not ingestible, breakable and not breakable for the venerid *Pelecyora isocardia* (n = 38) and lucinid *Loripes orbiculatus* (n = 76) at Banc d'Arguin and the venerid *Pelecyora ceylonica* (n = 60) and the lucinid *Pillucina fischeriana* (n = 2918) at Barr Al Hikman. Data for Banc d'Arguin was obtained by Piersma *et al.* 1993a (with breakforce conversion according to the breakfore-length relationships obtained by Yang *et al.*, 2013). Data for Barr Al Hikman was collected in this study.

Group	anti-predation trait	Barr Al Hikman % < x	Banc d'Arguin % < x	P	χ^2	df
venerids	depth (x = 4 cm)	42	44	0.10135	0.75	1
lucinids	depth (x = 4 cm)	17	49	2.194e-06	22.417	1
venerids	length (x = 16 mm)	16	100	< 2.2e-16	192.31	1
lucinids	length (x = 16 mm)	96	100	0.414	0.66559	1
venerids	breakforce (x = 40 N)	16	100	< 2.2e-16	193.09	1
lucinids	breakforce (x = 40 N)	55	100	3.04e-07	26.225	1



CHAPTER 3

The role of the intertidal mudflats of Barr Al Hikman, Sultanate of Oman, as feeding, reproduction and nursery grounds for brachyuran crabs

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Abstract

Intertidal mudflats along the shores of the Arabian Peninsula contain high densities and a large diversity of brachyuran crabs. These crabs have important ecological and economic values, yet most crab communities in the area remain unstudied. Here we provide density and diversity estimates of crabs at the intertidal mudflats of Barr Al Hikman, a relatively large and pristine wetland in the Sultanate of Oman. Across the winters of 2012–2015 crabs were sampled on a grid. 29 species were recorded. Yearly mean densities varied between 12 to 54 crabs/ m^2. Burrow-hiding deposit-feeding crabs and swimming crabs were the most abundant species across all winters. Size frequency and oviposition data suggest all studied crabs, except for the blue swimming crab *Portunus segnis*, reproduce in the intertidal area. However, the blue swimming crab, which is the most important crab for local fisheries, uses the area as a nursery ground. We analysed the relationship between the two most abundant crab species and the four environmental variables namely seagrass density, tidal elevation, median grain size and sediment depth using Random Forest models. The predictive capacity of the models and the relative importance of the environmental predictors varied considerably between years but some generalities emerged. Particularly, across all years crab densities were in general positively associated with seagrass densities and sediment depth and negatively associated with tidal elevation and median grain size. Our study demonstrates that the intertidal mudflats at Barr Al Hikman provide essential feeding, reproduction and nursery grounds for a large number of ecologically and economically important crabs.

Introduction

The densities and diversity of crabs (infraorder Brachyura) at the intertidal mudflats adjacent to the Arabian Peninsula are exceptionally high compared to other intertidal mudflat areas (Simões *et al.* 2001; Ng *et al.* 2008; Naderloo *et al.* 2013). These crabs are important for the ecological functioning of Arabian intertidal ecosystems and likewise intertidal ecosystems are important for these crabs. For example, crabs in the area are an important food source to millions of shorebirds, crabs exert strong top-down selection pressure on molluscs and it can be expected that they accelerate nutrient cycling by decomposing organic material and increase the water and air content in the soil by digging burrows (Qureshi & Saher 2012; Safaie 2016; Chapter 2). Furthermore intertidal mudflats can be important for crabs as a nursery ground (Hill *et al.* 1982; Potter *et al.* 1983; Seitz *et al.* 2005). Thus, a basic description of the crabs and the relationship with the intertidal environment are important from an ecosystem perspective. This is also a timely issue, as mudflats in the region are under rapidly increasing human pressure (Naderloo *et al.* 2013; Burt 2014), while most Arabian crab communities remain poorly studied. The purpose of this study was to provide fundamental data on crabs found on the intertidal mudflats of Barr Al Hikman in the Sultanate of Oman.

The intertidal area of Barr Al Hikman is characterized by slightly sloping, seagrass-covered mudflats, intersected by some coral outcrops above or just below the surface (Chapter 2 & 5). Due to environmental variability and associations with habitat, crabs are expected to be heterogeneously distributed across the intertidal zone. Previous descriptions of crabs communities across intertidal areas showed that crabs are often found in seagrass beds, for instance because seagrass provides crabs with shelter (Kunsook *et al.* 2014) and food (Edgar 1990). Crab distribution were also found to be related to exposure time which may correlate with feeding time (Henmi 1992), with the duration that crabs are exposed to marine and avian predators and with fluctuations in temperature and oxygen (Flores *et al.* 2005; Jensen *et al.* 2005). Sediment grain size is an important variable imposing limitation on burrowing activity of crabs (Henmi 1992) and it is related to the hydrodynamics due to tide and waves (Hovel *et al.* 2002). Sediment depth relates to the depth to which burrowing crabs can burrow or lay buried.

Here we first qualitatively and quantitatively describe the crabs present in the ecosystem on the basis of data collected on a spatial grid across four subsequent winters (2012–2015). Next, in order to better understand the spatial distribution of the most abundant crabs, we analysed the relationships between crab densities and the environmental variables seagrass density, median grain size, tidal elevation (as a measure of exposure time) and sediment depth using Random Forest (RF) algorithm. Random Forests are useful for explorative studies such as ours because of its ability to model non-linear relationships and complex interactions among predictor variables (Cutler *et al.* 2007). Another goal was to improve our knowledge on the life cycle of the crabs of Barr Al Hikman. Specifically, we investigated if crabs, after larval settlement, permanently stayed and reproduced in the intertidal zone, or if they used the intertidal area as a nursery ground and moved to the sublittoral for spawning. We conclude with a discussion on the ecological and economical importance of crabs in Barr Al Hikman.

Methods

Study area

Barr al Hikman (20.6° N, 58.4° E) is a peninsula of approximately 900 km^2, located in the central-east of the Sultanate of Oman, 25 km west of the island Masirah (Fig. 3.1). The peninsula is surrounded with about 190 km^2 of intertidal mudflats (Fig. 3.1). These mudflats provide foraging habitat to a large variety of species, including, fishes, shrimps (Ross 1985; Fouda & Al-Muharrami 1995; Mohan & Siddeek 1996) and waterbirds (Chapter 5). The area features an abundant and diverse community of crabs which, however, remain poorly studied (Fouda & Al-Muharrami 1995; Chapter 2).

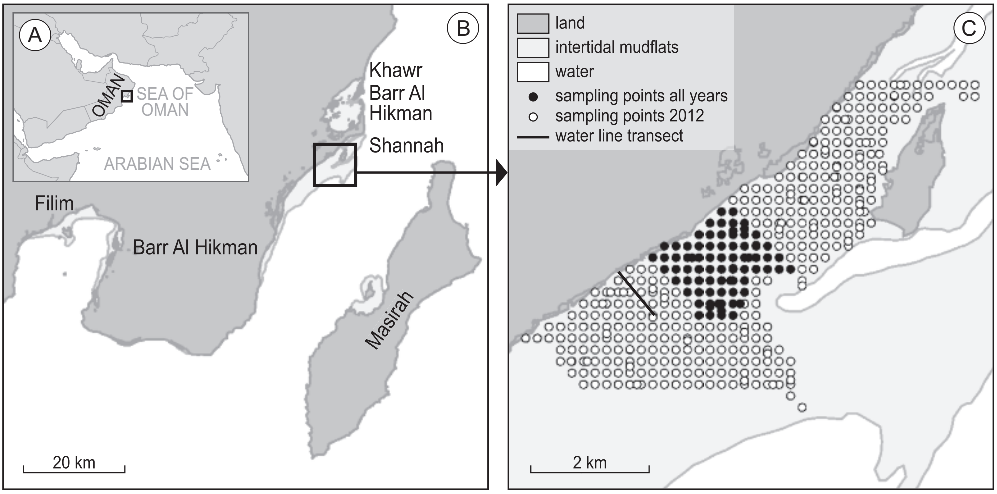

Figure 3.1. (A) The Sultanate of Oman with Barr Al Hikman in the red square. (B) Barr Al Hikman, with the study area in the red square. (C) The study area with the grid sampling points and the water line transect. Black points refer to the small grid of 80 points. Black and white points refer to the large grid.

The intertidal mudflats are flooded twice per 24.8 hours. The tide is mixed semidiurnal, meaning that the two daily high- and low tides differ in height. The tidal amplitudes range between 0.1 m at neap and 3 m at spring tides (Chapter 5). The climate is arid, with an average annual rainfall for Masirah of 70 mm, and mean monthly temperature ranging from 22.3°C in January to 30.4°C in May (Mettraux *et al.* 2011). In early summer the water is warm and nutrient-poor. Between June and October, cool, turbid and eutrophic water enters the area driven by the yearly Somali coastal upwelling (Jupp *et al.* 1996). The salinity of the water varies between 36‰ in winter and 40‰ in summer (Mohan & Siddeek 1996). The intertidal mudflats are characterized by a patchwork of barren areas, alternating with pools and seagrass beds that are intersected by smaller and larger gullies, which reach into the sabkha. The main seagrass species that occur in the area are *Halodule uninervis* and *Halophila ovalis* and occasionally *Syringodium isoetifolium* and *Thalassia hemprichii* (Fouda & Al-Muharrami 1995; Jupp *et al.* 1996). Raised fossil reefs and reefs formed by the polychaete *Pomatoleios kraussiireefs* are found scattered throughout the intertidal zone.

Our study area was situated on the east coast of the Barr al Hikman peninsula south of Shannah, in an area of about 6×8 km (Lat 20.6714 – 20.7772, Long 58.6366 – 58.7122, Fig. 3.1). This area consists almost exclusively of intertidal mudflats, with only a few reef structures just below or above the surface. The study area was sampled during each winter in the period 2012-2015. The sample periods were: 7 November – 15 December 2012, 5–20 December 2013, 7 November – 15 December 2014 and 6–18 November 2015.

Crab density sampling & life cycle

In all years crabs were sampled on a grid with an inter-sampling distance of 200 m, with 20% additional random stations on the gridlines (Fig. 3.1C) (Bijleveld *et al.* 2012). In the first year 2012 a large grid with 440 stations (including random stations) was sampled. In the three successive years subsets of the large grid (hereafter: small grid) were sampled (Fig. 3.1C). The number of stations sampled on the small grid were 80, 73,75 and 72 in 2012, 2013, 2014 and 2015 respectively. Sampling took place during low tide. At each station, four sediment samples were taken within a square meter with a 15 cm diameter corer to a depth of 20 cm. Presumably a sample depth of 20 cm ensures that all crabs living in the sediment are captured (unpublished data). The samples were sieved separately over a mesh size of 1 mm and crabs were collected. During the sampling we also noted all crabs encountered on the mudflats to compile the list of the crabs in Barr Al Hikman as comprehensive as possible.

The collected crabs were stored in a 4% formalin solution and shipped to the NIOZ Royal Netherlands Institute of Sea Research. Here, each crab was identified, measured and inspected for eggs. Crabs were identified using keys given in Naderloo (2017). Carapace width and length were measured to the nearest 0.1 mm. Biomass in gram ash-free dry mass (AFDM) was obtained by drying the samples (at 55°C for a minimum of 72 hours), weighing (to the nearest 0.1 mg), incineration (at 560°C for 5 hours) and weighing again (Compton *et al.* 2013).

The densities of the eight most abundant species were calculated for each sampling year. For the year 2012 densities were calculated both for the large grid and the small grid. Yearly mean numerical and biomass densities were calculated from the average densities of the four samples taken per station. We used the average of four samples to compute the yearly means and standard deviation. The data contained many zeros (i.e. in most years most species were absent from more than 50% of the sampled stations) and the average number of crabs per station did not follow a normal distribution.

To study the live cycle of the eight most abundant crabs we present size range (carapace width) and oviposition rates. While sampling in the area we observed seemingly large numbers of blue swimming crabs *Portunus segnis* moving in and out the area with the tidal flow. To estimate the size (carapace width) of *P. segnis* in the water column we walked square line transect (Fig. 3.1C) in which we counted all crabs observed within 1 m^2 in front of the observer in the watercolumn to a maximum depth of 40 cm. For each observed crab the size was visually estimated using the following categories: 0–25 mm, 25–50 mm, 50–100 mm and >100 mm. A second observer sampled (with a scoop net) a subset of P segnis in the water column to estimate oviposition rates. The number of transects were 18, 10, 17 and 9 covering 28,400 m, 19,200 m, 25,600 m and 25,700 m in 2012, 2013, 2014 and 2015 respectively. The number of *P. segnis* caught in the water column and checked for oviparous females equalled 326, 38, 255 in 2012, 2014 and 2015 respectively.

Environmental variables

SEAGRASS DENSITIES

Seagrass in the study area consisted exclusively of *Halodule uninervis* and *Halophila ovalis*. Aboveground seagrass density of both species was visually assessed at each grid station following the classification of Braun-Blanquet (Braun-Blanquet 1932). This scale separates seagrass cover into five classes based on the following coverage: 0–1%, 1–5%, 5–25%, 25–50%, 50–75% and 75–100%. We combined the class "r" and "+" proposed by Braun-Blanquet (1932) into the 0-1% coverage class (Fig. 3.2A).

ELEVATION

The elevation of the intertidal area was derived from an intertidal elevation model developed by Molenaar (2012, unpublished report summarized in Box A). The intertidal elevation model was constructed on the basis of the waterline method (Zhao *et al.* 2008). In this approach, waterlines were extracted from seven Landsat satellite images captured at known tidal height.

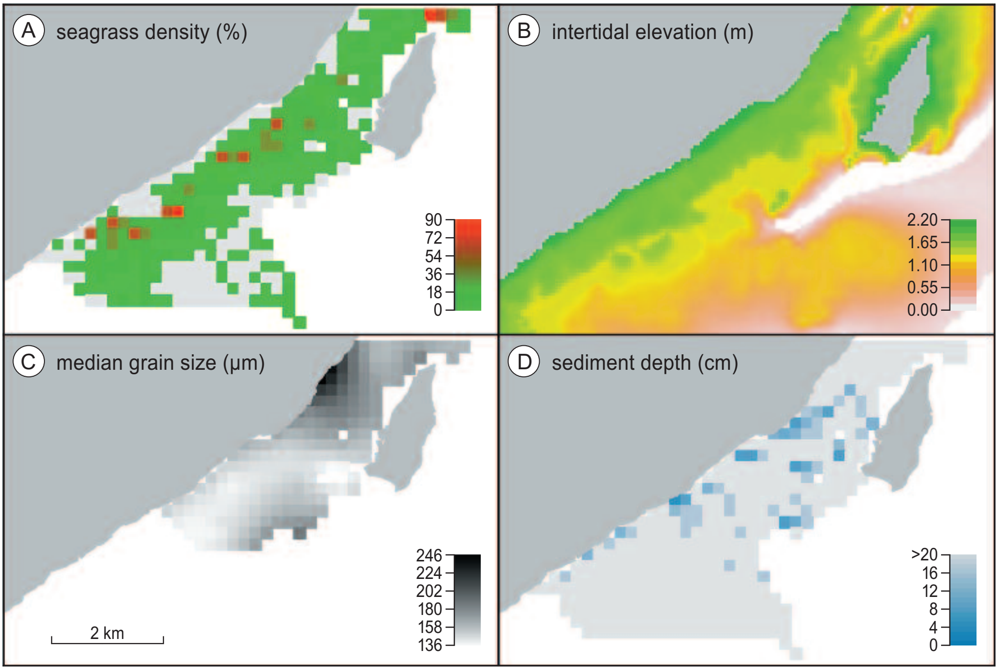

Figure 3.2. Environmental variable in the study area used for species distribution modelling. (A) Seagrass density sampled in November 2012, (B) tidal elevation based on satellite data collected between 2010 and 2012, (C) median grain size based on samples collected in November 2011, and (D) sediment depth based on samples taken in November 2012.

Based on the assumption that the waterline of each image represents a line of equal elevation, elevations were computed by means of interpolation (Fig. 3.2B).

SEDIMENT GRAIN SIZE

The upper 5 cm of the sediment was collected with a PVC tube of 19 mm diameter in November – December 2011 at 240 stations on the sampling grid (Fig. 3.2C). Samples were frozen and shipped to NIOZ. Grain size distributions were measured by means of a particle size analyser which uses laser diffraction and Polarization Intensity Differential Scattering technology (Coulter LS 13 320, optical module 'grey', grain sizes from 0.04 to 2000 µm in 126 size classes). For further details concerning sediment analysis we refer to (Compton *et al.* 2013). To reduce costs, only the sediment samples from the random stations (n = 39) were analysed. The median grain size (mgs, in µm) was used for further analysis. This variable was interpolated across the study area with universal kriging. As some station fall outside the interpolation range mgs could not be estimated for all stations (see below). Mgs was positively correlated with the squared distance to the coast. To improve interpolation accuracy we added mgs-squared as a covariate for modelling the variogram. For each station the shortest distance to the coast was measured using QGIS (Quantum GIS Development Team 2012). To meet the normality assumptions we used the log transformed value of mgs. In R (R Development Core Team 2013), using the package *gstat*, we checked if the assumptions of residual patterns and normally distributed residuals were met. For visualization purposes we back-transformed the interpolated values of mgs (Fig. 3.2C).

SEDIMENT DEPTH

At some of the grid stations a hard impenetrable layer was reached within the 20 cm of the corer used to sample the crabs. For these stations, the maximum sediment depth was recorded to the nearest cm (Fig. 3.2D).

Species distribution modelling

For the two most abundant crab species (*Macrophthalmus sulcatus* and *Thalamita poissonii*) the data was suitable to model the low-tide distributions as functions of the environmental variables. We used the Random Forest (RF) algorithm (Breiman 2001) which is a modelling technique that fits many classification trees to a data set, and then combines the predictions from all the trees (Cutler *et al.* 2007). For each tree about one third of the data is left out which are used for validation (the out-of-bag [OOB] sample) and combined in an overall OOB error estimate. RF makes no distributional assumptions (Cutler *et al.* 2007).

RF models were fitted using log-transformed numerical crab densities as response variables. Log-transformed values were used to reduce the relative importance of high densities. The value of 1 was added to all zero numerical densities to avoid taking the log of zero. Separate models were fitted for each species and each year. For 2012, models were fitted on the data collected on the large and small grid seperately. Because mgs could not be interpolated to all stations, the number of stations that were included equalled 228 for the large grid and 54 for the small grid. We only measured mgs in November 2011 and assume that it did not change in the period 2011–2015. We applied the RF algorithm within the R environment

(R Development Core Team 2013) using the package *randomForest* (Liaw & Wiener 2002). The performance of the RF model was examined as the percent variance explained: pseudo R^2 = 1– MSE_{OOB}/observed variance, where MSE_{OOB} is the mean square error between observations and OOB predictions (Wei *et al.* 2010). Predictor importance was determined as the difference in model performance in terms of contribution to prediction accuracy with or without a randomly permuting predictor variable (Breiman 2001). We analysed the nature of the relationships between crab densities and predictor variables by means of partial dependence plots. Partial dependence plots show the marginal effect of a response variable after accounting for the average effects of the other variables on the response (Friedman 2001). Partial dependence plots were fitted in R using the pdp package (Greenwell 2017).

Table 3.1. List of crab families and species observed on the intertidal mudflats of Barr Al Hikman, with reference to feeding types and, if collected on the grid, the mean winter densities (number per m2) over the period 2012-2015 (based on samples of the small grid).

Family	**species**	**feeding type**	**mean winter density** (# m^{-2} ± SD)
Dotillidae	*Dotillidae* sp.	deposit [1]	-
	Scopimera crabricauda	deposit [1]	0.71 (±1.05)
Dromiidae	*Dromia dormia*	predator[1]	-
Grapsidae	*Metopograpsus messor*	unknown	-
	Grapsus albolineatus	herbivore[2]	-
Leucosiidae	*Leucosiidae* sp.	unknown	1.94 (±1.44)
	Nursia sp.	unknown	-
Inachidae	*Camposcia* sp.	unknown	-
Matutidae	*Matuta victor*	scav/pred[1]	-
Macrophthalmidae	*Macrophthalmus depressus*	deposit[1]	0.20 (±0.39)
	Macrophthalmus grandidieri	deposit[1]	0.18 (±0.25)
	Macrophthalmus goneplacidae	deposit[1]	-
	Macrophthalmus laevis	deposit[1]	0.27 (±0.42)
	Macrophthalmus serenei	deposit[1]	0.14 (±0.09)
	Macrophthalmus sinuspersici	deposit[1]	0.54 (±0.51)
	Macrophthalmus sulcatus	deposit[1]	12.22 (±7.19)
Ocypodidae	*Ocypode saratan*	scav/pred[1]	-
	Ocypode rotundata	scav/pred[1]	-
	Ocypode platytarsis	scav/pred[1]	-
	Uca annulipes	deposit[3]	-
	Uca sp.	deposit[1]	0.14 (±0.29)
Pilumnidae	*Pilumnus* sp.	unknown	0.04 (±0.09)
Pinnotheridae	*Pinnotheres* sp.	deposit[1]	-
	Xenopthalmus sp.	deposit[1]	-
Portunidae	*Portunus segnis*	scav/pred[5]	0.27 (±0.30)
	Thalamita crenata	predatory[4]	-
	Scylla serrata	predatory[1]	-
	Thalamita poissonii	herbivore[1]	10.97 (±14.40)
Varunidae	*Asthenognathus* sp.	unknown	-
Xanthidae	*Xanthiidae* sp.	unknown	-

[1]own observation, [2]Naderloo *et al.* (2013), [3]de Boer and Prins (2002), [4]Cannicci *et al.* (1996), [5]Safaie (2016)

Results

The crabs species of Barr Al Hikman

In the grid samples we identified 14 crab species (Table 3.1). Outside the grid samples, we identified another 15 species (Table 3.1). These 29 crab species belong to 13 families. With seven species, members of the *Macrophtalmidae* family were the most common, followed by members of the *Ocypodidae* family (five species) and of the *Portunidae* family (four species). We identified 13 species to be burrow-hiding deposit-feeding crabs, eight species as scavengers/predatory crabs and two species as herbivorous (Table 3.1).

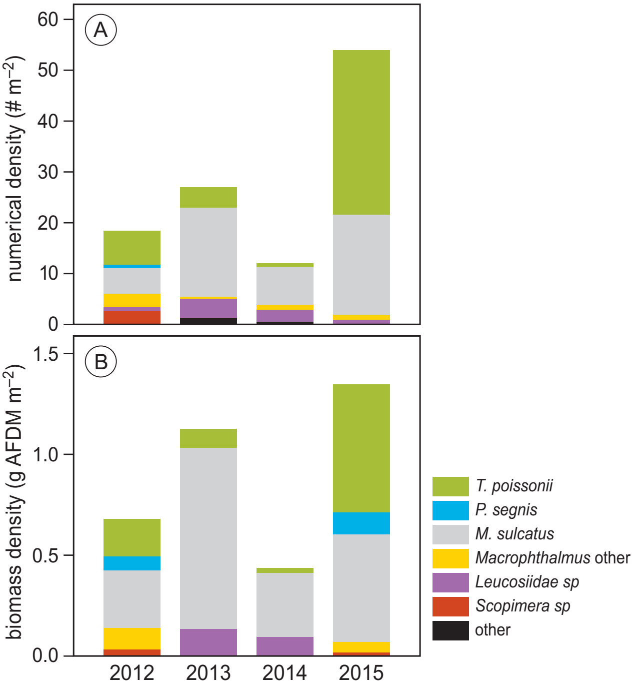

Figure 3.3. Average numerical densities (A) in number per m^2 and biomass densities (B) in g AFDM per m^2 of *M. sulcatus*, *T. poissonii*, *Leucosidae* sp, *P. segnis*, all other *Macrophthalmus* and all other crabs during five subsequent winters calculated from the samples taken on the small grid.

Crab densities & life cycle

Across the winters 2012–2015 the total numerical crab densities ranged from 12.1 to 53.9 crabs/m^2 and biomass densities ranged from 0.44 to 1.35 g AFDM/m^2 (Fig. 3.3). *M. sulcatus* and *T. poissonii* were the most abundant species; together they contributed for at least 60% of numerical and biomass density during all winters (Table 3.1, Table 3.2, Fig. 3.3 & Fig. 3.4). In 2012, the estimated densities on the large grid were similar to the densities estimated on the small grid, suggesting that the density estimates on the small grid are representative for the large grid.

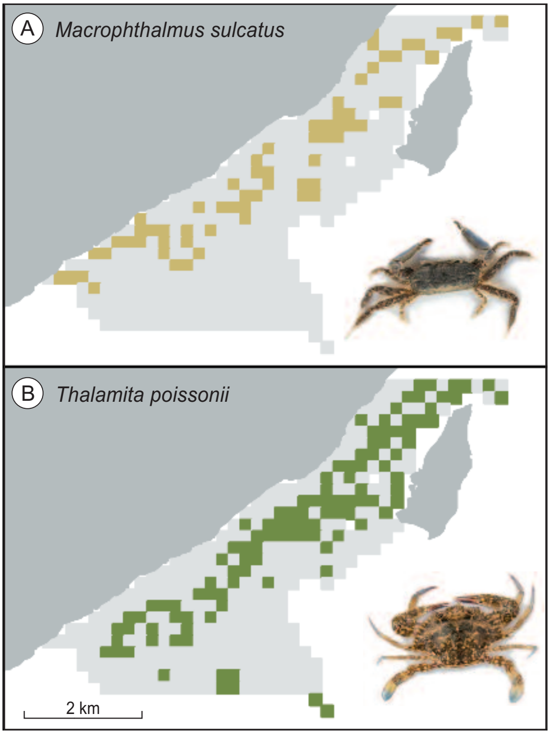

Figure 3.4. Spatial distribution (presence/absence) of (A) *Macrophthalmus sulcatus* and (B) *Thalamita poissonii*, the two most abundant crabs in the area, in November 2012. Coloured blocks denote presence and grey blocks absence.

Table 3.2. The average numerical and biomass density of the eight most abundant crabs across four years based on the samples collected on the grid (large and small) and in the water column. Species are ranked according to their abundance, with most abundant species on top.

		2012 large grid	**2012**	**2013**	**2014**	**2015**
numerical density (#/m^2)	*Macrophthalmus sulcatus*	3.47 (±8.71)	4.9 (±11.38)	17.26 (±20.68)	7.28 (±11.12)	19.44 (±23.82)
	Thalamita poissonii	7.29 (± 15.41)	6.65 (± 13.36)	4.03 (± 9.76)	0.93 (± 4.20)	32.28 (± 41.21)
	Leucosiidae	1.18 (± 4.43)	0.7 (± 3.07)	3.84 (± 8.50)	2.24 (± 6.92)	0.97 (± 4.29)
	Scopimera crabricauda	1.11 (± 7.51)	2.27 (± 10.55)	0.19 (± 1.64)	0.37 (± 3.23)	0
	Macrophthalmus sinuspersici	1.11 (± 4.13)	1.23 (± 4.56)	0.38 (± 2.30)	0.19 (± 2.76)	0
	Macrophthalmus laevis	0.45 (± 3.38)	0.88 (± 5.61)	0	0.19 (± 1.62)	0
	Portunus segnis	0.41 (± 2.55)	0.7 (± 3.79)	0.19 (± 1.64)	0	0.19 (± 1.65)
	Macrophthalmus serenei	0.32 (± 2.29)	0.18 (± 1.57)	0	0.19 (± 1.62)	0.19 (± 1.65)
biomass density (g AFDM/m^2)	*Macrophthalmus sulcatus*	0.27 (± 0.75)	0.28 (±0.70)	0.89 (±1.22)	0.32 (±0.54)	0.53 (±0.77)
	Thalamita poissonii	0.39 (± 1.23)	0.18 (±0.50)	0.09 (±0.41)	0.02 (±0.16)	0.64 (±1.10)
	Leucosiidae	0.03 (±0.16)	0.01 (±0.04)	0.12 (±0.29)	0.09 (±0.33)	0.02 (±0.08)
	Scopimera crabricauda	0.01 (±0.10)	0.03 (±0.14)	0 (±0.03)	0 (±0.01)	0
	Macrophthalmus sinuspersici	0.03 (±0.13)	0.02 (±0.07)	0 (±0.03)	0 (±0.01)	0
	Macrophthalmus laevis	0.05 (±0.36)	0.07 (±0.45)	0	0 (±0.01)	0
	Portunus segnis	0.08 (±0.65)	0.07 (±0.39)	0.01 (±0.08)	0	0.11 (±0.95)
	Macrophthalmus serenei	0.02 (±0.14)	0.02 (±0.15)	0	0 (±0.02)	0.04 (±0.31)

Mean and range of carapace width found in the grid samples and in the water column are given in Table 3.3. Oviparous females were found in all of the eight most abundant species, except for *P. segnis* (Table 3.3). In the water transect *P. segnis* was observed for 968, 15, 14 and 228 times in 2012, 2013, 2014 and 2015 respectively. The water transect method does not give an accurate number of densities, but relative number of *P. segnis* observed in the water column is consistent with the number of *P. segnis* sampled on the grid.

Table 3.3. Sample size, carapace width and oviparous rates for the eight most abundant crabs observed in the grid samples and in the water column.

species	# crabs	mean carapace width (range) (mm)	% oviparous female
Macrophthalmus sulcatus	338	12 (2–25)	54
Thalamita poissonii	421	9 (3–25)	31
Leucosiidae sp.	74	7 (3–11)	5
Macrophthalmus sinuspersici	40	6 (2–11)	100
Scopimera crabricauda	38	4 (2–9)	56
Macrophthalmus laevis	15	13 (8–17)	67
Macrophthalmus serenei	12	11 (6–15)	20
Portunus segnis (grid)	15	25 (13–44)	0
Portunus segnis (water)	1306	35 (12–125)	0*

*based on a sample of 619 crabs

Species distribution modelling

Model performance of RF for *M. sulcatus* and *T. poissonii* varied considerably between years. The variance explained by the RF models for the 2012 data covering the large grid was 7% for *M. sulcatus* and 21% for *T. poissonii* (Table 3.4). For these models seagrass was the environmental variable which explained most of the variance of the crab densities (Table 3.5). The variance explained by the RF models covering the small grid ranged from –18% to 30% for *M. sulcatus* and from –9 to 10% for *T. poissonii*. For these models no single environmental variable could be selected as the best explaining environmental variable because $\mathrm{MSE}_{\mathrm{OOB}}$ differed substantially between years (Table 3.5). The shape of the relationships between crab densities and predictor variables is shown by means of partial dependence plots (Fig. 3.5). Some generalities emerged. Particularly crab densities were in general positively associated with seagrass densities and sediment depth and negatively associated with tidal elevation and median grain size.

Table 3.4. Percentage of variance captured by the RF model for the different years and sample grids. Negative values imply that the model does not predict better than a mean value.

	2012 large grid	2012	2013	2014	2015
Macrophthalmus sulcatus	7.08	29.53	29.58	–18.67	–7.20
Thalamita poissonii	25.01	7.20	4.62	-8.94	10.04

Table 3.5. Mean predictor importance (MSE_{OOB}) on numerical crab abundance for different years and sample grids. Values indicates the contribution to RF prediction accuracy for that variable. Higher values mean higher prediction accuracy.

	2012 large grid	2012	2013	2014	2015
Macrophthalmus sulcatus					
seagrass	14.22	14.43	16.33	–1.07	–1.67
Mgs	0.51	7.5	7.06	–0.58	0.33
elevation	6.69	9.38	8.64	4.31	5.13
sediment depth	9.13	15.38	16.06	–0.07	7.87
Thalamita poissonii					
seagrass	19.48	6.59	2.66	1.06	0.52
Mgs	10.79	10.25	12.69	6	6.94
elevation	17.17	6.88	6.16	2.94	6.77
sediment depth	7.46	3.14	–0.32	–1.5	11.65

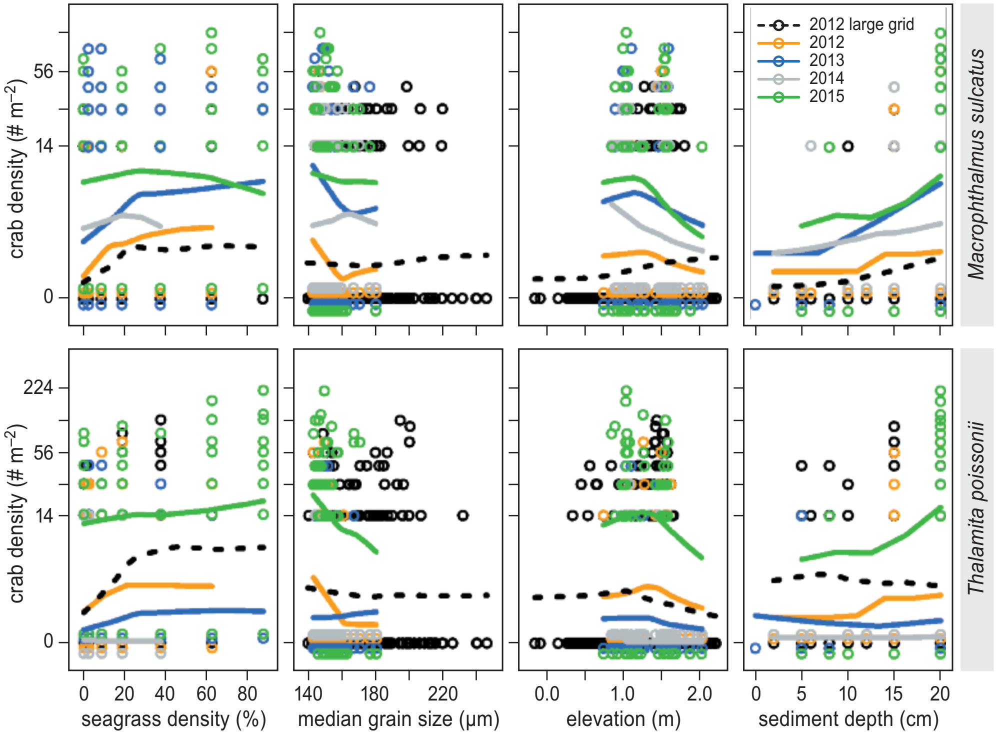

Figure 3.5. Partial dependence plots for the modelled relationships between crab densities and the predictor variables. Lines indicate modelled relationships and points represent the data. Note the log scale on the y-axis.

Discussion

Crabs of Barr Al Hikman

Our study shows that at least 29 species of crabs occur on the intertidal mudflats of Barr Al Hikman. All these species were previously observed in the Arabian region (Simões *et al.* 2001; Naderloo *et al.* 2013; Naderloo 2017) and nine of them had previously been reported from Oman (Clayton 1996; Clayton & Al-Kindi 1998; Khorov 2012). The diversity of crabs at Barr Al Hikman is similar to other nearby areas such as intertidal mudflats in Iran, Kuwait, Yemen, India and Mozambique (Cooper 1997; Simões *et al.* 2001; de Boer & Prins 2002; Al-Yamani *et al.* 2012; Naderloo *et al.* 2013; Shukla *et al.* 2013). Note that we sampled only the intertidal mudflats and not the intertidal reefs and mangroves, which usually have a more diverse crab community than intertidal mudflats (Simões *et al.* 2001; Naderloo *et al.* 2013).

The crab community at Barr Al Hikman shows similarities with crab communities at other (tropical) intertidal mudflats. For instance, deposit-feeding burrow-hiding crabs and herbivorous swimming crabs also dominated many other tropical intertidal mudflats (Simões *et al.* 2001; Naderloo *et al.* 2013; Naderloo 2017), which typically reach densities in the same order of magnitude as we found (Swennen *et al.* 1982; Clayton & Al-Kindi 1998; Karlsson 2009; Otani *et al.* 2010). Likewise, 5-fold inter-annual fluctuations in crab/invertebrate densities on intertidal mudflats are not unusual (Beukema 1989; Beukema 1991b; Clayton & Al-Kindi 1998).

Species distribution modelling

The model performance of random forest models explaining the distribution of *M. sulcatus* and *T. poissonii* varied considerably between years. In some years, up to 30% of the variance could be explained but in most years the variance explained was close to 0. Note that species distribution models usually have equally low performance when examining the spatial distribution of invertebrates at intertidal mudflats (Compton *et al.* 2013). Models performed best in years when the crab densities were intermediate (2012 and 2013) and worst in years with low (2014) and high (2015) crab densities.

In general, the crab densities were positively associated with seagrass density and sediment depth and negatively associated with median grain size and elevation. The positive association between seagrass and crab densities may indicate that crabs use seagrass as a food resource. Isotope data collected in 2014 are in line with this suggestion as it showed that seagrass is the main food resource for both *T. poissonii* and *M. sulcatus*, either by direct consumption or by the consumption of seagrass detritus (Al Zakwani *et al.*, unpublished data). Furthermore, analysis of gut contents of crabs collected at Barr Al Hikman in December 2012 showed seagrass roots in *T. poissonii* (n = 12, unpublished data). The positive association may also be caused by the safe-habitat function that seagrass meadows provide (Kunsook *et al.* 2014) as both species are subjected to predation by a large number of avian predators (Chapter 2 and 8). Vice versa, seagrass may also profit from the presence of detritus-eating crabs as too high levels of organic material can be detrimental for seagrass (Koch 2001; Folmer *et al.* 2012) and seagrass could benefit from soil aeration promoted by burrowing crabs (Smith *et al.* 1991).

The cause of the observed correlations with other environmental variables remains more speculative. The negative association between crab densities and intertidal elevation is in agreement with the idea that closer to the shore crabs face problems related to desiccation and fluctuations in temperature and oxygen (Flores *et al.* 2005; Jensen *et al.* 2005). The negative association with mgs and the positive association with sediment depth may be related to the burrowing and burying behaviour of the studied crabs. The burrowing and burying behaviour may also explain why crabs were positively associated with sediment depth.

Across all four years of study, the slopes between crab densities and environmental variables were in general similar, but the heights of the response curves differed. This suggests that crab abundance fluctuates around some long-term average, driven by biotic environmental factors and by factors that vary over time, rather than in space (van der Meer 1999). At Barr Al Hikman crab abundance may be related to the amount of seagrass and the detritus that is produced (i.e. the total amount of food in the system) as the low number of crabs in 2014 coincided with low seagrass densities in the area and the high crab densities in 2015 with high seagrass densities (Fig. 3.6B). Yet, also other time-related variables such as weather conditions can affect juvenile crab survival in intertidal ecosystems (Beukema 1991a; Seitz *et al.* 2005).

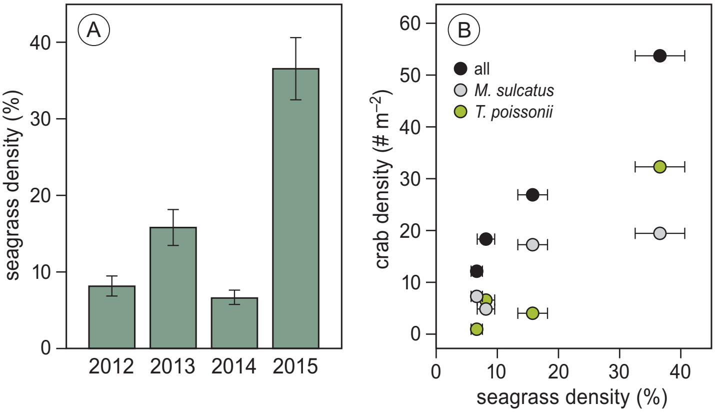

Figure 3.6. (A) Mean % seagrass density between years and (B) annual mean % seagrass density plotted against mean numerical density. Error bars represent standard errors.

Life cycle

Our finding that oviparous females were found in seven of the eight most abundant crabs species (Table 3.3) indicates that reproduction of most species occurs in the intertidal zone. The maximum size of the smaller burrow-hiding deposit feeding crabs, mainly *Macrophthalmus*, matches closely with the maximum size class for these species (Clayton & Al-Kindi 1998; Chapter 7). This suggests that these species are intertidal after larval settlement until the adult stage (Fig. 3.7). The blue swimming crab *P. segnis* was the only species in which no berried females were found, despite that over 600 crabs were checked (Table 3.3). In contrast, landings of *P. segnis* caught in the sublittoral in the Gulf of Oman show that ovigerous females can be found year round, with up to 50% of the females carrying eggs in fall (Safaie *et al.* 2013a; Safaie *et al.* 2015). However, the crabs caught were considerably larger. The average size of

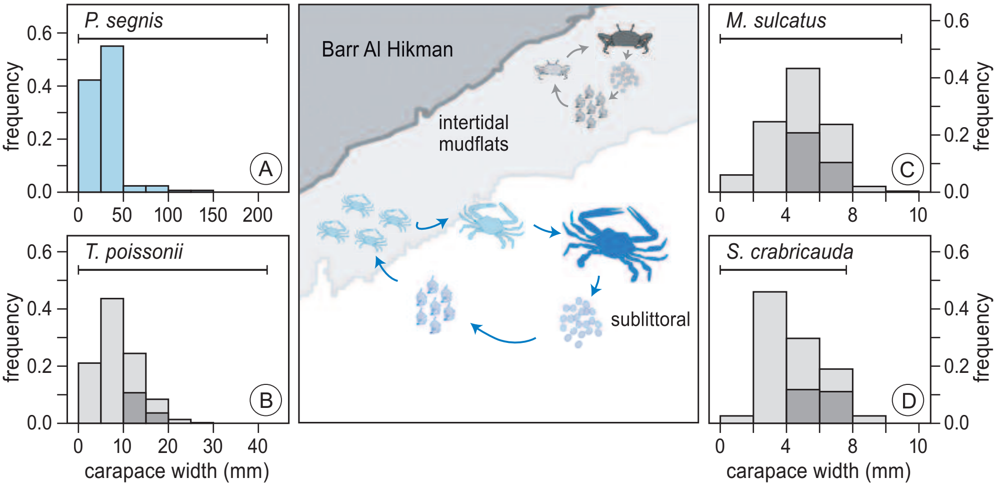

Figure 3.7. Carapace width frequency distribution of *P. segnis* (A), *T. poissonii* (B), *M. sulcatus* (C) and *S. crabricauda* (D) based on crabs encountered in the grid samples and along the water line transect (all years combined) and (E) a description of life-cycle. Black lines above figures denote maximum size known for each species. Size-range data are obtained from Mehanna et al. (2013); Bom *et al.* (unpublished); Chapter 7 and Clayton and Al-Kindi (1998). Light colours show non-ovigerous crabs, dark colours show ovigerous females. This led to the proposed life cycles in (E): after larval settlement *T. poissonii* and the burrow-hiding crabs reside in the intertidal area which they also use for reproduction (species in grey), whereas the area function as a nursery ground for blue swimming crabs *P. segnis* (in blue).

P. segnis landed on several sites in Oman, including a site 25 km away from Barr Al Hikman, in winter and spring, was 15 cm and with a maximum of 20 cm (Mehanna *et al.* 2013). These results suggest that small *P. segnis* are mainly linked to the intertidal zone and large ovigerous *P. segnis* are linked to the sublittoral, although we cannot exclude that landings did not contain small crabs (Bellchambers & de Lestang 2005). Our results suggest that Barr Al Hikman act as a nursery function for *P. segnis* (Fig. 3.7) in a similar way as intertidal areas act as nursery ground for other species of swimming crabs (Hill *et al.* 1982; Potter *et al.* 1983; Seitz *et al.* 2005).

Economic importance

The nursery function of Barr Al Hikman for *P. segnis* highlights the direct economic value of intertidal mudflats for Oman as, *P. segnis* provides a major income for local fisheries (Mehanna *et al.* 2013; MAFW 2014; Giraldes *et al.* 2016). Likely, all sampled *P. segnis* were below one year of age as growth rates measured on *P. segnis* at various places along its geographical range show that specimen larger than 100 mm is about 5 months old (Safaie *et al.* 2013a). Thus, with densities up to 0.7 crabs m^{-2} and an intertidal area encompassing 190 km^2, the entire annual production in Barr Al Hikman is in the order of hundreds of millions of *P. segnis*. This is probably still a conservative estimate because we sampled during one period in winter whereas spawning continues throughout the winter (Safaie *et al.* 2013b; Safaie *et al.* 2015). Although we do not know how many crabs reach the harvestable size of 10 cm, the estimated production number shows the enormous potential that intertidal areas can have for *P. segnis*. Effective conservation planning is therefore not only important for conservation of biodiversity but also important to sustainable crab fisheries. This is a timely issue as currently *P. segnis* is overexploited in the region (Safaie *et al.* 2013b; Giraldes *et al.* 2016).

Conclusion

We have shown that the intertidal mudflats of Barr Al Hikman provide habitats to a large number of crabs. Seagrass acts as an important food resource and habitat as is shown by the positive relationships with crab densities, both in space and time. Most crabs were found to reproduce in the area, but a noticeably exception is the economically important blue swimming crab *P. segnis*, for which the area is as a valuable nursery ground. Therefore it is important to include the role of crabs and seagrass beds in conservation management plans of the area.

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Box A

Bathymetry model

As no bathymetry model exists for the intertidal area of Barr Al Hikman a bathymetry model was newly created using the waterline method (Ryu *et al.* 2002; Foody *et al.* 2005; Zhao *et al.* 2008). This approach consists of deriving waterlines (i.e. boundaries between submerged and exposed areas) from satellite images captured at different tidal heights. These lines are subsequently used as contour lines in an interpolation procedure, as it is assumed that they represent lines of equal elevation. Several methods can be adopted for waterline mapping, ranging from manual digitization to fully automated procedures (Ryu *et al.* 2002; Foody *et al.* 2005; Zhao *et al.* 2008). Here we adopted a semi-automated approach: the waterlines were automatically mapped based on a threshold value of the Normalized Difference Vegetation Index (NDVI). This threshold was allowed to vary between images to deal with the problem of varying atmospheric conditions. To this end, the waterlines were edited according to decision rules based on expert knowledge of the location of gullies and reefs.

Seven Landsat ETM+ images were obtained (Table A.1; source: http://glovis.usgs.gov). The tidal heights at the capture dates of the images at the Ras Hilf port on Masirah (approx. 18 km from the study area) were subsequently acquired (http://easytide.ukho.gov.uk). The exact water heights h at the imagery times were calculated with the formula:

$$h = h_1 + (t_2 - t_1) + Cos(A) + 1)/2]$$

where $A = \pi[t - t_1)/(t_2 - t_1)] + 1)$ *radians*

t denotes the decimal time at imagery capture
t_1 and h_1 denote the decimal time and tidal height of the tide preceding time t, t_2 and h_2 denote the decimal time and tidal height of the tide following time t (Tidal Information, New Zealand Nautical Almanac 2011–12).

Table A.1. The obtained Landsat ETM+ images with their corresponding water heights and NDVI threshold values for separating exposed and submerged mudflats.

Capture date (d-m-y)	**Local time** (hh.mm)	**Water height** (m)	**NDVI threshold**
26-3-2011	10.22	0.975	–0.17
8-4-2010	10.21	1.326	–0.18
24-4-2010	10.21	1.353	–0.18
10-3-2011	10.23	1.674	–0.15
20-10-2011	10.23	1.946	–0.15
10-5-2010	10.21	1.977	–0.19
24-1-2012	10.23	2.588	0.02

Waterlines were digitized using the *Topo to Raster* tool in ArcMap 10 (ESRI 2011), an interpolation method specifically designed for creating hydrologically correct Digital Elevation Models from contour lines (http://webhelp.esri.com 2012). The seven obtained waterlines in some locations intersected or overlapped. As this is in reality impossible, intersecting parts were deleted and parallel waterlines were drawn instead.

As no satellite images where available for the more extreme high and low tides (Table A.1), we manually added two waterlines, which correspond with 2.8 m when the water is at the coast line and with 0.1 m when the outer fringes of the intertidal area are exposed (own observations). The outer fringes are visible on the satellite images and correspond with our observations of the waterline at 0.1m.

The final bathymetry (Fig. A.1) model was created with the TIN to Raster tool in ArcMap. In this procedure an elevation model was created with the nearest neibour procedure (ESRI 2011).

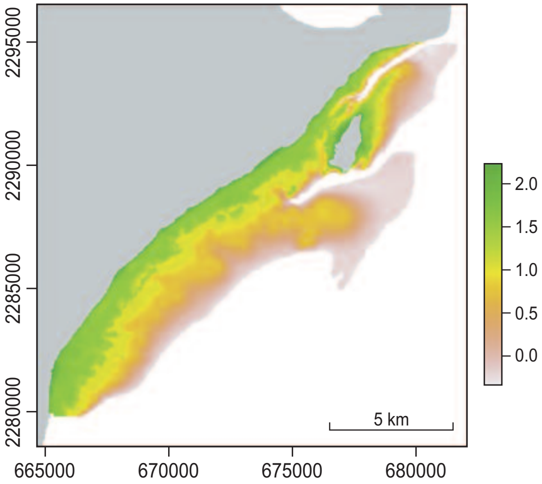
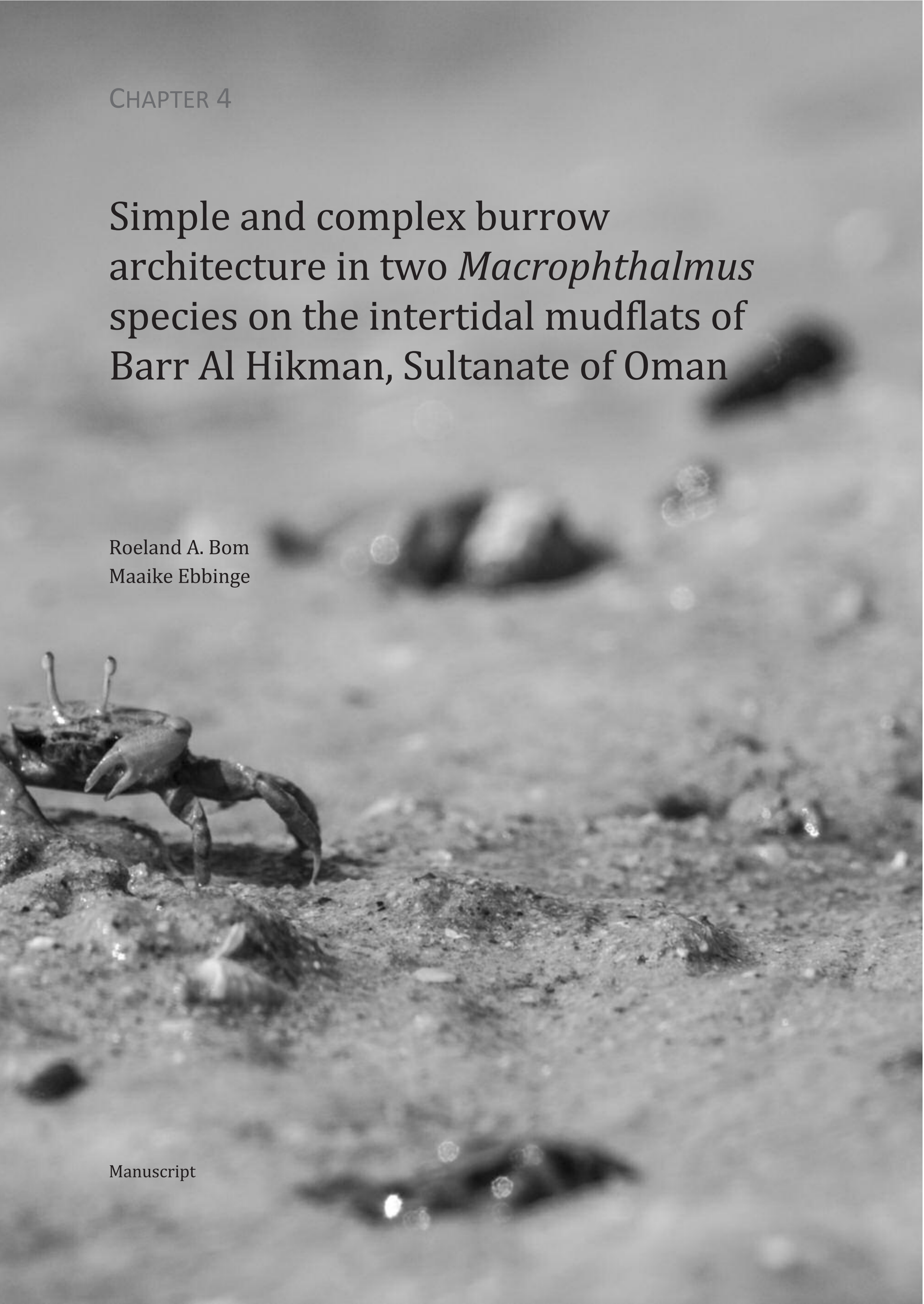


Figure A.1. The obtained bathymetry map for the south-east coast of Barr Al Hikman. Thick values refer to UTM.



CHAPTER 4

Simple and complex burrow architecture in two *Macrophthalmus* species on the intertidal mudflats of Barr Al Hikman, Sultanate of Oman

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Manuscript

Abstract

We studied the burrow architecture of *Macrophthalmus sulcatus* and *Macrophthalmus depressus* on the intertidal mudflats of Barr Al Hikman in the Sultanate of Oman. Casts (n = 7) and excavations (n = 8) show that *M. sulcatus* construct single tunneled burrows with one or two sharp curves. Each of the studied burrows was inhabited by one crab, except for one burrow where a large male and female was found. There was a strong relation between *M. sulcatus* carapax width and burrow size at entrance. Casts (n = 10) and excavation (n = 16) of burrows show that *M. depressus* constructs complex burrows, with multiple entrances and many branches. Burrows with up to five entrances were found, but we never managed to cast an entire burrow, so burrows are more extensive than described. Maximum depth of a cast was 35 cm. In six burrows more than one crab was encountered (up to four crabs per burrow, both males and females). There was no relation between *M. depressus* carapax width and burrow size at entrance. We argue that the difference in burrow architecture can be related to environmental factors. *M. sulcatus* burrows in a zone that is flooded every day, where simple burrows may suffice as a place to hide for predators, waves and desiccation and as a place for reproduction. Contrary, *M. depressus* burrows in a zone that is only flooded at spring tide. In this area, complex burrows could be beneficial for crabs in order to avoid desiccation. Complex burrows were found in an area with relatively fine sediments, so also sediment structure could play a role in the found burrow architecture. Finally, also social factors may account for complex burrow architecture.

Introduction

Crabs of the Ocypodoidea superfamily (families *Macrophthalmidae Ocypodidae*, *Ucididae*, *Dotillidae*) are well known for their burrowing behaviour (Bellwood 2002). Burrows of Ocypodoidea crabs are thought to have several adaptive functions; it may provide crabs a safe refuge from predators (Nye 1974; Yong *et al.* 2011; Qureshi & Saher 2012), a place to protect from waves, desiccation and extreme temperatures (Lim & Diong 2003) and a place for moulting and reproduction (Christy 1982; Chan *et al.* 2006; Yong *et al.* 2011; Sal Moyano *et al.* 2012). Most burrows of Ocypodoidea crabs have been described as rather simple, often in the shape of a J, Y, S or U, sometimes including a small chamber for reproduction (Christy 1982; Chan *et al.* 2006; Yong *et al.* 2011). Some studies report on Ocypodoidea crabs constructing complex burrows (Koo *et al.* 2005; Qureshi & Saher 2012; Vachhrajani & Trivedi 2016; Odhano & Saher 2017) but little is known what causes some species to construct such complex burrows.

This study reports on the burrow architecture of two species within the genus *Macrophthalmus* found on the intertidal mudflats of Barr Al Hikman in the Sultanate of Oman: *Macrophthalmus sulcatus* and *Macrophthalmus depressus*. Both species were found to construct strikingly different burrows.

Methods and Material

Study area & Macrophthalmus crabs

The present study was conducted at the intertidal mudflats that surround the Barr Al Hikman Peninsula in the Sultanate of Oman (N20.68°, E58.65°). The intertidal ecosystem in this area is relatively pristine and is acknowledged for its high biodiversity (Chapter 5). Burrowing crabs are an important part of the benthic community of Barr Al Hikman (Chapter 2 & 3). *M. sulcatus* was found to be the most abundant crab, locally reaching densities of >100 crabs/m^2 (Chapter 3). The species occurs in a zone of around 1 km broad at intermediate distance from the coastline in an area that is flooded with every high tide, i.e. twice per lunar day. *M. sulcatus* burrows in medium grained sediments (median grain size ~ 150 m), often in association with seagrass beds (Chapter 3). *M. depressus* is less abundant than *M. sulcatus* and occurs mainly in a zone within 100 m from the coastline in fine-grained sediments (median grain size ~ 300 m, Chapter 3). This zone is flooded with spring tides only, approximately 12 times per lunar cycle (28 days).

Burrow architecture

The burrow architecture of both *M. sulcatus* and *M. depressus* was studied by making a cast of the burrows using plaster (Krone Moulding Plaster). On 16 December 2014 plaster was poured into seven entrances of burrows of *M. sulcatus* and ten entrances of burrows of *M. depressus*. After 30 minutes the resulting casts were hard enough to be excavated using a small spoon (Fig. 4.1). For the burrows of *M. sulcatus* the length and depth of the burrow was measured in relation to burrow size at entrance. The burrows of *M. depressus* appeared to be complex and

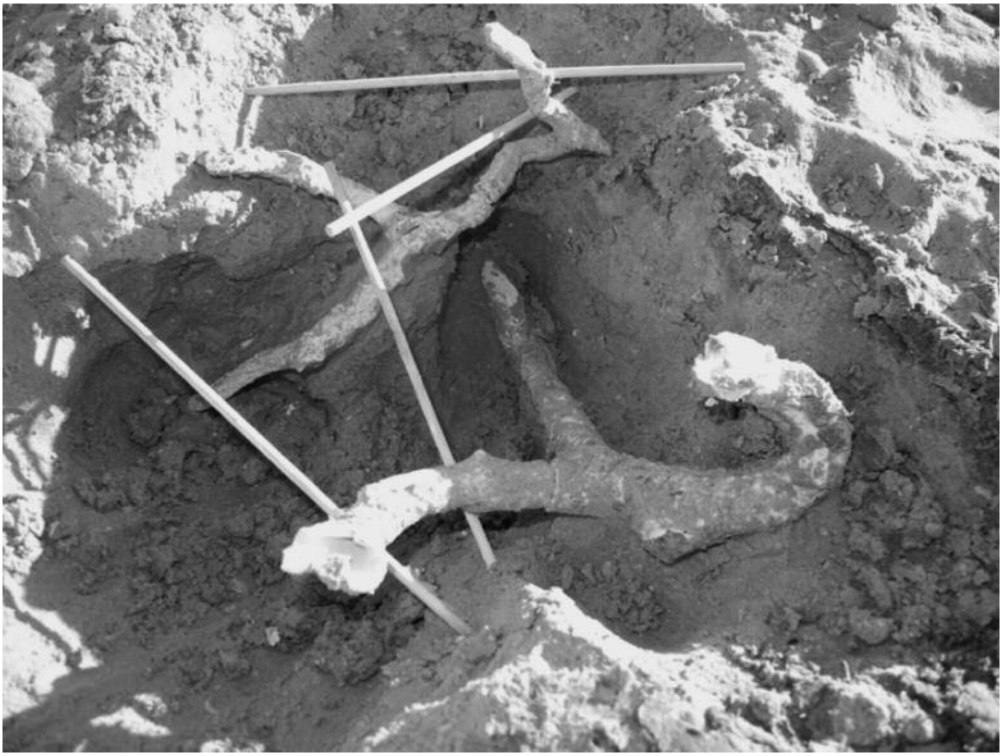

Figure 4.1. Cast of a burrow of *M. depressus*. Note that the two casts were connected and broke during excavation.

are here described in terms of their general morphology. For both species, the burrow size at entrance was measured in relation to size (carapax width) of the crab(s) found inside. To boost the sample size for this latter relation, the burrow size at entrance was measured for another eight burrows of *M. sulcatus* and 16 burrows of *M. depressus* and subsequently excavated to measure the size of the crab(s) found inside. Size was measured using a calliper and was recorded to the nearest 0.1 mm. The relation between burrow size at entrance and crab size was tested for the two species using linear models. All analysis were done using the R software (R Development Core Team 2013)

Results

Macropthalmus sulcatus

All seven casted burrows of *M. sulcatus* appeared to be a single tunnel (Fig. 4.2). Burrows had one or two sharp curves at the beginning into any direction after which the burrow continued into one direction. The end of each burrow consisted of a small pool of water in which in all but one cast a single crab was caught. Burrows were on average 21.3 cm long (range 11.2 – 26.6

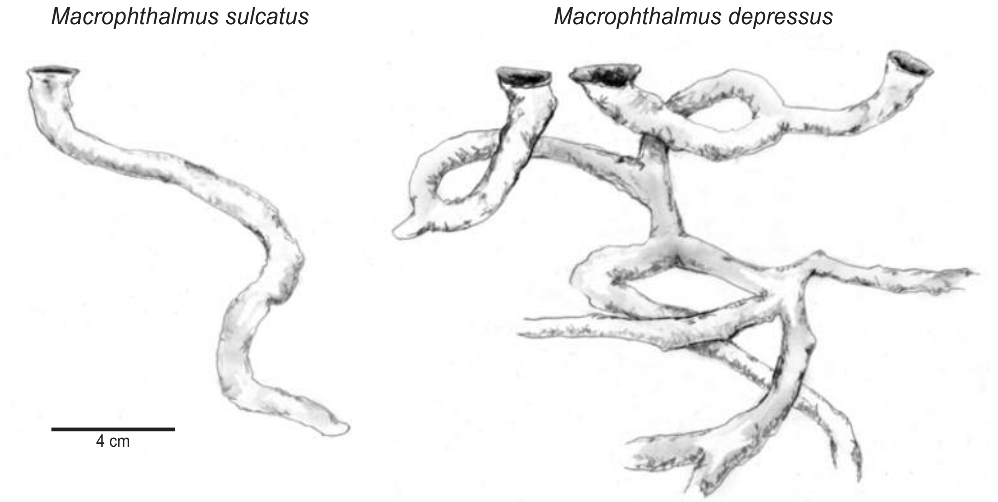

Figure 4.2. Typical cast of the burrow of the two crabs studied. The burrow ends of the burrow of *M. depressus* are open as the burrows were more extensive than our casts.

cm) and 10.3 cm deep (range 8.3 – 12.5 cm). One of the burrows that was excavated was occupied by two relatively large crabs; a male and a female (Fig. 4.3). There was a positive relation between burrow size at entrance and the carapax width of the crab caught inside (t = 8.020, $P < 0.01$, $R^2 = 0.82$, Fig. 4.3).

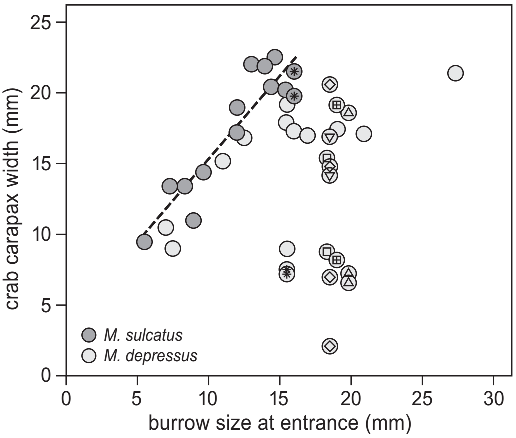

Figure 4.3. Relationship between crab carapax width and burrow size at entrance for the two studied crab species. The dashed line gives the significant linear model relating *M. sulcatus* carapax width to burrow size at entrance. Symbols within the points refer to burrows in which more than one crab was encountered; similar symbols refer to the same burrow.

Macrophthalmus depressus

The casted burrows of *M. depressus* appeared to be complex, with multiple entrances and branches (Fig. 4.1 and 4.2). In fact, we never managed to make a complete cast of an entire burrow as the tunnels always continued where the plaster stopped. One burrow appeared to have five entrances and another had two entrances (thus the ten burrow entrances into which plaster was poured belonged to five burrows). Branches were observed in any direction and tunnels had all possible slopes and angles. Maximum depth of a cast was 35 cm, at which the water level was reached. In two casted burrows a single crab was found (in the three other burrows the crabs probably could escape as the burrows were more extensive than our casts). In six out of the 16 excavated burrows more than one crab per burrow was encountered (up to four crabs per burrow, Fig. 4.3). Both males and females were caught. There was no relation between burrow size at entrance and crab size ($t = 1.109$, $P = 0.28$, $R^2 = 0.01$, Fig. 4.3).

Discussion

This study shows that within the same area, the burrow architecture of two closely related crabs can be strikingly different. *M. sulcatus* was found to construct rather simple burrows whereas *M. depressus* was found to construct complex burrows. Why do these related species construct such different burrows?

We suggest that the observed differences in burrow architecture can be linked to the different environmental conditions in which they were found. Simple burrows of *M. sulcatus* were found at an intermediate distance from the coast in coarse sediments in an area that is flooded every day. In this zone simple burrows may suffice as a place to hide for predators, strong waves and desiccation and as a place for reproduction. Furthermore, the coarse sediments perhaps limit the possibilities to construct and maintain complex burrows. Indeed, during excavation, several burrows of *M. sulcatus* collapsed before a crab was encountered (these burrows are not included in this study). The complex burrows of *M. depressus* were found in an area close the shore which is not flooded daily. Crabs living in this area may be challenged not to get desiccated. Complex burrows with deep rooting branches may in this respect help crabs to retain and to access water. Furthermore, it could be supposed that deposit-feeding *Macrophthalmus* crabs burrowing in an area that his not flooded daily are often deprived from food, as these crabs feed on organic material that comes with the flooding tide (Schuwerack *et al.* 2006). In deposit-feeding *Thalassinidean* shrimps it has been described that they do not only forage outside their burrows but also make use of the organic material that has been drifted inside their complex burrows (Nickell & Atkinson 1995). To our knowledge it has never been described that deposit-feeding crabs feed inside their burrows, but perhaps *M. depressus* may use the particles that has fallen into their complex (i.e. extensive) burrows as an additional food supply. In addition it should be noted that the burrows of *M. depressus* were found in relatively fine sediments which, contrary to the area in which *M. sulcatus* burrows, perhaps allows for more complex burrow constructions.

That environmental conditions are important to explain the observed burrow architecture is further suggested by a study on the burrow architecture of *M. depressus* at intertidal mudflats in India. Here in sandy and muddy sediments in an area that is flooded daily, burrows were found to be U-shaped (Silas & Sankarankutty 1967). Thus, under different environmental conditions the burrows of *M. depressus* in India were found to be much simpler then at Barr Al Hikman.

Other factors that could affect burrow construction include social interaction in crabs and predation pressure (Atkinson 1974; Yong *et al.* 2011). Complex burrows in Gonoplax crabs were associated with their highly developed social behaviour (Atkinson 1974). Diverse social behaviour is also found in *Macrophthalmus* crabs (Kitaura *et al.* 2006) but it is unclear to which extend the social life of the two studied crabs differ and thus whether social behaviour could imply the difference in burrow complexity. Precise engineering of burrows in Ocypode crabs was suggested to be an anti-predation mechanism (Yong *et al.* 2011). We do not know how much the predation pressure, by shorebirds (Chapter 2), exposed on the studied crabs differ. We conclude that more detailed observations and experiments are needed to further understand the burrow architecture of the studied crabs.

Acknowledgements

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CHAPTER 5

Barr Al Hikman, a major shorebird hotspot within the Asian–East African flyway: results of three winter surveys

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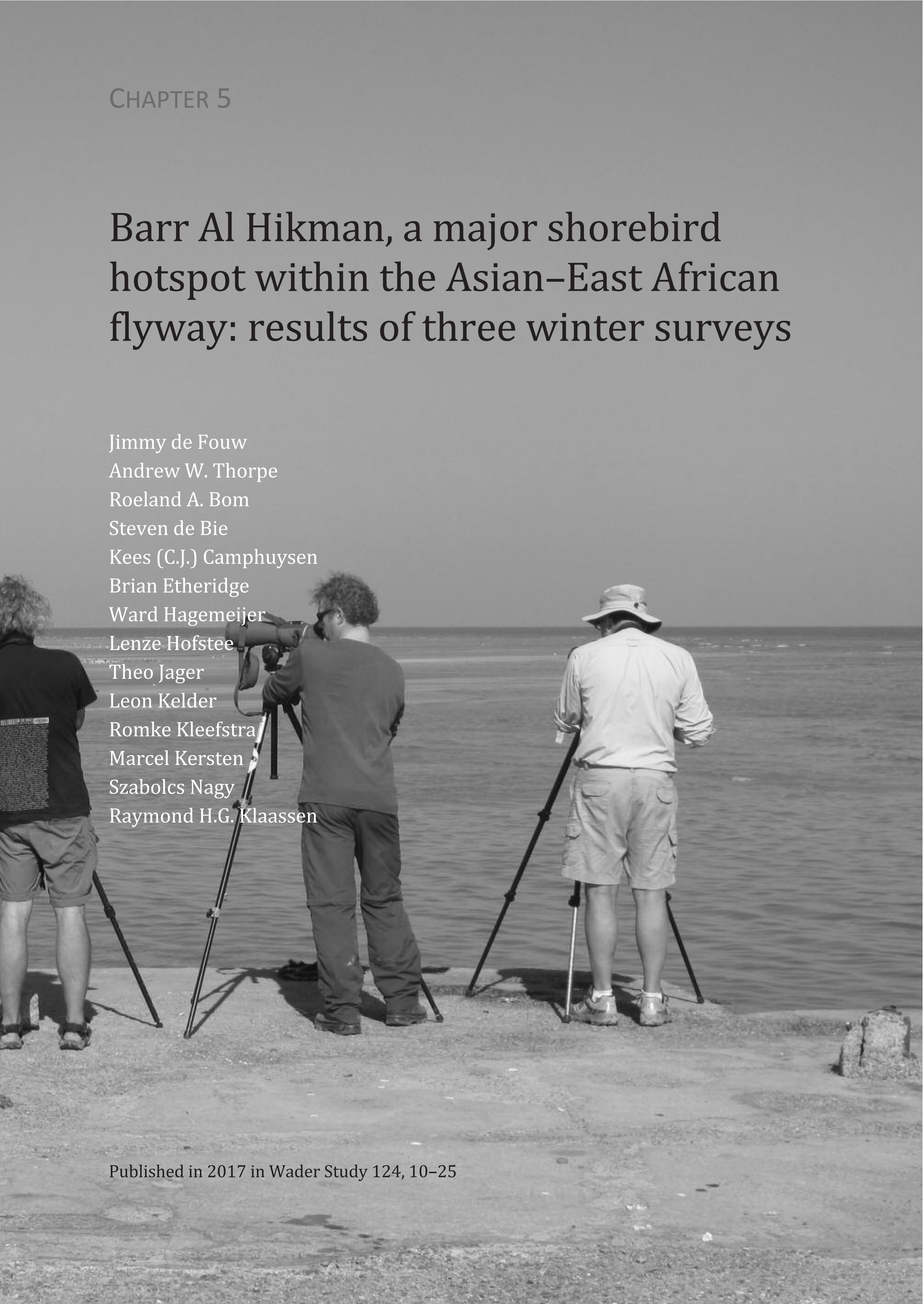

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Abstract

Barr Al Hikman, a large intact coastal wetland in the Sultanate of Oman, is an important wintering site for migratory waterbirds in the Asian–East African Flyway. The last reported systematic survey of the area is from 1990. Here, we present results of three surveys in 2007/2008, 2013/2014 and 2015/2016. Up to a half a million waterbirds of 42 species were counted. Shorebirds were by far the most numerous group (>410,000). For 18 shorebird species numbers wintering at Barr Al Hikman exceeded 1% of their flyway population. Therefore, our results confirm that Barr Al Hikman is still an important wintering ground, not only with respect to the number of birds, but also in terms of species diversity. Furthermore, a comparison with past surveys shows that numbers have tripled since the 1990s. We argue that, taking into account methodological issues, habitat degradation at other wintering sites in the Gulf region of the flyway may be an important factor leading birds to shift to Barr Al Hikman. However, the future of Barr Al Hikman is uncertain: recent rapid urban growth and road construction have drastically changed the Oman coast, and potentially threatening developments are being planned in the area. Therefore, to preserve the Barr Al Hikman area, clear conservation guidelines and actions are needed and the site deserves to be designated as a Ramsar site.

Introduction

Barr Al Hikman is a relatively undisturbed tropical intertidal wetland ecosystem located in the Sultanate of Oman. Already in the 1970s the ornithological importance of Barr Al Hikman was recognised, and since the 1980s the area has been considered the most important site for migratory shorebirds in Oman (Gallagher & Woodcock 1980; Eriksen 1996). Although the site was visited regularly during the 1980s, it was not until 1989–1990 that an attempt was made to carry out a complete survey of the area (Green *et al.* 1994; Eriksen 1996). This survey revealed that Barr Al Hikman hosted about 134,000 wintering shorebirds of 24 species, and in addition there were significant numbers of non-shorebirds such as cormorants, herons, flamingos, gulls and terns (Green *et al.* 1994, Eriksen 1996). For several species, Barr Al Hikman was found to be the most important wintering site within the Asian–East African Flyway known at the time, and for eleven waterbird species it was estimated that the area held one- to two-thirds of the entire Asian–East African Flyway population (Eriksen 1996).

The shorebird species that winter in Oman have very different breeding origins (Delany *et al.* 2009). About half are long-distance migrants that breed in the Arctic or Sub-arctic, in an area stretching across the Palaearctic from Scandinavia (e.g. broad-billed sandpiper *Calidris falcinellus*), via central Siberia (e.g. bar-tailed godwit *Limosa lapponica*) to eastern Siberia (e.g. great knot *Calidris tenuirostris*; Fig. 5.1). Other species are medium- to short-distance migrants breeding in Central Asia (e.g. lesser sandplover *Charadrius mongolus* and greater sandplover *C. leschenaultii*) or locally within the Arabian Gulf Region (e.g. crab plover *Dromas ardeola*; Chapter 11). Moreover, Barr Al Hikman is thought to constitute an important stopover site for shorebirds wintering further south on the east coast of Africa (Delany *et al.* 2009). This includes some of the same shorebird populations that overwinter at Barr Al Hikman, such as bar-tailed godwit, and also some species that have their main wintering areas further south, and only stopover at Barr Al Hikman, such as whimbrel *Numenius phaeopus*, Terek sandpiper *Xenus cinereus* and little stint *Calidris minuta*. Therefore, the area can be considered one of the major shorebird sites within the network of intertidal ecosystems that make up the Asian–East African migratory flyway.

The key importance of Barr Al Hikman makes the site's long-term conservation an important issue. Although the area has been proposed as a Ramsar Site and recently declared a National Nature Reserve, Barr Al Hikman is far from safe. Over the last decade, rapid anthropogenic development (e.g. industrial and urban growth and road construction) has drastically changed Oman, particularly the coastline. In many areas these rapid changes are in potential conflict with safeguarding the natural heritage. Current ecological threats to Barr Al Hikman are plentiful, e.g. increased economic activities that include export-driven fisheries (likely a direct effect of increased access to the area due to major road constructions) (Fouda & Al-Muharrami 1995; Al-Rashdi & Claereboudt 2010; Mehanna *et al.* 2012). Furthermore, on the mainland of the peninsula a large aquaculture shrimp industry is under consideration, as is the construction of a major oil terminal at Duqm, just 100 km south of Barr Al Hikman (with the associated risk of spills).

In addition to local pressure on the shorebird habitats of Barr Al Hikman, there is an ongoing loss of these habitats at a global scale (Davidson 2014; Ma *et al.* 2014) and in the

Middle-East in particular (e.g. Green & Richardson 2008; Delany *et al.* 2009). Given the critical international importance of Barr Al Hikman as a stopover and wintering site for many waterbirds, regular monitoring of the site is needed. The last known systematic survey of the whole area dates back to the 1990s (Green *et al.* 1994, Eriksen 1996). Therefore there is a clear need for an update on the number of birds wintering at Barr Al Hikman.

Here, we present the results of three systematic surveys of the whole Barr Al Hikman peninsula conducted in the winters 2007/2008, 2013/2014 and 2015/2016. Results are compared with the 1989-1990 survey (Green *et al.* 1994) and we discuss possible reasons for changes in numbers of wintering birds. Finally, in order to put the survey results in perspective, we also compare our results with estimates of the flyway population from literature.

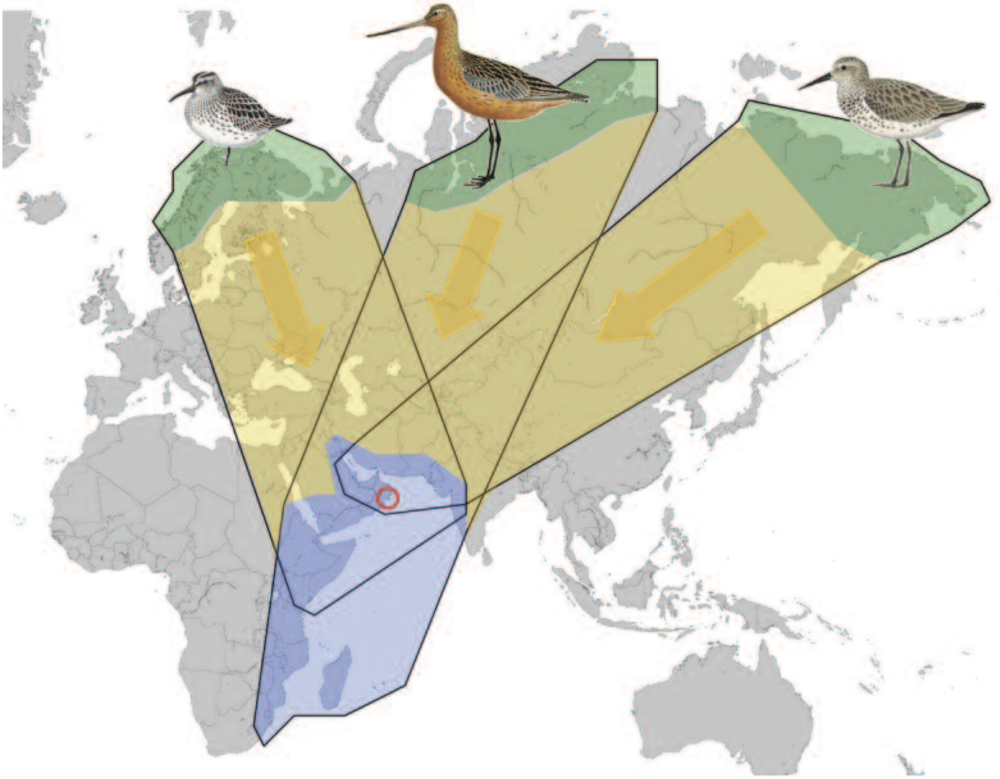


Figure 5.1. The migratory flyways of three populations of arctic shorebirds wintering and stopping over in the Middle East (from west to east): broad-billed sandpiper, bar-tailed godwit, and great knot. This shows that Oman is a wintering and stopover site for birds with a western origin, but also for birds with an eastern origin. Birds wintering further south, notably on the east coast of Africa and Madagascar, presumably make a stopover in the Middle East during their spring and autumn migrations.

Methods

Study area

Barr Al Hikman is a large (30×30 km) peninsula, located on the coast of the Arabian Sea, in the Al Wusta region, Sultanate of Oman (20.6°N, 58.4°E). The area is famous for its abundant birdlife, turtle habitat, and the passage of dolphins and whales around Masirah Island (Salm *et al.* 1993; Eriksen 1996; Jupp *et al.* 1996; Claereboudt 2006). The waters surrounding the Barr Al Hikman peninsula and Masirah Island contain seagrass beds, coral reefs and mangrove forest that harbour a large diversity of marine life (Ghazanfar 1999; Burt *et al.* 2016; Chapter 3) and form important nursery grounds for fish, crabs and shrimps (Mohan & Siddeek 1996; Chapter 3).

The interior of the peninsula consists of sabkha, a mixture of sand, salt and mud. Two types of sabkha are distinguished: lower 'coastal' sabkha (1–5 metres above mean sea level, MSL), which is regularly flooded during high tides and occasionally after heavy rains, and higher 'continental' sabkha (5–15 metres above MSL), which is fed by continental groundwater (see for details: Mettraux *et al.* 2011) (hereafter 'sabkha' is used for both as we did not distinguish between them in the field). All along the coast of the peninsula, low coastal dunes are found that support a typical coastal vegetation described as an *Astriplex*-*Suaeda* community, dominated by *Limonium stocksii*, *Suaeda vermiculata* and *Arthrocnemum macrostachyum* (Ghazanfar 1999). Throughout the study area, several patches of the mangrove *Avicennia marina* can be found, especially along a few creeks on the east coast, just south of the village of Shannah, at Ghubbat Hashish near the village of Filim, and at both the islands of Mahawt and Ma'awil (Fouda & Al-Muharrami 1995).

The peninsula is surrounded by intertidal mudflats that cover about 190 km^2. A large part of the mudflats is covered by seagrass meadows containing the seagrasses *Halodule uninervis* and *Halophila ovalis*. In the sublittoral zone, the seagrass *Thalassia hemprichii* is also found (Jupp *et al.* 1996; Chapter 3). The intertidal mudflats are an important feeding habitat for shorebirds. Three main mudflat areas can be distinguished:

- The Ghubbat Hashish bay area: about 52 km^2 of mudflat is located in the sheltered bay on the west side of the Barr Al Hikman peninsula. Here, mudflats are characterised by silty sediment with low densities of seagrass.
- The east coast: about 88 km^2 of intertidal mudflat is found on the east side of the peninsula (south of the village Shannah) (Fig. 5.2). These mudflats vary between bare sand and dense seagrass, the latter with more silty sediment.
- The Khawr Barr Al Hikman area: the large inlet situated at the east coast just north of Shannah includes about 49 km^2 of mudflats.

On the south coast of the peninsula there are some sandy lagoons with dense Salicornia sp. stands (Khawr Al Milh) and about 10 km^2 of sandy mudflats that stretch along the shore. Finally, there are two small islands in the survey area: Mahawt at Ghubbat Hashish, and Ma'awil at the edge of the intertidal flats on the east coast (Fig. 5.2).

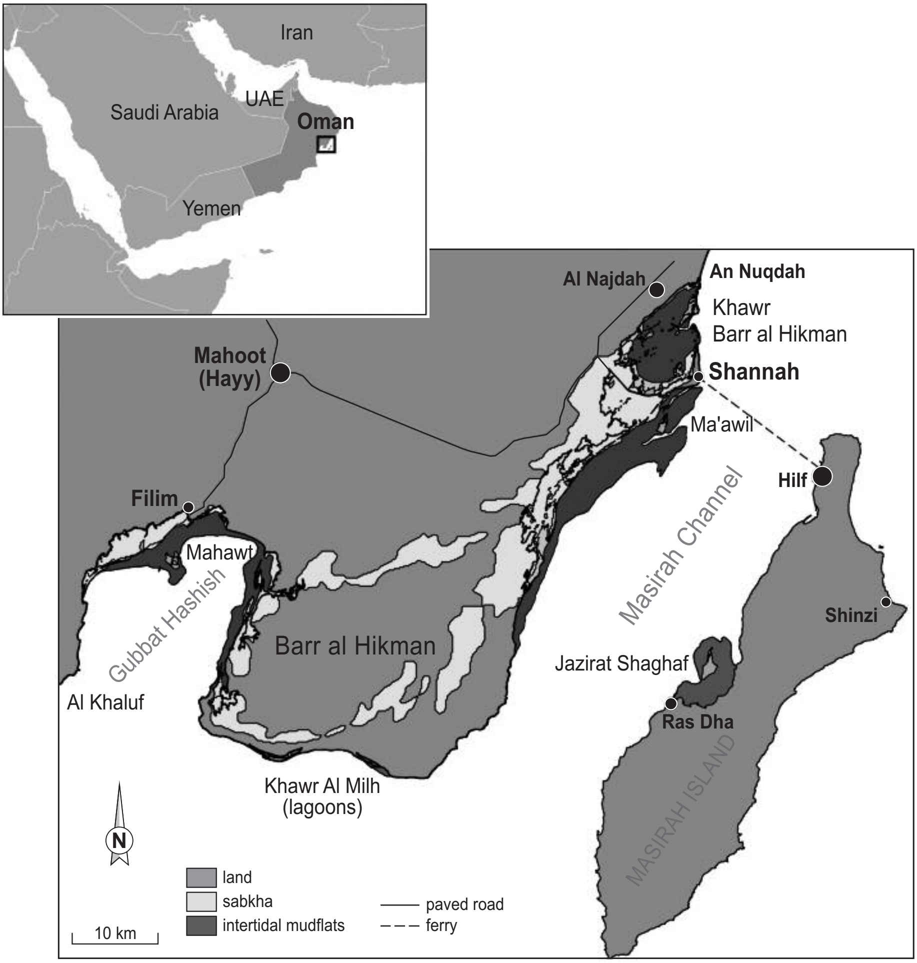


Figure 5.2. The Arabian Peninsula with the Barr Al Hikman area indicating the locations mentioned in the text. Intertidal mudflats and adjacent counting sections are indicated by dark grey shading. Mahoot, Al Najday and Shannah are the most important human settlements. Black lines show paved roads.

Climate and tidal regime

Barr Al Hikman has a hot desert climate with hot summers and warm winters, and is strongly influenced by a complex monsoon wind regime along the coast (Honjo & Weller 1997; Homewood *et al.* 2007; Mettraux *et al.* 2011). Precipitation is low, on average 58 mm annually, and the average winter temperature is around 24°C (range: 19–28°C) (http://www.wunderground.com; Mettraux *et al.* 2011). During survey years, weather conditions were similar although in both 2013/2014 and 2015/2016 a one-day sandstorm event occurred and due to poor visibility the count session was cancelled and partly cancelled respectively.

The tidal regime of Barr Al Hikman is a mixed semidiurnal tide, characterised by two high and two low tides per day, both differing in height (Fig. 5.3A). Consequently, the area of mudflat exposed can vary dramatically between tides. For example, at high tide the water level can be so low that a significant part of the mudflat remains exposed, whereas at low tide the water level can be so high that almost 60% of mudflats remains unexposed. These intermediate tides are alternated with extreme low-low and extreme high-high tides, 0.1 and 3.0 metre respectively (predicted tidal heights above Lowest Astronomical Tide (LAT), http://www.ukho.gov.uk/Easytide/easytide/). The coastal sabkha gets (partly) flooded when water levels exceed 2.6 metres.

Surveys

The study area was surveyed in three winters: 2007/2008 (6–23 January), 2013/2014 (14–23 December) and 2015/2016 (22–30 January). The coastline of the area was divided into count sections (Fig. 5.4). Birds were counted for a period of approximately two hours before and after high tide, when they were distributed along the high water line as well as on the adjacent sabkha. Surveys were only conducted during high tides when the water level reached at least 2.0 metres above LAT (see above). Usually two survey teams operated at the same time. A team of six counters divided over two survey teams would need about eight days to cover the whole area. In practice it invariably took longer, as it is impossible to survey on all days due to unfavourable tides or weather conditions. This means that the counts were carried out consecutively (not simultaneously) and we made the assumption that birds moving between sections, which could potentially lead them to be missed or counted twice, would still lead to an unbi-

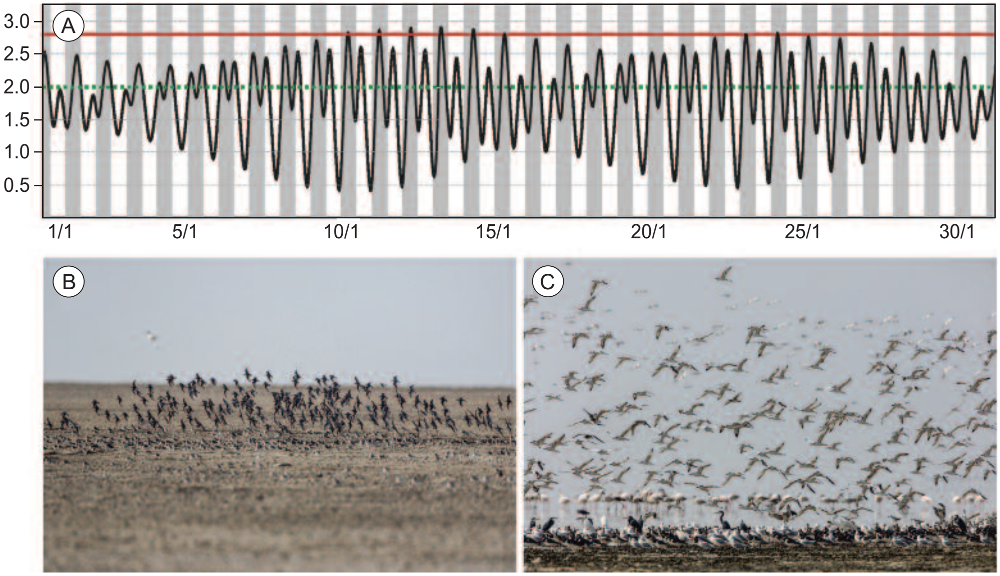


Figure 5.3. (A) The tidal regime at Barr Al Hikman in January 2016. A 2.0 meter water level is needed to conduct a waterbird survey (dotted green line). During a period of extremely high tides (>2.8 metres, red line) the area becomes largely inaccessible. (B) Small shorebirds roosting on sabkha. (C) Densely-packed, mixed waterbird species roost at the waterline on the coast.

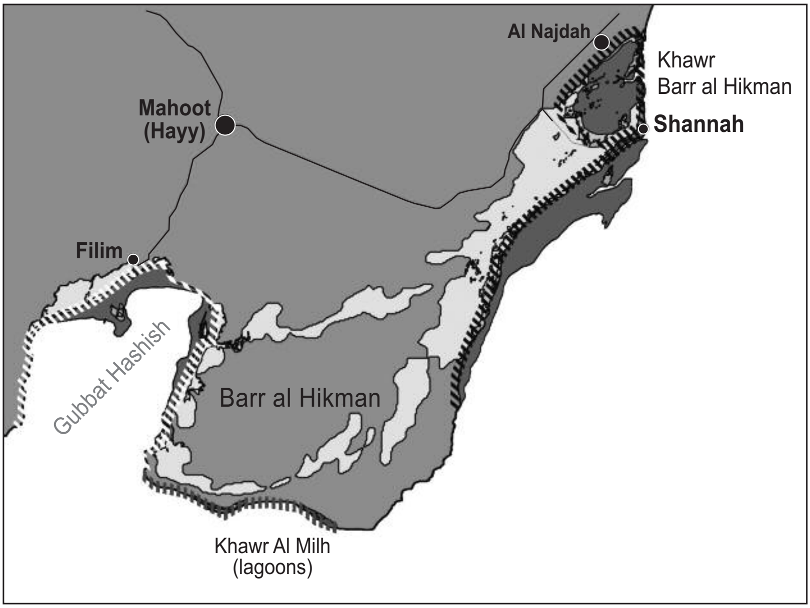


Figure 5.4. Three main count sections (shaded) can be distinguished: the bay of Ghubbat Hashish, East coast south of the village Shannah with the Khawr Barr Al Hikman a large inlet situated north of Shannah and the south coast sandy inlets Khawr Al Milh.

ased estimate, as these biases could go either way during the count period of approximately 10 days.

Coastal sections on the east and west coast of the peninsula could generally be accessed by four-wheel drive vehicles and were surveyed by slowly driving along the coast, regularly stopping to scan for flocks on the tide line or on the sabkha. Areas inaccessible by car, for example lagoons, small creeks or inlets, were surveyed on foot. In 2007/2008, the small islands of Mahawt and Ma'awil were counted from small fishing boats (assisted by teams on foot). Neither of the islands was included in the two subsequent counts due to logistic difficulties and time constraints (note that in the 2007/2008 survey only relatively small numbers were observed on the islands, 5,900 and 4,200 on Mahawt and Ma'wil respectively). Besides the lagoons we did not survey the shores of the south coast of the peninsula as we never encountered significant numbers of birds on these sheltered bays with sandy beaches and fringing coral reefs during occasional visits.

The sabkha appears to be a very important roosting area for shorebirds and it deserves special attention in surveys. Eriksen (1996) and Green *et al.* (1994) noted 'massive flocks flying inland as high tide approaches', presumably roosting on the dry sabkha. As we got more acquainted with the study area, we became aware of a large number of small shorebirds roosting far inland on the sabkha, up to around five kilometres from the shore. Although the sabkha can be notoriously difficult to access (see below), in 2013/2014 we made an attempt to survey the sabkha from the east coast during a single high tide. At every opportunity to do so (roughly every 2–5 km), a team drove inland as far as possible, constantly scanning for shorebird roosts. In 2015/2016, however, the sabkha was flooded by the time the sabkha survey was planned, rendering it inaccessible by car and making a full sabkha survey impossible. It is unknown whether the flooding prevented the birds from roosting on the sabkha. If that was the case, birds might have moved even further inland to higher sabkha or might have stayed to roost with the other shorebirds along the coast.

Birds were counted using binoculars and telescopes. Roosts were approached to within a few hundred metres in order to get good views of the birds. In most cases, bird numbers could be counted to species level. For small flocks (approx. <200 birds) all individuals were identified. For large flocks, first flock size was determined, and subsequently flock composition was estimated on the basis of the identification of several subsets of individuals. Subsets were spread regularly throughout the whole flock in an attempt to count a representative sample of the flock, in which the number of subsets counted was not standardised but plausibly increased with flock size. As we did not study the spatial distribution of species in flocks in detail, we do not know how well this approach really worked, but the strong impression from the experienced surveyors was that only relatively rare shorebirds were underrepresented by this method (see Discussion). On some occasions when flocks were distant and viewing conditions poor (e.g. heat haze), species could not be identified accurately. In these circumstances the number of birds was estimated, divided between ‘small’ and ‘large’ shorebirds. These estimates were then partitioned between species according to the species composition of ‘small’ and ‘large’ shorebirds within each counting section. In 2012/13, 7% and in 2015/16, 23% of the total number of birds counted could not be identified to species level and were therefore treated in this way.

Survey complications

Counting birds at any large inter-tidal site has its difficulties and Barr Al Hikman is no exception. A specific problem for surveying Barr Al Hikman is the unreliability of driving on sabkha, which seriously complicates accessing the area. Although it is very convenient to drive on dry sabkha, cars, including four-wheel drive vehicles, will get seriously stuck in wet sabkha. This makes the area almost completely inaccessible after very high tides, when the sabkha gets flooded, and after heavy rains. A four-wheel drive vehicle (equipped with ground plates) is nevertheless essential to move around safely in the study area as only the main roads to Filim and Shannah are paved (Fig. 5.2). A direct implication of the effect of high tides on the accessibility of the area is that one should carefully plan the survey during a time period when tides do not exceed 2.8 metres (day and night) but are always above 2.0 metres during the count. If the tide exceed 2.8 metres (Fig. 5.3A), the area is inaccessible, and the birds roost far inland on the wetter sabkha, where they are impossible to count. However, when tides are below 2.0 metres, large numbers of birds do not roost and keep on feeding.

Another complication, albeit not specific to Barr Al Hikman, is the disturbance of high tide roosts by raptors, mainly marsh harriers *Circus aeruginosus*. Shorebird flocks take flight at every approaching raptor. Therefore, as a considerable amount of time is needed to identify and count all the different shorebird species, frequent disturbances by raptors can seriously interfere with and delay surveys.

Results and Discussion

Survey results

More than half a million waterbirds use Barr Al Hikman in December and January. A total of 358,000 waterbirds were counted in 2007/2008, 472,000 in 2013/2014, and 521,000 in 2015/2016. Altogether 42 species were identified. These figures do not include birds of prey and we did not separate the species of the large white-headed gull complex comprising *Larus fuscus*, *L. cachinnans*, *L. barensis* and *L. heuglini* (Table 5.1). Species which were observed less than five times during the survey are not included in Table 5.1. Most birds were found on the east coast (including Khawr Barr Al Hikman) (Table 5.1).

Numerically, shorebirds were by far the most dominant group, with totals of 305,000, 393,000 and 414,000 (23 species) for the three winters, respectively. The dominant shorebird species was dunlin *Calidris alpina*, followed by bar-tailed godwit, lesser sandplover and redshank *Tringa totanus* (Table 5.1).

Other important waterbird groups were cormorants, herons & flamingos (27,000, 33,000 and 39,000), gulls (20,000, 31,000 and 62,000) and terns (5,700, 14,700 and 6,700), in the three winters respectively. Khawr Barr Al Hikman has a large great cormorant *Phalacrocorax carbo* roost, which either can be counted during low tide when the birds stand on the sandy mudflats north of Shannah, or when the birds are flying from the roost to the sea. The largest numbers of gulls and terns were found near human settlements, particularly at fish-landing sites, small harbours and rubbish dumps. The variation in the number of gulls and terns observed between years and locations can most likely be explained by the fact that these groups are not as confined to Barr Al Hikman as the others. They roam over a larger area and concentrations might occur at Barr Al Hikman in one year but not another. In 2015/2016, however, gulls and terns were targeted in a count as they flew to their roosts on islands near Shannah, and this might explain the high number counted that year. slender-billed gull *Larus genei* is the only gull species that occurs throughout Barr Al Hikman and seems less associated with harbours and rubbish dumps.

The two most common birds of prey were marsh harrier and osprey *Pandion haliaetus*. Only three falcon species (peregrine falcon *Falco peregrines*, lanner falcon *Falco biarmicus* and saker falcon *Falco cherrug*) occur in the area. They hunt over the inter-tidal flats, but are rare and their occurrence varies between years. Compared with important intertidal sites elsewhere in the world, the numbers of falcons at Barr Al Hikman are remarkably low.

Distribution of shorebirds

Several key sites for shorebird feeding and roosting were identified within the study area (Fig. 5.5). All mudflats along the east coast are important feeding grounds. These mudflats are widest just south of Shannah. Further south they become narrower and consequently host fewer birds. The birds that feed on these mudflats during low tide roost at high tide either along the water line, or on neighbouring sabkha (Fig. 5.5). Interestingly, although both the high water line and the sabkha are important for roosting, the relative use of these habitats differs between species. Generally, the larger, long-legged species roost at the high water line (e.g. crab plover, Eurasian oystercatcher *Haematopus ostralegus*, redshank and Eurasian curlew

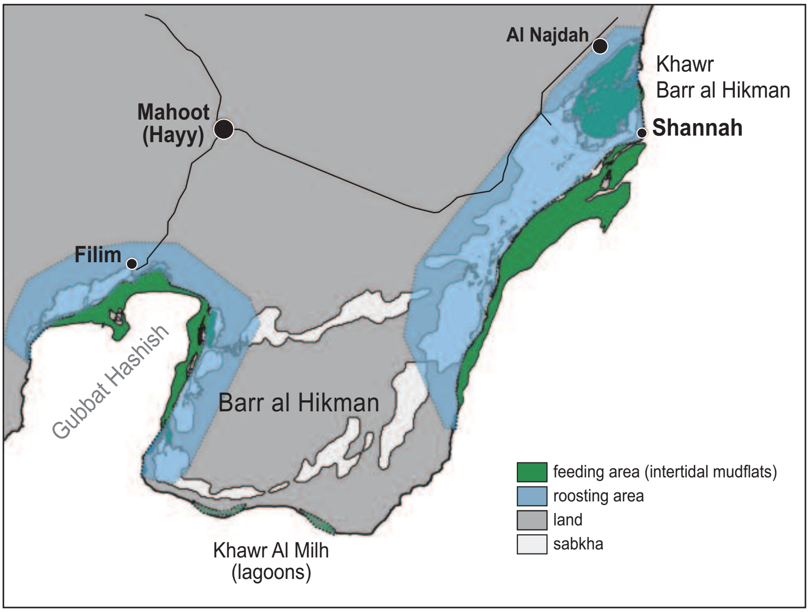


Figure 5.5. Important feeding and roosting site of waterbirds in the Barr Al Hikman area (Note: this map does not include important areas for pelagic feeding birds (e.g. terns and cormorants) that feed on open water. Surveys with boats are needed to identify these areas).

Numenius arquata), and the small sandpipers and sandplovers roost on the sabkha, although 5–20% of the latter may roost at the high water line. Roosts on the sabkha can occur up to a few kilometres from the high water line. On the east coast in particular, large numbers of dunlin (100,000), lesser sandplovers (38,000) and little stints (10,000) were found roosting on the sabkha. Therefore the abundance of these species might have been underestimated during our counts (and especially in previous counts when the sabkha was not included in the area surveyed), as it is extremely difficult to find all flocks inland on the sabkha (see also below).

Khawr Barr Al Hikman, the large inlet just north of Shannah, is another important roosting and feeding site. At Gubbat Hashish, the most important feeding areas are found on the large mudflats in the northern and north-western end of the bay. The sabkha on the northwest side of Gubbat Hashish and inlets at the northeast side are the important roosting area. However, there, birds mainly roost in the large inlets or khawrs and to a lesser extent far inland on the sabkha (in contrast to the situation at the east coast). Thus the inland sabkha near the west coast of the peninsula might not form an important roosting habitat for the birds in the bay (Fig. 5.5). The two lagoons on the south coast of the peninsula host smaller numbers than Ghubbat Hashish and the east coast. These shorebirds also both feed and roost in the lagoons.

Comparing results between years

Total shorebird numbers at Barr Al Hikman increased by about 36% over the five years between 2007/2008 and 2016/2016 (Table 5.1). The survey methodology, the area surveyed,

Table 5.1. Counts of wintering birds at the wetlands surrounding the Bar Al Hikman peninsula, Oman, between 1989 and 2016. Numbers for 2007/2008, 2013/2014 and 2015/2016 are from this study, the count data for 1989/1990 are adapted from Green *et al.* (1994). EC = East coast, GH = Ghubbat Hashish, SC = South coast.

	1989/1990			**2007/2008**				**2012/2013**				**2015/2016**			
	EC	GH & SC	Totals	EC	GH	SC	Totals	EC	GH	SC	Totals	EC	GH	SC	totals
Cormorants, herons, flamingos															
great cormorant *Phalacrocorax carbo*	2,700	5,446	8,146	5,298	4,251		9,549	14,465	3,174		17,639	14,573	6,138	90	20,801
Socotra cormorant *Phalacrocorax nigrogularis*	0	1,085	1,085												
greater flamingo *Phoenicopterus ruber*	3,837	3,651	7,488	7,134	5,731	168	12,865	7,741	4,344	98	12,183	10,085	4,313	111	14,509
Eurasian spoonbill *Platalea leucorodia*	26	95	121	82	96	7	178	182	35	0	217	179	43		222
grey heron *Ardea cinerea*	73	515	588	147	733	11	880	376	237	36	649	371	305	38	714
great egret *Egrettta alba*	12	226	238	11	89	5	100	168	51	14	233	112	32	6	150
little egret *Egrettta garzetta*				2	13		15					5		1	6
western reef egret *Egretta gularis*	1,023	735	1,758	1,907	988	47	2,895	1,914	421	30	2,365	1,816	573	36	2,425
Shorebirds															
crab plover *Dromas ardeola*	2,149	794	2,943	5,195	1,706		6,901	6,067	2,596	96	8,759	7,507	955		8,462
Eurasian oystercatcher *Haematopus ostralegus*	2,969	1,408	4,377	2,501	1,355	17	3,856	3,596	1,818	20	5,434	3,402	840	40	4,282
ringed plover *Charadrius hiaticula*	1	2	3	53	9	5	62	91	4		95	225	63	34	322
Kentish plover *Charadrius alexandrinus*	103	117	220	1,139	740	198	1,879	921	116	29	1,066	1,175	435	30	1,641
lesser sandplover *Charadrius mongolus*		65	65	23,241	10,597	865	33,838	60,925	11,222	222	72,369	107,289	14,812	1,268	123,369
greater sandplover *Charadrius leschenaultii*	160	19	179	1,197	1,313	319	2,510	2,977	545	21	3,543	12,802	1,790	197	14,789
sandplover spp. *C. mongolus/leschenaultii*	3,423	6,660	10,083												
plover spp. *Charadrius spp*	3,035	285	3,320												
grey plover *Pluvialis squatarola*	1,941	648	2,589	1,110	976	82	2,086	3,289	712	105	4,106	2,918	769	115	3,802
ruddy turnstone *Arenaria interpres*	801	923	1,724	4,121	955	684	5,076	2,441	1,443	1,569	5,453	4,320	2,251	369	6,940
sanderling *Calidris alba*	1,151	557	1,708	1,216	991	865	2,207	1,824	108	834	2,766	2,522	660	457	3,638
great knot *Calidris tenuirostris*	1,104	89	1,193	94	267		361	107			107	271	119		390
curlew sandpiper *Calidris ferruginea*				26,371	10,540	873	36,911	7,242	219	61	7,522	11,588	2,651	394	14,633
dunlin *Calidris alpina*				68,178	12,168	4,109	80,346	113,973	9,124	5,950	129,046	110,424	13,576	1,658	125,659
curlew sandpiper/dunlin *C. ferruginea/alpina*	22,928	9,269	32,197												
little stint *Calidris minuta*	2,152	3,231	5,383	6,685	4,229	782	10,914	15,271	1,975	693	17,940	5,921	1,828	89	7,838
broad-billed sandpiper *Limicola falcinellus*	366	1,282	1,648	184	27	3	211	168	2	14	184	161	681	11	853
medium-small calidrid *spp. C. ferruginea/ alpina/falcinellus*	10,940	1,875	12,815												
Eurasian curlew *Numenius arquata*	869	850	1,719	4,444	2,593	97	7,037	2,924	3,442	110	6,476	9,673	4,811	34	14,518
whimbrel *Numenius phaeopus*	162	63	225	61	603	4	664	85	266	36	387	91	247	14	352

Table 5.1. Continued

	1989/1990			2007/2008				2012/2013				2015/2016			
	EC	GH & SC	Totals	EC	GH	SC	Totals	EC	GH	SC	Totals	EC	GH	SC	totals
Shorebirds continued															
bar-tailed godwit *Limosa lapponica*	19,720	11,170	30,890	46,340	18,252	718	64,592	69,124	17,194	862	87,180	51,582	9,138	255	60,976
redshank *Tringa totanus*	10,350	2,771	13,121	25,958	8,174	363	34,132	33,146	3,643	55	36,845	16,265	1,936	284	18,485
spotted redshank *Tringa erythropus*				6	1		7					2	3	1	6
greenshank *Tringa nebularia*	238	99	337	351	171	20	522	1,182	301	18	1,501	572	537	40	1,149
marsh sandpiper *Tringa stagnatilis*	9	6	15	9	40	2	49	8	2		10	16	109	24	150
Terek sandpiper *Xenus cinereus*	101	358	459	426	185	90	611	523	886	317	1,726	381	1,134	69	1,583
common sandpiper *Actitis hypoleucos*	4	2	6	4	4	1	8	21	1	2	24	28	20	16	64
medium-small *Tringa/Calidris*	3,210	3,248	6,458												
pied avocet *Recurvirostra avosette*	2	46	48												
Gulls															
slender-billed gull *Larus genei*	9,837	10,098	19,935	4,119	3,850	1,874	7,969	2,862	2,181	6,490	11,533	5,046	1,634	2,602	9,282
great black-headed gull *Larus ichthyaetus*				15	8	216	23	358	8	133	499	187	101	423	711
sooty gull *Larus hemprichii*	111	6,298	6,409	306	1,017	39	1,323	223	614	1,198	2,035	2,836	1,533	888	5,257
large white-headed gull sp. *Larus fuscus/ cachinnans/barensis/heuglini*	3,374	18,417	21,791	1,855	4,943	1,970	6,798	1,763	5,516	9,663	16,942	25,805	5,147	15,662	46,614
gull spp.	100	741	841												
Terns															
gull-billed tern *Gelochelidon nilotica*	22	69	91	168	14		182	545	11	2	558	351	17	0	368
Caspian tern *Sterna caspia*	158	1,208	1,366	41	1,794	21	1,835	126	968	46	1,140	401	1,650	38	2,089
swift tern *Sterna bergii*				368	1,326	441	1,694	377	333	230	940	373	702	1,264	2,339
lesser crested tern *Sterna bengalensis*	27	2	29	10	37	54	47	439	480	2,140	3,059	177	193	178	548
sandwich tern *Sterna sandvicensis*	2,321	8,835	11,156	405	222		627	288	187	6,442	6,917	119	418	87	624
Saunders's tern *Sterna saundersi*	8	26	34	658	21	100	679	487	21	168	676	182	118	102	402
white-winged black tern *Chlidonias leucopterus*				19			19	61	0	100	161				
common tern *Sterna hirundu*								0	0	1,270	1,270	351	17	0	368
tern spp.	100	741	841								0				
Birds of prey															
osprey *Pandion haliaetus*				14	27		41	19	32		51	36	39	1	76
marsh harrier *Circus aeruginosus*				26	20		46	54	25		79	48	12	3	63

and survey effort was generally similar across the three winters, except that in 2007/2008 the sabkha roosts far inland were less well known and therefore missed; so this could explain at least part of the increase. In 2013/2014, large flocks of Calidrid sandpipers and sandplovers were found during the extra effort to pick up shorebirds roosting inland on the sabkha. However, inspection of the results (Table 5.1) shows that this difference in survey effort can only explain the changes in numbers of sandplovers and Calidrid sandpipers, so the increases in the other shorebird species appear to be genuine.

Larger shorebirds roosted at the high water line and were only rarely observed on the sabkha. They are also relatively easy to identify, therefore misidentification is not an issue and survey results should be reliable. Thus we believe that the increases in crab plover (+23%), Eurasian oystercatcher (+11%), grey plover *Pluvialis squatarola* (+75%) and Eurasian curlew (+104%) are real. Likewise we believe that the observed increase in bar-tailed godwits in 2013/2014 (+33%) and decrease in 2015/2016 are real, and similarly for redshanks, which were more or less stable until 2013/2014 but dropped remarkably in 2015/2016 (–46%).

For sandplovers and Calidrid sandpipers, there are two concerns about the survey results: misidentification and variation in survey effort between years. Identifying these small species is not easy in closely-packed and dense-mixed-species flocks. For example, the dunlins occurring at Barr Al Hikman (*C. a. centralis*) are relatively long-billed which makes it surprisingly difficult to distinguish between dunlin and curlew sandpiper *Calidris ferruginea*, especially when viewing conditions are not perfect. Second, the survey effort for these species was not constant between surveys because in 2013/2014 there was a special survey of the inland sabkha which revealed a total of 54,000 of these small bodied shorebirds. In 2015/2016 conditions were different, as the sabkha was partly flooded and this precluded a thorough survey of the sabkha.

If we look at the combined numbers of the two most common sandplover species (lesser and greater sandplover), we see that about 39,500 and 100,000 more individuals were counted in 2013/2014 and 2015/2016 respectively compared to 2007/2008. The apparent increase between 2007/2008 and 2013/2014 can partly be explained by the additional sandplovers found roosting inland on the sabkha (19,000). Thus we conclude that sandplovers (either or both species) have genuinely increased, and this is supported by the even higher number in 2015/2016, when the inland sabkha was largely flooded.

Interpretation of the fluctuations in the numbers of Calidrid sandpipers is different and more complex. Their total number seems to have increased since 2007/2008, (+20,000 to 2013/2014 and again +15,000 to 2015/2016). However, the number of Calidrid sandpipers found during the sabkha survey was greater than the increase in their numbers from 2007/2008 to 2013/2014. Therefore fewer Calidrid sandpipers were counted in the main survey area (i.e. excluding the sabkha).

So what can we say about the numbers of individual Calidrid species? Sanderling *Calidris alba* and broad-billed sandpiper occur in relatively small numbers, especially in comparison with dunlin and curlew sandpiper. Given the difficulties of picking out these species in large flocks, we consider that there is no clear evidence for a change in their numbers at Barr Al Hikman.

About 7,000 more little stints were counted in 2013/2014 compared with 2007/2008 (Table 5.1). However, as 8,700 little stints were found during the sabkha survey, the numbers in the main survey area decreased by about 1,700 (–15.5%). This decrease might be real as numbers in 2015/2016 (7,800) indicate a further decrease.

In 2013/2014, about 24,000 more dunlins were counted in the main survey area (i.e. deducting about 25,000 counted in the sabkha survey) compared with 2007/2008. Numbers increased further in 2015/2016 by 45,000. These figures indicate that the dunlin population increased substantially – by about 50% – between 2007/2008 and 2015/2016. However, over the same period the number of curlew sandpipers first decreased, dropping by almost 30,000 between 2007/2008 and 2013/2014 (from 36,900 to 7,500) and then increased by 7,000 in 2015/2016. These changes make one wonder whether this is not a result of a misidentification of the two species. During the 2013/2014 and 2015/2016 surveys, it was noticed by the survey teams they were not finding the numbers of curlew sandpipers they had expected based on the 2007/2008 count. Hence, some extra attention was given to Calidrid flocks; nevertheless the surveyors failed to find larger numbers of curlew sandpipers during more detailed flock scans. Moreover, we have no evidence that observers overestimated the number of curlew sandpipers during the 2007/2008 survey. In that survey the ratio of dunlins to curlew sandpipers (69:31) was very similar to the ratio in birds captured during ringing activities (62:38). These ratios were different in 2013/2014 and 2015/2016 (94:6 and 80:20 respectively). Unfortunately there were no ringing activities during these surveys for comparison.

We consider that the increase in dunlins and decline in curlew sandpipers between the surveys is real. Interestingly, curlew sandpipers have shown a strong decline in the East Atlantic Flyway, in which their numbers reached an historic low in the winter of 2013/2014 (van Roomen *et al.* 2015). Moreover, in Banc d'Arguin, Mauritania, the number of curlew sandpipers dropped by 70% between 2000 and 2014 (Marc van Roomen, pers. comm.). The breeding success of curlew sandpipers is strongly correlated with lemming cycles (Underhill 1987; Summers *et al.* 1998); therefore the numbers of wintering birds can vary dramatically between years. In addition, recent studies showed that faltering lemming cycles, probably caused by changes in the Arctic due to climate change, are an important factor leading to changes in the population sizes of migratory birds (Nolet *et al.* 2013). Therefore these are factors that could have led to the changes we observed in the numbers of Curlew Sandpipers; however, a longer time series of data are needed before firm conclusions can be reached.

Overall, there are strong indications that sandplovers and Calidrid sandpipers have increased since 2007/2008. However, it is clear that the tidal regime strongly dictates how birds distribute themselves spatially on the sabkha during roosting. More in-depth research on bird distribution (e.g. tagging individual birds, specific sabkha counts) is needed before firm conclusions can be made on numbers and distribution.

Notes on the occurrence of great knots and broad-billed sandpipers

Great knot and broad-billed sandpiper are species that occur at Barr Al Hikman in small to moderate numbers, but we consider that they were underestimated during the survey. The small Arabian Sea population and western Indian Ocean of great knots (ca. 2,000–5,000) is recognised as a distinctly separate population (Delany *et al.* 2009), and Barr Al Hikman is considered an important wintering site for these birds. Great knots mainly roost within dense bar-tailed godwit flocks, in which they are difficult to detect. Not surprisingly, only small numbers of great knots were counted during our surveys (107–390, Table 5.1); therefore we consider that we probably underestimated their numbers. This idea is fuelled by frequent observations of small feeding flocks of great knots during low tide. Our judgement is that the site hosts around 1,000 birds. Others have estimated that about 1,200 great knots winter at Barr Al Hikman (Evans 1994, Green *et al.* 1994). Our slightly more conservative estimate of 1,000 would nevertheless mean that Barr Al Hikman holds 20–50% of the flyway population (Table 5.2). The same is true for broad-billed sandpiper. They are common throughout Barr Al Hikman, but at the same time it is difficult to find all individuals in dense mixed Calidrid-sand-plover flocks. During low tide, flocks of foraging broad-billed sandpipers are frequently encountered, and these can consist of up to a hundred individuals. This suggests that, like great knot, the species is more common than indicated by the surveys; however the true status of this species at Barr Al Hikman is difficult to establish because of the problems in carrying out accurate counts. Eriksen (1996) recorded 5,000 broad billed-sandpipers at Barr Al Hikman on 3 January 1993, which was an estimate of a large single species foraging flock at Ghubbat Hashish (Jens & Hanna Eriksen, pers. comm.). We estimate that at least a few thousand (almost certainly >2,000) broad-billed sandpipers winter at Barr Al Hikman, which represents 8% of the flyway population (Table 5.2).

Table 5.2. Shorebird species wintering at Barr Al Hikman in numbers that exceed 1% of the estimated flyway population, as estimated by Delany *et al.* (2009). The number at Barr Al Hikman is the maximum count from 2008, 2013 and 2016.

Species	Flyway population estimate	Year of maximum count	Maximum count as % of flyway population
crab plover	60,000–80,000	2013	11–15%
Eurasian oystercatcher	27,000–40,000[1]	2013	14–20%
Kentish plover	25,000–100,000	2008	1–8%
lesser sandplover	100,000–125,000	2016	>100%
greater sandplover	25,000–100,000	2016	15–60%
grey plover	90,000	2013	5%
ruddy turnstone	100,000	2016	7%
sanderling	150,000	2016	2%
great knot	2,000–5,000	-	24–60%[2]
curlew sandpiper	400,000	2008	9%
dunlin	500,000	2013	26%
little stint	1,000,000	2013	2%
broad-billed sandpiper	61,000–64,000	-	8%[3]
Eurasian curlew	25,000–100,000	2016	15–58%
bar-tailed godwit	100,000–150,000	2013	58–65%
redshank	100,000–1,000,000	2013	4–37%
greenshank	100,000–1,000,000	2013	0–2%
Terek sandpiper	100,000–1,000,000	2013	0–2%

[1] Roomen *et al.* (2015)
[2] Green *et al.* (1994), Evans (1994)
[3] Eriksen (1996)

Has there been a significant increase in shorebird numbers since the 1990s?

The last complete systematic survey of Barr Al Hikman was conducted in 1989/1990 (Green *et al.* 1994, Eriksen 1996). If we compare the results of our study with the 1989/90 survey, we see that generally waterbird numbers have increased massively, almost threefold (Fig. 5.6, Table 5.1). Large shorebirds increased twofold and small shorebirds increased fivefold (Fig. 5.6, Table 5.1). The main increase has occurred on the east coast of the peninsula (Table 5.3). This is mainly due to the increase of small shorebirds which to a large extent roost on the sabkha (e.g. sandpipers and sandplovers). Green *et al.* (1994) were not able to separate these groups to species level so comparison between their survey and ours is not possible. Larger shorebirds also showed a general increase. For example, crab plovers almost tripled (2,900 to 8,500), bar-tailed godwits doubled (31,000 to 61,000) and Eurasian curlews increased massively from 1,700 to 14,500. Also flamingos and cormorants showed a notable increases between 1990 and 2016 of 7,500 to 14,500 and 8,100 to 21,000 respectively (Table 5.3). As large-bodied shorebirds are relatively easy to survey, and as they invariably roost along the shoreline, we are confident that the increase in their numbers is genuine.

Table 5.3. Waterbird numbers per coastal area, Numbers for 2007/2008, 2013/2014 and 2015/2016 this study. Count from 1989/1990 adapted from Green *et al.* (1990).

		1989/90	2007/08	2012/13	2015/16
Shorebirds (small)	East coast	48,200	134,000	209,800	260,000
	Ghubbat Hashish	25,400	51,900	36,200	45,500
Shorebirds (large)	East coast	39,700	84,900	116,100	89,100
	Ghubbat Hashish	20,500	34,100	30,500	19,300
Terns and gulls	East coast	16,100	8,000	7,500	35,800
	Ghubbat Hashish	46,400	17,900	38,200	32,800
Herons, flamingos and cormorants	East coast	7,700	14,600	24,800	27,100
	Ghubbat Hashish	11,800	12,100	8,400	11,700
Waterbirds total	East coast	111,600	241,400	358,300	412,100
	Ghubbat Hashish	104,000	116,100	113,300	109,200

Determination of long term population trends can be problematical if there are differences between surveys in methodology, but we are sure that such differences cannot explain the large-scale population increases we recorded. Indeed we are rather confident that the different surveys are comparable as effort and coverage have been similar. In addition, one of the surveyors in 1989/1990 (Mick Green) introduced us to the area during a joint pilot study in January 2007, during which we surveyed the east coast together (Klaassen *et al.* 2007). It seems that the only major difference between our study and the study of Green *et al.* (1994) is the fact that we made extra effort to pick up small shorebirds roosting on the inland sabkha. However, this would only explain the increases to a relatively minor extent, as we also found substantial increases in the numbers of large shorebirds (Fig. 5.6), which can be surveyed more accurately as they mainly roost along the tide line.

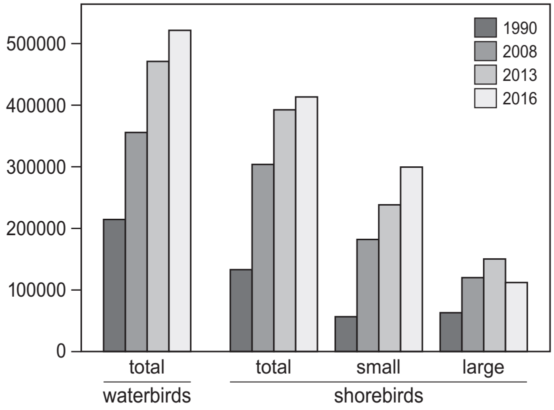


Figure 5.6. Total bird numbers of all species counted in surveys between 1990 and 2016. Bird counts in 1990 adapted from Green *et al.* (1994).

Why are shorebird numbers increasing?

The notable increases in shorebirds wintering at Barr Al Hikman since 1989/1990, and within our survey period are surprising, as globally shorebirds generally are in decline (Fernández & Lank 2008; Delany *et al.* 2009; Hua *et al.* 2015; van Roomen *et al.* 2015). So what could possibly explain these increases?

First, conditions within the Asian-East African flyway might have improved and shorebird populations just might have increased. It is impossible to know whether this is the case because surveys of the breeding areas are virtually non-existent, mainly because of the logistical difficulties of working in the high-arctic. For that reason, these shorebird populations are only monitored by surveying the birds in their wintering areas.

Second, the increase in shorebird numbers at Barr Al Hikman could be the result of a redistribution of wintering birds. Individual shorebirds are generally faithful to their particular wintering site (e.g. (Smith *et al.* 1992; Leyrer *et al.* 2006; Conklin & Colwell 2007), and only move to another site if the original site is lost (Lambeck *et al.* 1989; Schekkerman *et al.* 1994; Burton & Armitage 2008; Rakhimberdiev *et al.* 2011; Verkuil *et al.* 2012). Currently, the Arabian Gulf is developing rapidly and the anthropogenic impact on marine systems is particularly high (Halpern *et al.* 2008; Sheppard *et al.* 2010; Sale *et al.* 2011; Van Lavieren *et al.* 2011; Naser 2014). Although a detailed analysis of inter-tidal wetland change in the Arabian Gulf is lacking, a recent study revealed a major loss of wetlands due to coastal developments in the United Arab Emirates resulting in a major shorebird decline (Green & Richardson 2008). These birds may now winter at Barr al Hikman which is one of the relatively few remaining key sites for shorebirds in the Middle East. If a redistribution of shorebirds due to the loss of their original wintering areas is the reason for the increase at Barr Al Hikman, then the increase cannot be viewed as a positive development but as evidence that the flyway populations are threatened. Clearly, a more regional view on changes in shorebird numbers and distributions in the Middle East is urgently required.

Significance of Barr Al Hikman from an international perspective

Our surveys confirmed that Barr Al Hikman is the single most important wetland for wintering birds in the Middle East, not only with respect to the number of birds, but also in terms of species diversity (Delany *et al.* 2009). Moreover the surveys revealed that the number of birds wintering at Barr Al Hikman have increased substantially. We used Asia-East African flyway population estimates as compiled by Delany *et al.* (2009) to calculate the percentage of the flyway population wintering at Barr Al Hikman (Table 5.2). For no less than 18 shorebird species, numbers wintering at Barr Al Hikman exceeded 1% of the flyway population (the critical minimum threshold value that defines an area of conservation concern; Delany *et al.* 2009). For nine of these species, at least 10% of the flyway population winters at Barr Al Hikman, and for seven a very large proportion of the flyway population winters there: redshank (4–37%), Eurasian curlew (15–58%), greater sandplover (16–60%), great knot (24–60%), dunlin (26%), bar-tailed godwit (58–65%), and lesser sandplover (>100% meaning that the 2016 count at Barr Al Hikamn is higher than the flyway population estimate made by Delany *et al.* 2009) (Table 5.2). This is rather remarkable, and from this one might conclude that an update of the flyway population estimates for shorebirds in the Asian-East African flyway is urgently needed.

It should be noted that pied avocet *Recurvirostra avosetta* was recorded by Green *et al.* (1994), but not during our surveys. Pied avocet is an irregular and rare visitor to Barr Al Hikman and Oman in general (Eriksen & Victor 2013). A record in the International Waterbird Census database of 1,400 avocets at Barr Al Hikman in January 1997 is believed to be erroneous (Jens Eriksen & Wetlands International, pers. comm.). Although there are historic records of slender-billed curlew *Numenius tenuirostris* from Barr Al Hikman (Delany *et al.* 2009), we have not considered the species as it is now believed to be extinct (Kirwan *et al.* 2015).

Conservation

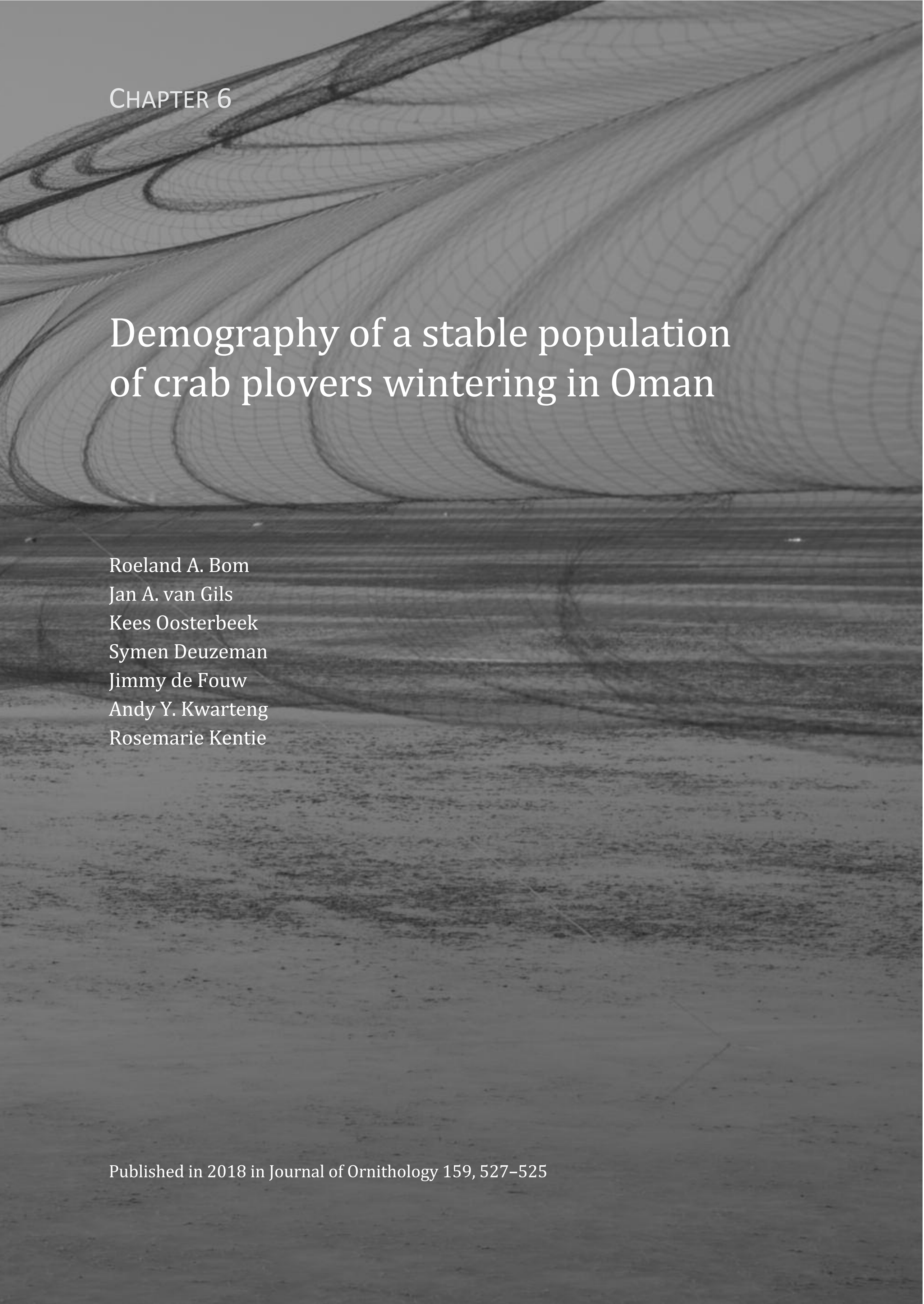
The huge numbers of shorebirds utilising Barr Al Hikman during the non-breeding season makes the area of major conservation concern. Over the last decade, rapid urban growth and road construction have drastically changed the coast of Oman. At this stage the Barr Al Hikman area is still relatively untouched, but several planned developments could quickly change this situation. For example, at the Barr Al Hikman Peninsula a large aquaculture shrimp industry is under active planning and exploration. The environmental impact of shrimp farms can be disastrous and sound environmental impact assessments using expert knowledge are vital before decisions are made allowing such developments to take place. In addition, there are plans for the development of offshore oil extraction close to the area, and together with the oil refineries at the Duqm dock such activities carry with them the risk for oil spills. It is not clear whether ecological and natural resource interests are considered during the planning of economic activities, and whether and how the current conservation status (National Nature Reserve) can help to halt economic activities that are detrimental to the area.

Last but not least, the area is known for its extensive fisheries for swimming crabs, shrimps, fish and sea cucumber (Mohan & Siddeek 1996; Al-Rashdi & Claereboudt 2010; Safaie *et al.* 2013a). Although fishing is mainly carried out from small boats, its impact can be large as there are many boats in the area. At this stage it is not clear if over-fishing is a threat for fish and crab stocks and their impact on the ecosystems. However, a recent study showed that over-fishing of sea cucumbers resulted in a rapid decline of the species in the area (Al-Rashdi & Claereboudt 2010). Furthermore, extensive turtle poaching and falcon hunting was observed regularly by the authors during the surveys. All of the above stresses the need for accurate monitoring programmes for conservation purposes.

In conclusion, Barr Al Hikman is one of the major sites within the network of intertidal ecosystems that make up the Asian-East African migratory flyway. The large numbers of shorebirds wintering at and migrating through Barr Al Hikman makes it of international conservation concern and therefore deserves to be designated as a Ramsar site. However, given the on-going planned coastal developments on a local and international scale in the region, wetlands along the flyway are not adequately safeguarded. Therefore, a deeper understanding of changes in waterbird populations at a flyway level and of local ecosystem functioning is urgently required to further inform conservation management.

Acknowledgements

We thank the Ministry of Environment and Climate Affairs for permission to work at Barr Al Hikman; we are especially grateful to Thuraya Al Sariri, Ali al Kiyumi, Ahmed Said Al-Shukaili, Badr Al Balushi, Salim Samir Bait Bilal. We thank Reginald Victor and Andy Y. Kwarteng (Sultan Qaboos University) for their collaboration and logistic support. Karin Stuut of Aladin Travel helped with logistics during the first years. We thank Waheed Abdullah Al Fazari, Zahran Abdulsalaam, Salim Al-Rubaie, Peter Olsson, Petter Ohlsson and Wietske Lambert for help in the field, and Jens Eriksen for sharing data and comments on bird numbers. We especially thank Shell Development Oman for their consistent financial support during the years, especially Muna Al Shukaili and Joanne Robinson. The surveys were also financially supported by Petroleum Development Oman (PDO), Natural Research Ltd, Embassy of the Kingdom of The Netherlands in the Sultanate of Oman, Carex The Netherlands, Wetlands International, the Ornithological Society of the Middle East and the Swedish Ornithological Society. Finally, we thank the two reviewers who helped us to make this manuscript stronger.



CHAPTER 6

Demography of a stable population of crab plovers wintering in Oman

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Abstract

The monotypic crab plover *Dromas ardeola* winters around the shores of the Indian Ocean and breeds in colonies on islands around the Arabian Peninsula. The IUCN lists the world population of crab plovers as stable, but long-term survey data or demographic estimates regarding the species status are lacking. Here, we use survey and demographic data collected from 2011–2015 to study the status of the population of crab plover at their most important wintering area: the Barr Al Hikman Peninsula in the Sultanate of Oman. Our survey data showed that the population of crab plovers initially increased and then stabilized. The overall observed finite rate of population change ($\bar{\lambda}_{obs}$) was estimated at 1.004 (0.995–1.013 95% Bayesian credible interval [BCI]), indicating a stable population (7,000–9,000 birds), that is possibly at carrying capacity. Based on mark-recapture data, the mean annual apparent survival probability of crab plovers was estimated to be 0.90 (0.85–0.94 95% BCI). We used counts of adults and yearlings to estimate the mean annual fecundity rate at 0.06 young per pair. Using these demographic values, the overall mean expected finite rate of population change ($\bar{\lambda}_{exp}$) was estimated to be 0.949 (0.899–0.996 95% BCI), so there is a low chance that $\bar{\lambda}_{obs}$ and $\bar{\lambda}_{exp}$ overlap. $\bar{\lambda}_{obs}$ and $\bar{\lambda}_{exp}$ would completely match if about 450 crab plovers immigrate to Barr Al Hikman each year. Regional surveys show that yearling densities are higher closer to the breeding areas, so immigrants could be birds that during their first winter stayed close to their natal area. Our study support the IUCN listening of crab plover as stable, but further population-wide monitoring is required. From a conservation point of view it is important to continue monitoring because crab plovers breed and winter in a region that is rapidly developing.

Introduction

The coastal areas of the Arabian Peninsula and East-Africa provide essential breeding and wintering habitat for a large number of shorebirds traveling within the Asian–East African Flyway (Delany *et al.* 2009). In contrast to shorebird populations in other parts of the world (Fernández & Lank 2008; van Roomen *et al.* 2015; Piersma *et al.* 2016), the status of shorebirds breeding and wintering along the Arabian and East-African coasts remains largely unknown (Delany *et al.* 2009). Coasts along the Arabian Peninsula and East-Africa are rapidly changing under increasing human pressure (Halpern *et al.* 2008), including habitat loss, climate warming, and overfishing (Sheppard *et al.* 2010; Sale *et al.* 2011). To understand if shorebirds in this part of the world can keep up with their changing environment, long-term survey data and demographic estimates are urgently needed.

The monotypic crab plover *Dromas ardeola* is endemic to the coastal areas of the Indian Ocean and the main breeding areas are located in the Arabian/Persian Gulf and the Red Sea (Chapter 11). Crab plovers breed in colonies on sandy islands where they nest in self-excavated burrows (De Marchi *et al.* 2008). Suitable breeding habitat seems scarce as only 56 breeding sites are known to exist worldwide (Chapter 12). Crab plovers are unusual among shorebirds a their modal clutch size is one, or rarely two eggs (Tayefeh *et al.* 2013). Crab plovers exhibit extended parental care, which is biparental at the breeding areas (Almalki *et al.* 2015) and probably uniparental at the wintering areas (De Sanctis *et al.* 2005). Parental care extends up to 8 months, which is longer than any other shorebird (De Sanctis *et al.* 2005). A small clutch size and extended parental care are life-history characteristics typical of long-lived species with low fecundity rates (Newton 1998; Sæther & Bakke 2000; Sandercock 2003), but the demography of crab plovers has not been studied before. Potentially, as crab plovers require specific breeding- and wintering habitat, they may suffer from rapid environmental changes in coastal areas. Egg collecting, destruction of burrows, or harvesting of adults may seriously affect breeding success and survival of crab plovers at the breeding areas (De Marchi *et al.* 2006; Behrouzi-Rad 2013; Tayefeh *et al.* 2013), whereas habitat destruction and overexploitation of preferred crab prey may affect the species at the wintering areas (Safaie *et al.* 2013b). Based on counts at the wintering areas, the world population of crab plovers has been estimated to be 60,000 to 80,000 birds (Wetlands International 2002). The population of crab plovers is currently considered to be stable (IUCN 2016), but this has not been substantiated with data (Delany *et al.* 2009).

In this study, we assessed the status of the population of crab plover wintering at the Barr Al Hikman Peninsula in the Sultanate of Oman (Fig. 6.1A). The area supports 10–15% of the world population of crab plovers and is therefore the most important wintering area for the species (Delany *et al.* 2009). Based on survey data and demographic estimates collected from 2011 to 2015, we developed an Integrated Population Model (IPM) (Schaub & Abadi 2011) in which we estimated observed and expected finite rates of population change (λ_{obs} and λ_{exp}). IPMs combine population counts and demographic data in a single model, and are particularly useful for studies with small datasets (Schaub *et al.* 2007), or studies where not all demographic parameters could be accounted for by data collected in the field (Schaub & Abadi 2011). Here we estimated λ_{obs} using existing survey data (Chapter 5) whereas λ_{exp} was calcu-

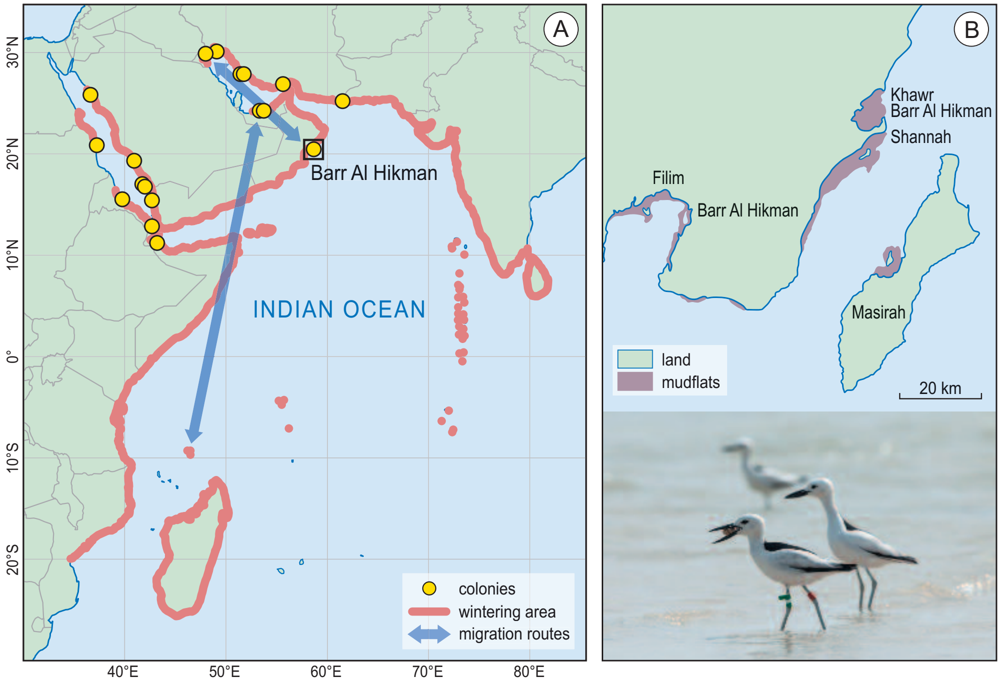


Figure 6.1. The distribution of crab plovers is confined to coastal areas of the Indian Ocean (A). Breeding areas (yellow dots) are adapted from Chapter 11, and wintering areas (red coast line) from Delany et al. (2009). Arrows show the known connections between breeding and wintering areas (Chapter 11; Javed *et al.* 2011). The study area at Barr Al Hikman is shown in the black square and in (B), with the main localities that are mentioned in the text. The inset in (B) shows a colour-ringed crab plover.

lated from newly estimated survival and fecundity rates. Apparent annual survival rates were estimated based on sightings of 169 individually colour-marked birds, and annual fecundity rates were based on the percentage of yearlings (first-winter birds) in the population. In addition to survival and fecundity, population dynamics of local populations also depend on immigration and emigration (Newton 1998). We did not measure immigration and emigration directly, but calculated potential immigration rates by matching observed (λ_{obs}) and expected (λ_{exp}) finite rates of population change (e.g. Doxa *et al.* 2013). We discussed the generality of our results by looking at population dynamics of crab plovers at other winter areas.

Methods

Study area & data collection

Our study was conducted at the intertidal mudflats that surround the Barr Al Hikman Peninsula in the Sultanate of Oman (20.6° N, 58.4° E). The intertidal mudflats encompass 190 km^2 and can be found south of Shannah, in the Khawr Barr Al Hikman, near Filim and on Masirah Island (Fig. 6.1B). Local industries included fisheries and salt mining, but the area is relatively pristine. Crab plovers can be found in the area almost exclusively in winter (Eriksen & Victor 2013). Six GPS tracks and four ring observations show that crab plovers wintering in Barr Al Hikman are connected to breeding areas in the Arabian/Persian Gulf in colonies in Kuwait and South-West Iran (Fig. 6.1A, Chapter 11). Barr Al Hikman was surveyed for shorebirds including crab plovers in the four winters of 1989/90 (Green *et al.* 1992), 2007/08, 2013/14 and 2015/16 (Chapter 5; Table 6.1).

Table 6.1. Survey results on wintering crab plovers at Barr Al Hikman, Oman, 1989–2016. In the present study, survey results collected over the period 2007/08 – 2015/16 were used to estimate the survey-based finite rate of population change.

Year	No. of crab plovers	Source
1989–1990	2943	Green *et al.* 1992
2007–2008	6901	chapter 5
2013–2014	8759	chapter 5
2015–2016	8462	chapter 5

We collected mark-recapture data on crab plovers at Barr Al Hikman during ten winter expeditions between 2007/08 and 2015/16 (one winter included two expeditions). During seven expeditions, crab plovers were caught with mist nets and individually marked with colour rings. All catching took place on the mudflats close to the shore 3 to 22 km south of Shannah in the nights around a new moon. In 2008/2009 and April 2010, all newly captured crab plovers received a unique combination of a single colour ring (white or orange) with a single letter inscription on each tibia and a metal ring on the right tarsus. During later years, birds were marked with four coloured rings and a green flag on their tibia, and a metal ring on the tarsus. An initial mark-recapture analysis showed that there was no difference in the resighting probability between the two types of colour rings as the Bayesian credible interval (BCI) for an effect of marker type overlapped zero (BCI 95% [–0.481; 1.459]).

Crab plovers were aged as yearlings (i.e. born in the previous summer) or adults (i.e. birds older than 1 year, Table 6.2) at first capture. Yearlings of are easy to recognize by their spotted

Table 6.2. Number of adult and yearlings crab plovers that were individually marked with colour rings at Barr Al Hikman per field visit.

Period	no. of ringed adults	no. of ringed yearlings
Dec 2008– Jan 2009	58	11
Apr 2010	2	4
March 2011	5	6
Nov–Dec 2011	29	3
Nov–Dec 2012	9	0
Nov 2014	22	7
Nov 2015	12	1

crown and hind neck and their greyish mantle (Cramp *et al.* 2004). We could not confidently age second-winter birds and we suspect that all yearling crab plovers had moulted into their adult plumage prior to our catching expeditions (Appendix A6.1). During all expeditions, observation effort to resight the marked birds was concentrated along the coast south of Shannah, but during most expeditions all other sites in the area were visited and checked as well at least once.

From 2011–2015, during early winter (November–December), we collected data on the annual fecundity of crab plovers by regularly counting the number of yearlings and adults in foraging or roosting groups all along the coast south of Shannah. Roosting groups were only counted if all birds were visible, because it appeared that birds at flock edges were often foraging yearlings. We counted between 8 and 22 groups per year, and between 10 and 666 individuals per group (Table 6.3).

Table 6.3. The number of groups in which the percentage yearlings of crab plovers were counted and the total number of birds counted. The final column give the model estimates of the percentage of yearlings in the population per year.

Year	no. groups counted	total no. birds counted	% of yearlings (mean ± 95% BCI)
2011/12	12	986	6.88 (5.41 – 8.53)
2012/13	12	766	6.77 (5.11 – 8.63)
2013/14	8	479	5.81 (3.89 – 8.14)
2014/15	22	1492	6.23 (5.10 – 7.49)
2015/16	11	2364	3.01 (2.42 – 3.80)

Integrated population model

We combined survey data and demographic data in a Bayesian Integrated Population Model (IPM) (Schaub & Abadi 2011) to estimate the annual-dependent survey-based finite rate of population change (λ_{obs}) and the annual-dependent demographic-based finite rate of population change (λ_{exp}) for the five-year period 2011/12 – 2015/16.

SURVEY-BASED FINITE RATE OF POPULATION CHANGE λ_{obs}

λ_{obs} was estimated from population counts as:

$$\lambda_{obs} = N_{t+1} / N_t$$

where N_t is the total population size at year t and N_{t+1} is population size in the year t + 1. To calculate N_t for winters in which no surveys were performed we simulated N_t by fitting a quadratic polynomial function with a Poisson distribution through the survey data over the period 2007/08 – 2015/16 in the Markov Chain Monte Carlo (MCMC) framework that we used in our Bayesian model (Fig. 6.2). We calculated year-specific λ_{obs} and also the geometric mean of $\bar{\lambda}_{obs}$ over all five years. The geometric mean was calculated as:

$$\bar{\lambda}_{\text{obs}} = \left(\sum_{t=1}^{T} \lambda_t \right)^{1/T}$$

(Stevens 2009).

Our estimation of λ_{obs} assumes perfect detection or equal probability of detection. Imperfect detection is widespread in surveys of roosting birds (Sutherland 2006) and we cannot guarantee perfect detection during our crab plover surveys. Arguably, probability of detection between years is equal, as all surveys reported in Table 6.1 are comparable in the sense that they covered exactly the same area and that there has been overlap between observers during all surveys (Chapter 5). In addition, crab plovers roost in well-defined congregations at the high-waterline and their conspicuous black-and-white plumage make them hard to miss. Furthermore, tracking data show that crab plovers have limited movements in their wintering area (unpublished data), making it unlikely that birds are counted twice when surveys are conducted over subsequent days.

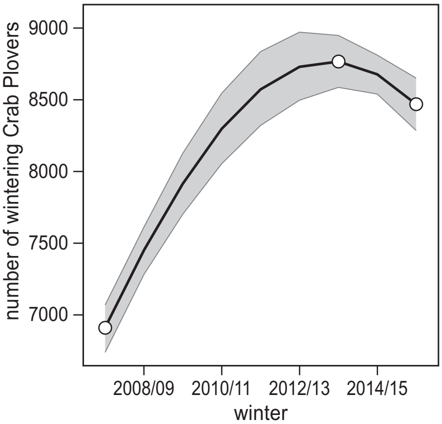


Figure 6.2. Number of wintering crab plovers in Barr Al Hikman in the study period based on surveys (open circles) and modelled population estimates. The thick line represents posterior means and shaded area represents 95% BCI.

DEMOGRAPHIC-BASED FINITE RATE OF POPULATION CHANGE λ_{exp}

We estimated λ_{exp} following assumptions shown in a post-reproductive census life cycle diagram (Fig. 6.3). Accordingly, as we could not age second-winter birds, the crab plover population at Barr Al Hikman in year t consists of yearlings (Y) and reproducing adults (A). The number of adults that will be in the area at year t+1 depends on age-specific survival probabilities (S_y and S_a) and age-specific site fidelity (ψ_y and ψ_a), and on immigration rate (ω).

The number of yearlings in the area in year t+1 depends on the annual fecundity rate (ft), which is the proportion of yearlings per pair. We could not measure side fidelity (ψ) and immigration (ω) directly. Instead we estimated apparent survival (φ) as the product of true survival (S) and ψ (Lebreton *et al.* 1992) and immigration rate (ω) as the difference between λ_{obs} with λ_{exp} (see below).

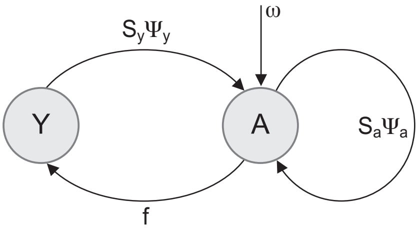


Figure 6.3. The life cycle diagram used for a population model of crab plover wintering at Barr Al Hikman. The two stages are the yearlings (Y) ≤ 1 year, and adults (A) birds > 1 year. The demographic parameters are age-specific survival (S_y, S_a), age-specific site fidelity (ψ_y, ψ_a), annual fecundity (f) and immigration of adults (ω).

We used a Cormack-Jolly Seber model to estimate apparent survival (φ), which corrects for the probability that not each bird is seen each year (resighting rate, p) (Lebreton *et al.* 1992), which we constructed in a Bayesian framework (Kéry & Schaub 2012). We first assessed the Goodness-of-Fit (GOF) in program Release in Mark to ascertain that the underlying assumptions for mark-recapture models are met (Pradel *et al.* 2005). Test 2, which tests the assumption that all individuals have an equal probability to be resighted and is therefore referred to as a test of trap-dependence, was significant ($\chi^2 = 40.7049$, df = 11, $P < 0.01$), and Test 3, which tests the assumption that all individuals have the same probability of survival to the next time step, was not ($\chi2 = 16.4881$, df = 9, $P = 0.0574$). To account for trap-dependence, we therefore used individual as random effect in the resighting probability (Kéry & Schaub 2012). The intensity of fieldwork varied each year, and resighting probability was modelled to vary among years. Test 3 of the GOF was almost significant, which could be caused by a differing apparent survival rate between adults and juveniles. We therefore tested preliminarily if apparent survival between yearlings and adults differed, which was not as the 95% BCI of their survival rates overlapped considerably (φ yearlings = 0.867, 95% BCI [0.657–0.994], φ adults = 0.893, 95% BCI [0.844–0.938]). Then, with a time-since-marking test, we tested whether catching influenced survival probability in the first year after catching, which could be caused by higher mortality or permanent emigration after the disturbance of handling, or by age-dependent survival probabilities (Sandercock 2006). We could find a weak effect of catching on apparent survival (φ first year after catching = 0.821, 95% BCI [0.672-0.982], φ years after first year after catching = 0.905, 95% BCI [0.855-0.950]). Given that there was overlap in BCI, all age classes and years after catching were treated as one group. Given our low sample size (Table 6.2), we did not calculate year-dependent annual apparent survival to avoid over parameterization.

We estimated year dependent fecundity (f_t) as the proportion of yearlings within a group (Y/[Y+A]), within the Bayesian framework. Because crab plovers lay (mostly) a single egg per year, fecundity could be estimated with a generalized model using a binomial error structure, and hence equals the fraction of success pairs (assuming that sex ratios of yearlings and adults in Barr Al Hikman are equal). As we estimated fecundity over the total number of birds older than one year (see below), we probably slightly underestimated the true fecundity in crab plovers, as crab plovers probably start breeding after their second winter (Chapter 11). However, given that fecundity rates in crab plovers are low (see below), this bias is probably small.

Because apparent survival between adults and yearlings did not differ, we could calculate λ_{exp} as:

$$\lambda_{exp} = \varphi + \varphi\, f_t$$

We estimated year specific λ_{exp} and the geometric mean of $\bar{\lambda}_{exp}$ over all the years.

IMMIGRATION

We regard immigrants as birds that have been in other areas during previous winters (hence, adult birds only). We calculated the per capita immigration rate ω for each year except the first year as:

$$\omega = (N_t - \lambda_{exp} * N_{t-1})/N_t$$

All parameters were estimated in one IPM. MCMC simulations for parameter estimation were obtained by running the JAGS program (Plummer 2003) implemented in the R environment (R Development Core Team 2013) using the *R2JAGS* package (Su & Yajima 2012). We used uninformative priors for all parameters. We ran three independent chains of 50,000 iterations of which the first 10,000 were discarded, and kept every 6th observation to avoid autocorrelation. We checked the R-hat for convergence of the parameters (in all cases < 1.01). Estimates are presented as the posterior means and with a 95% BCI.

Results

The geometric mean $\bar{\lambda}_{obs}$ for the five-year period 2011/12 – 2015/16 was 1.004 (0.995–1.013). The yearly λ_{obs} ranged between 0.98 and 1.02 and decreased over the years (Fig. 6.4). Annual apparent survival probability was 0.895 (0.847–0.940) for the period 2008/09 – 2015/16. The annual resighting probability increased from 0.080 (0.025–0.169 95% BCI) to 0.744 (0.097–0.915 95% BCI) over the years 2008/09 – 2015/16 (Appendix A6.2). The estimated annual fecundity rate varied over the period 2011/12 – 2015/16 between 0.03 and 0.07 (proportion of yearlings), with 95% BCI ranging between 0.02 and 0.08. On average, the annual fecundity rate was 0.06 (Table 6.3). Based on the estimated apparent survival probability and fecundity rate, the geometric mean $\bar{\lambda}_{exp}$ over the period 2012/13 – 2015/16 was 0.949 (0.899 – 0.996 95% BCI) and annually ranged between 0.92 and 0.96 (Fig. 6.4). As we did not estimate a yearly dependent apparent survival probability, variation in λ_{exp} was solely due to variation in the estimated fecundity rate, which was particularly low in the last year (Table 6.3). To explain differences between λ_{obs} and λ_{exp}, we estimated yearly per capita immigration rates of 0.056 (0.006–0.107 95% BCI) in 2012/13, 0.052 (0.027–0.104 95% BCI) in 2013/14, 0.034 (0.026–0.086 95% BCI) in 2014/15 and 0.051 (0.103–0.026 95% BCI) in 2015/16. Our estimated immigration rates correspond to 315–508 individuals per year.

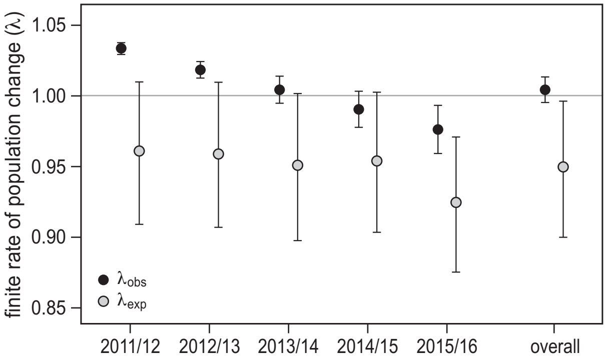


Figure 6.4. Annual finite rates of population change based on population surveys (λ_{obs}, black dots) and based on demographic estimates (λ_{exp}, grey dots) and the overall $\bar{\lambda}_{obs}$ and $\bar{\lambda}_{exp}$. Error bars show 95% BCI. The grey line at $\lambda = 1$ indicates the level at which the population would be stable. The difference between λ_{obs} and λ_{exp} was used to calculate immigration rates (ω).

Discussion

Annual survival

We estimated the annual apparent survival rate of crab plovers at 90%, which shows that, consistent with our expectations based on low fecundity rates, the crab plover is a long-lived shorebird (Sandercock 2003). Similar high survival rates are known from other large-bodied shorebirds including Eurasian curlew *Numenius arquata*, bar-tailed godwit *Limosa lapponica*, black-tailed godwit *Limosa limosa* and Eurasian oystercatchers *Haematopus ostralegus* (Sandercock 2003; Duriez *et al.* 2012; Taylor & Dodd 2013; Conklin *et al.* 2016; Kentie *et al.* 2016). Compared to other shorebirds, crab plovers exhibit more extreme life-history characteristics, including a clutch size of one egg and extended parental care, so it is perhaps remarkable that the annual apparent survival rate was similar high instead of higher than other large-bodied shorebirds. Since we could not separate true survival from permanent emigration, it could be that the true survival estimate is higher than our apparent survival rate (Lebreton *et al.* 1992). In general, shorebirds are extremely site faithful to their wintering area (Leyrer *et al.* 2013; Lourenço *et al.* 2016), but we do not know site fidelity for crab plovers as they move around in a part of the world where few observers are out on the shores looking for colour-ringed birds. An observation in winter 2012/13 in south India of a bird that was ringed by us in 2011/12 in Barr Al Hikman as an adult and never seen in the area afterwards, shows that permanent emigration can occur, suggesting that our apparent survival estimates are a conservative estimate of true survival in crab plovers. Note that the dispersal event to India could also explain why the apparent survival in the first year was lower (but with overlapping BCI) than the estimated apparent survival over the years after the year of catching.

Finite rate of population change and immigration

Survey data suggest that the population of crab plovers at Barr Al Hikman over the period of study (2011/12 – 2015/16) was stable, as in this period the overall survey-based finite rate of population change $\bar{\lambda}_{obs}$ did not differ from one (Fig. 6.4). A finite rate of change close to one indicates that the population at Barr Al Hikman is possibly at carrying capacity (Newton 1998). Note that prior to the study period, between 1989/90 – 2007/08, the population increased from 2,943 to 6,901 birds (Chapter 5; Table 6.1). As discussed in Chapter 5, the effort and area covered in 1989/90 did not differ from the more recent surveys; thereby the observed increase is thought to be genuine. Our demographic data did not cover the period 1989/90 – 2007/08, hence the origin of this increase remains unexplained.

Based on demographic data over the period of study (2011/12 – 2015/16), we estimated the overall demographic-based finite rate of population change ($\bar{\lambda}_{exp}$) to be 0.95 (Fig. 6.4). The upper value of the 95% BCI of $\bar{\lambda}_{exp}$ (0.996) slightly overlapped with the lower value of the 95% BCI of the overall $\bar{\lambda}_{obs}$ (0.995), indicating that there is a small chance that $\bar{\lambda}_{exp}$ did not differ from $\bar{\lambda}_{obs}$, (Fig. 6.4). Given the small overlap of the BCI, we reason that it is more likely that the observed population stability cannot be explained by our survival and fecundity estimates alone. Thus our study population likely received immigrants as part of a larger metapopulation, which matches our observation that crab plovers emigrate from Barr Al Hikman. The annual means of λ_{obs} and λ_{exp} predict net immigration ranging from 315 to 508 crab plovers per year. Immigrants could, for instance, originate from areas where the population of crab plovers is at carrying capacity, or crab plovers may immigrate to Barr Al Hikman when conditions at their original wintering site are deteriorating (Chapter 5). Limited data show that populations in other wintering areas are stable or increasing (Fig. 6.5), leaving the scenario open that immigrants could originate from other areas that are already at carrying capacity.

Immigrants could also be second-year crab plovers that during their first winter have stayed close to the breeding areas. Differential migration is widespread among migratory

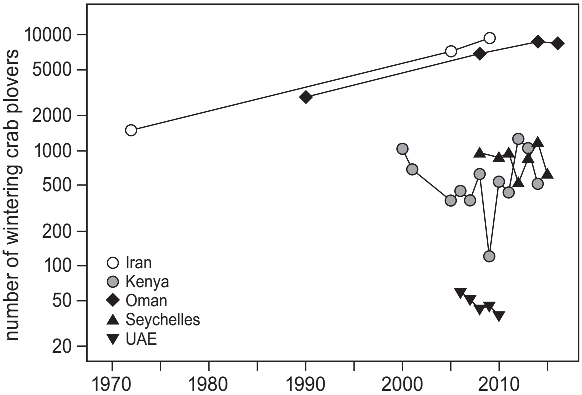


Figure 6.5. Survey-based population estimates of crab plovers in five countries on a $\log_{10}$ scale. The large wintering population of crab plovers in Iran, which likely have shared breeding areas with the Barr Al Hikman population, was observed to increase (data from Summers *et al.* 1987; Amini & van Roomen 2009). A small population of wintering crab plovers in the United Arab Emirates decreased from 60 to 30 birds from 2006–2010 (Javed *et al.* 2012). Two winter populations along the shores in East-Africa (Miday Creek in Kenya, data C. Jackson) and Aldabra in the Seychelles (data: the Seychelles Islands Foundation) were apparently stable during the last decade.

shorebirds (Cristol *et al.* 1999; Nebel 2007). If this is the case, percentages of yearling crab plovers in wintering groups closer to the breeding areas should be higher than the 3–7 % of yearlings found at Barr al Hikman. Only few surveys of crab plovers exist, yet these surveys supported this possibility: A winter population near breeding areas in Eritrea consisted on average of 8% of yearlings (18 groups counted during winter over the period 2002–2009, total adults = 1160, yearlings = 99, G. De Marchi, unpublished data). A group of 104 wintering crab plovers in January 2016 close to the breeding areas in Kuwait consisted of 16% of yearlings (P. Fagel, pers. comm). Likewise, a group of 550 wintering crab plovers in the Gulf of Kutch in India consisted of 17% yearlings, but it is unknown if crab plovers breed in this area (Palmes & Briggs 1986). Thus, although the origin of immigrants remain unknown, available data suggest that immigrants are birds that stayed close to their natal area during their first winter.

Conclusion

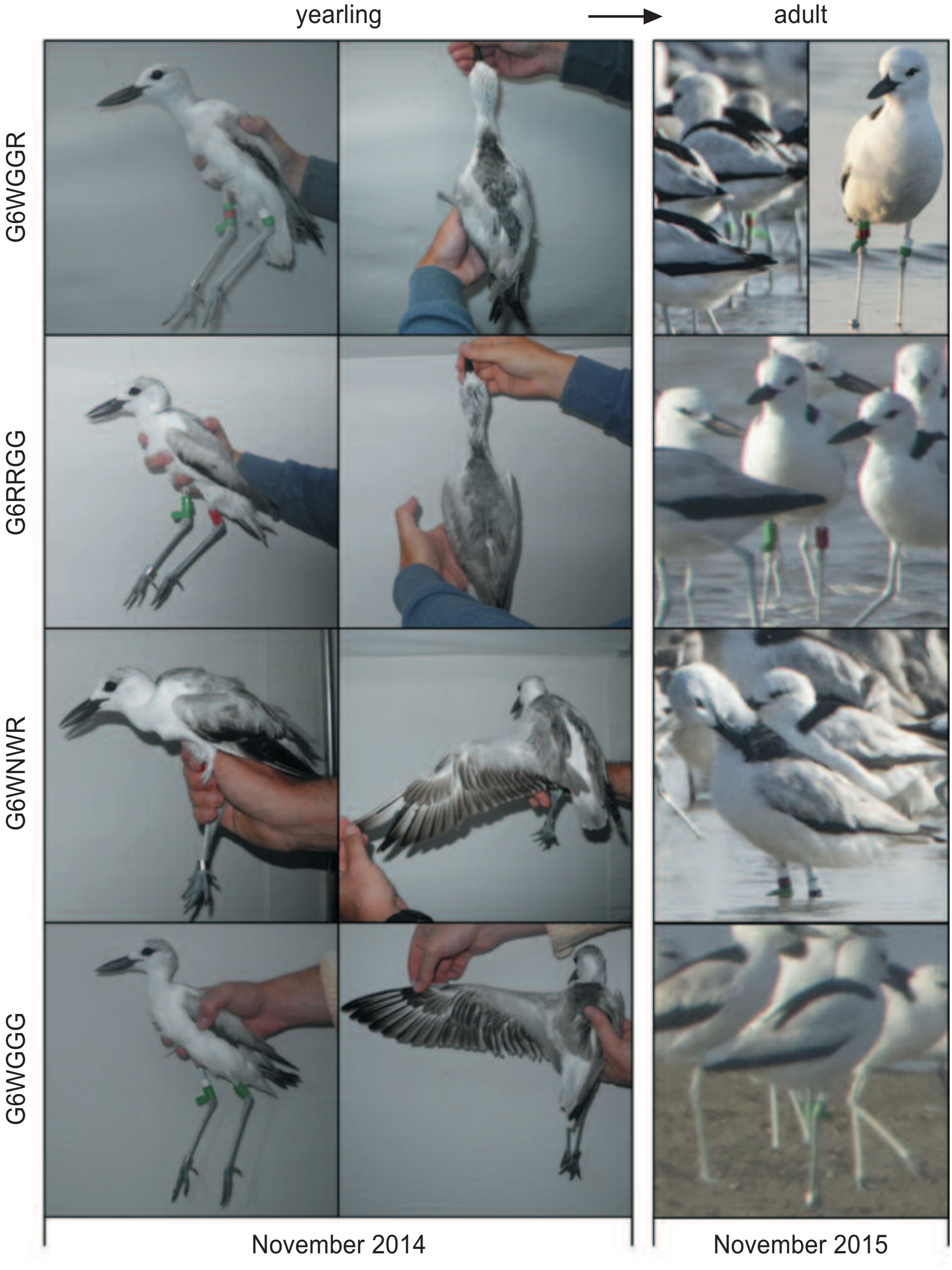
Our results support the current IUCN listing of the world population of crab plover as stable (IUCN 2017). Stability may be unexpected given that the species is under human pressure in their wintering grounds and especially in their breeding grounds where colonies remain subject to egg-collecting and harvest of chick and adults (De Marchi et al 2006; Behrouzi-Rad 2013; Tayefeh *et al.* 2013). We emphasize that survival and fecundity estimates indicate that the population of crab plovers wintering at Barr Al Hikman received immigrants, but their origin remains speculative. Finding the origin of these immigrants is a prerequisite to better understand the status of crab plovers wintering and breeding in the Arabian/Persian Gulf. Moreover, range-wide survey and ringing activities are needed to better understand the *global* status of crab plovers.

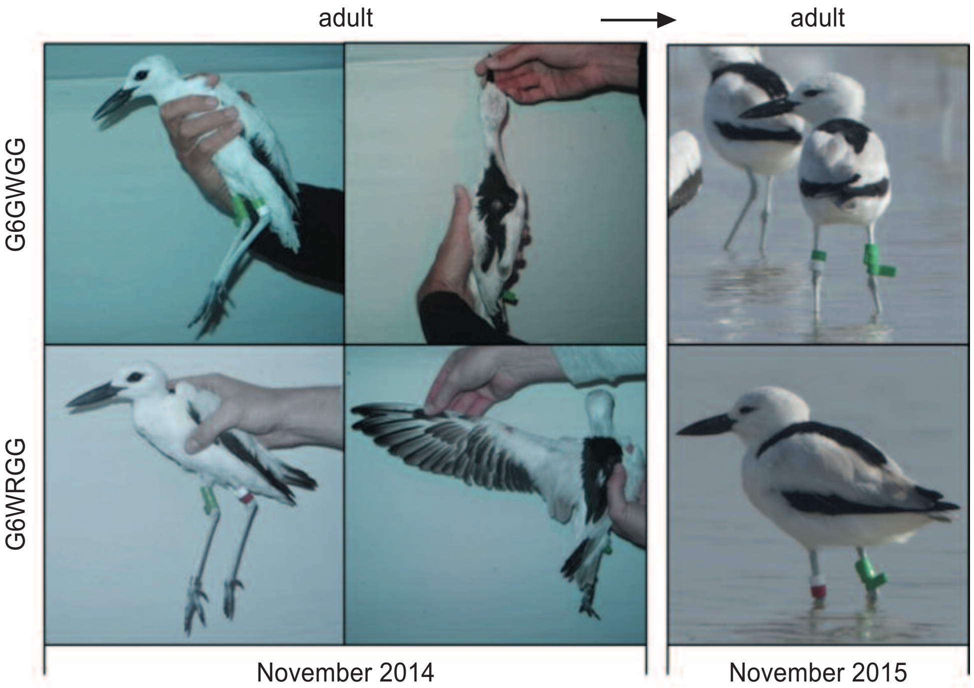
To our knowledge, our study is the first to report demographic parameters of a shorebird population wintering in the coastal areas of the Arabian Peninsula and East-Africa. The observed population stability contrasts with the rapid declining populations of many other shorebird species elsewhere in the world (Fernández and Lank 2008; Piersma *et al.* 2016; van Roomen *et al.* 2015); declines that are thought to be caused by environmental change, affecting particularly wintering- and stopover areas of shorebirds (Pearce-Higgins *et al.* 2017). Thus, shorebirds may still be able to find vital wintering grounds along the coasts of the Arabian Peninsula and East-Africa. From a conservation point of view, it is timely to protect those habitats and to continue monitoring the status of their inhabitants. Only then, unique birds such as the crab plover can be safeguarded for the future.

Acknowledgements

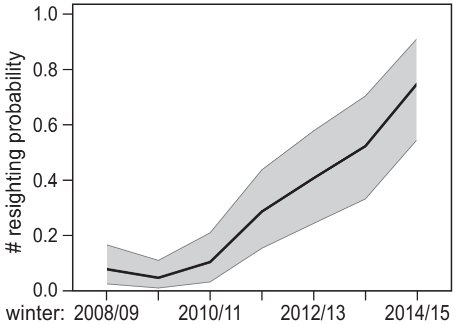
The presented work relies on the effort of many volunteers that were in the heat of the day out on the shabkha or mudflats to look for colour-ringed crab plovers. We thank all observers and in particular Irene Landman, Thijs Fijen, Jelle Abma, Jan van de Kam and Leon Kelder. Raymond Klaassen, Peter Olsson, Petter Ohlson and Gabriel Norevik provided indispensable help during catching. We thank Collin Jackson and the Seychelles Islands Foundation for sharing their data on crab plover surveys and Giuseppe De Marchi and Pekka Fagel for sharing their fecundity estimates. Dick Visser prepared the figures. Brett Sandercock, Giuseppe De Marchi and an anonymous reviewer gave excellent comments on previous versions of this manuscript. Our study was financially supported by Shell Development Oman, the Embassy of the Kingdom of The Netherlands in Muscat, the Research Council (TRC) of the Sultanate of Oman (ORG/EBR/12/002 grant awarded to AYK) and by NWO in the Netherlands (ALW Open Programme grant 821.01.001 awarded to JAvG). RK was funded by The Royal Society. Catching and banding of crab plovers was carried out under permission of the Ministry of Environment and Climate Affairs, Sultanate of Oman. We are grateful to the assistant Director-General Ms. Thuraya Said Al-Sairiri, Director-General Mr Sulieman Al Akhzami and the former Director-General, Mr Ali Al-Kiyumi for their assistance.

Appendices


yearling
adult
G6WGGR
G6RRGG
G6WNWR
G6WGGG
November 2014
November 2015



Appendix A6.1. Observations showing that crab plovers in their 2nd calendar year can moult into a plumage that is indistinguishable from adults. Pictures in each row show the same bird as referred to by a unique colour ring code. Left and middle pictures show birds at capture (November 2014) and right pictures show the same bird in the field a year later (November 2015). The upper four rows show pictures of birds that were captured as yearlings (identified by the greyish mantle and the spotted crown) and photographed a year later. The pictures show that 2nd calendar year crab plovers lost their spotted crown and largely lost their greyish back feathers. Only the third bird (G6WNWR) appears to remain some of the greyish back feathers, the back feathers of the other birds changed black. The last two rows show an example of the plumage of adults at capture (November 2014) and photographed a year later (November 2015). These show that also adults in winter plumage can have a slight spotted crown and a greyish mantle, which is according to Cramp *et al.* (2004).
Skakuj *et al.* (1997) reports that 2nd calendar year crab plovers prior to autumn moult are easily distinguished from adults by their spotted crown. Our pictures show, in line with an unsupported description of Cramp and Simmons (2004), that 2nd calendar year crab plovers lost their spotted crown after autumn moult. We conclude that the plumage of 2nd calendar year crab plovers in winter is like adult non-breeding. Thus, in winter, only yearlings and adults can be confidently aged.



Appendix A6.2. Resighting probability over the years of fieldwork. The thick line represents posterior means and shaded area represents 95% Bayesian Credible Intervals.

CHAPTER 7

Stomach fullness shapes prey choice decisions in crab plovers (*Dromas ardeola*)

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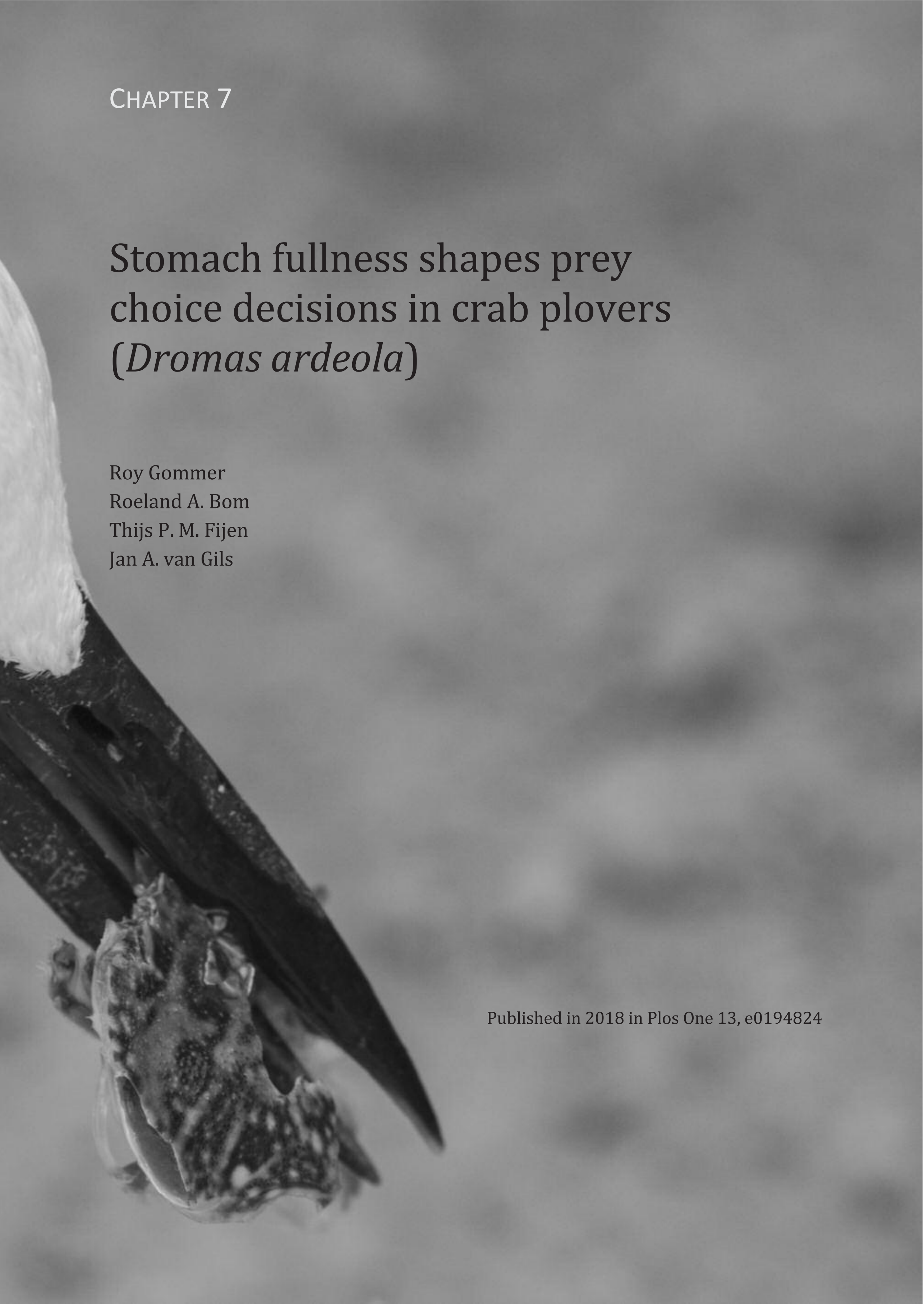

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Abstract

Foragers whose energy intake rate is constrained by search and handling time should, according to the contingency model (CM), select prey items whose profitability exceeds or equals the forager's long-term average energy intake rate. This rule does not apply when prey items are found and ingested at a higher rate than the digestive system can process them. According to the digestive rate model (DRM), foragers in such situations should prefer prey with the highest digestive quality, instead of the highest profitability. As the digestive system fills up, the limiting constraint switches from ingestion rate to digestion rate, and prey choice is expected to change accordingly for foragers making decisions over a relative short time window. We use these models to understand prey choice in crab plovers *Dromas ardeola*, preying on either small burrowing crabs that are swallowed whole (high profitability, but potentially inducing a digestive constraint) or on larger swimming crabs that are opened to consume only the flesh (low profitability, but easier to digest). To parameterize the CM and DRM, we measured energy content, ballast mass and handling times for different sized prey, and the birds' digestive capacity in three captive individuals. Subsequently, these birds were used in *ad libitum* experiments to test if they obeyed the rules of the CM or DRM. We found that crab plovers with an empty stomach mainly chose the most profitable prey, matching the CM. When stomach fullness increased, the birds switched their preference from the most profitable prey to the highest-quality prey, matching the predictions of the DRM. This shows that prey choice is context dependent, affected by the stomach fullness of an animal. Our results suggest that prey choice experiments should be carefully interpreted, especially under captive conditions as foragers often 'fill up' in the course of feeding trials.

Introduction

Prey choice decisions in animals are thought to be the product of natural selection (Stephens & Krebs 1986). It is generally assumed that this has shaped carnivorous in such ways that they select prey that maximize their rate of energy gain (Stephens & Krebs 1986, but see some recent studies highlighting that predators also can make dietary decisions based on macro-nutritional composition or toxins :Simpson & Raubenheimer 2011; Oudman *et al.* 2014; Machovsky-Capuska *et al.* 2016b; Machovsky-Capuska *et al.* 2016a). This assumption was used in the optimal diet theory (MacArthur & Pianka 1966) to predict prey-choice decisions. The original and most frequently used optimal prey-selection model is the so-called 'contingency model' (CM) (Charnov 1976; Stephens & Krebs 1986). CM predicts which prey items should be included in the diet based on their profitability. Each prey item i has a certain metabolizable energy content (e_i) and a certain handling time (h_i). Only prey items whose profitability (e_i/h_i) exceeds or equals long-term average energy intake rate should be included in the diet and consequently prey items with a lower profitability should be rejected.

The CM is supported by many empirical tests on for example birds, mammals and insects (Sutherland 1982; Stephens & Krebs 1986; Sih & Christensen 2001). The CM applies to foragers which are so-called 'handling-constrained' (Farnsworth & Illius 1998), i.e. foragers that spend all their time searching and handling prey. Their energy intake is limited by the rate at which prey items can be found and handled. Problems with the CM arise when foragers are able to find and handle prey items faster than they can process them internally (Verlinden & Wiley 1989). These foragers, instead of being handling-constrained, are 'digestion-constrained' (Zwarts & Blomert 1990; Fortin *et al.* 2002; Jeschke *et al.* 2002). Digestive pauses have to be taken before a new prey item can be ingested (van Gils *et al.* 2003). These digestive pauses cause a digestively constrained forager, obeying CM rules, not to maximise its long-term energy intake, because time to forage is lost during digestive pauses (Fortin *et al.* 2002). In this case, another optimal diet model should be considered.

The digestive rate model (DRM) (Verlinden & Wiley 1989; Hirakawa 1997; van Gils *et al.* 2005b) is an optimal diet model in which long-term intake rate is maximised under a digestive constraint. Tests of the DRM have first been restricted to herbivorous mammals (Fortin *et al.* 2002; Illius *et al.* 2002) and only relatively recently a few have been conducted on carnivorous birds (van Gils *et al.* 2005b; Quaintenne *et al.* 2010). In this model, energy intake is limited by the rate of digestion and prey items are by and large selected on the basis of digestive quality (energy (e_i) per unit of indigestible ballast mass (k_i)), rather than profitability (Quaintenne *et al.* 2010). Foragers can use time, which would otherwise be lost to digestive pauses, to search for high quality (easy-to-digest) prey items (van Gils *et al.* 2005b). Whether a forager needs to obey the CM or DRM thus depends on whether the forager is handling or digestively constrained.

Also the time horizon over which a forager wants to maximise its energy intake is important when considering optimal prey choice (Quaintenne *et al.* 2010). A forager aiming at maximising long-term energy intake should obey the rules of the DRM in case it faces, or is expected to face, a digestive constraint (i.e. has, or is expected to get, a full stomach). However, a forager aiming to maximise energy intake over a relatively short time interval (Fortin *et al.*

2002), should obey the CM at the start of feeding when the stomach is still empty. As its stomach gradually fills up and the constraint switches from a handling to a digestive constraint, it should be optimal for a short-term rate maximizing forager to switch from CM-principles to DRM-principles (Jeschke *et al.* 2002; Whelan & Brown 2005; Molokwu *et al.* 2011).

Here we will use both diet models to understand prey choice decisions in crab plovers *Dromas ardeola*, a tropical shorebird that primarily consumes crabs, but also consumes fish and benthic invertebrates (Hockey *et al.* 1996). In our study area in the Sultanate of Oman, crab plovers mainly prey on two types of crabs: small burrowing crabs, *Macrophthalmus sulcatus* (hereafter *Macrophthalmus*), that are ingested whole and potentially induce a digestive constraint or large swimming crabs, *Portunus segnis* (hereafter *Portunus*) that are opened to consume the flesh only, potentially inducing a handling constraint. *Portunus* is opened, since it is physically impossible to swallow the whole crab. The processing dichotomy between these two species makes the system ideal to study prey choice in the light of the CM and DRM. We tested, under captive conditions, the prey choice of crab plovers when offered small *Macrophthalmus*, small *Portunus* and large *Portunus*. Both a dichotomous prey choice experiment (empty stomach) as well as a cafeteria experiment have been performed to test for changes in prey choice as the stomach fills up. We parameterized both the CM and DRM by estimating the energy content of the crabs, the ballast mass of the crabs and the handling times of crab plovers on different crabs. The predictions of the CM and DRM were used to explain the outcomes of our prey choice experiments.

Methods

Study area & study species

The study was conducted on the relatively pristine mudflats of Barr al Hikman peninsula, located at the central-east coast of the Sultanate of Oman (20.6° N, 58.4° E). Barr al Hikman is one of the largest and most important wetland areas in the Middle East and supports large numbers of shorebirds (Chapter 5). Among them is the crab plover, our study species. About 8,000 of these conspicuous black-and-white birds winter in the area, making it the most important wintering area for this species (Delany *et al.* 2009). Its breeding range covers the northwestern Indian Ocean and the Red Sea, while its wintering range covers most of the Indian Ocean (De Marchi *et al.* 2006; Chapter 11). Throughout its wintering range the diet of crab plovers mainly consists of crabs, but other invertebrates and fish are also eaten (Aspinall & Hockey 1996; De Sanctis *et al.* 2005).

Captive birds

The birds to be held in captivity were caught during the night using mistnets, early November 2015. After capture, these birds were housed in an aviary (2.5 m width × 2.5 m length × 1.25 m height), made out of wood and nets. It took about a week for them to get accustomed to these new conditions. During this start-up phase they were fed a mixed diet of both crab species to be used in our experiments in order to prevent them from getting used to a single prey species. After catching the weight of the birds initially decreased, but stabilized after about a week at on average 79% (SD ± 4%) of the catching weight. Two birds suffered from leg cramp, presumably caused by stressful conditions of catching, from which one recovered during the week before the experiments, leaving us with three birds to be used in our experiments. After this week, each bird was assigned to a series of feeding trials. To be able to parameterize the CM, we measured handling time in relation to crab size. To be able to parameterize the DRM, we conducted a maximum intake experiment. Prey choice was tested in a dichotomous prey choice experiment and a cafeteria experiment. The birds were released by the end of November 2015.

Prey species

For all experiments, we used *Macrophthalmus* and *Portunus*. As profitability and digestive quality of *Portunus* was expected to scale substantially with size, we used two size classes of these species: a small (carapax width: 30–50 mm) and a large (carapax width: 60–90 mm). For the interest of this study, we report for both crab species the metabolizable energy content, the undigestible (inorganic) part and the total mass (undigestible + digestible). Following Zwarts and Wanink (1993) we used ash-free dry mass (AFDM) as our measure of metabolizable energy, or digestible part of the prey. It is reasonable to assume that the energy value per unit AFDM does not vary with species and size (Zwarts & Wanink 1993). Likewise, the ash content of the prey was used as the undigestible part of the prey. The dry mass (DM) of the prey was used as the total mass, which was defined as the undigestible + digestible part of the prey. To predict for each crab offered in the experiments its AFDM, its ash content and DM on the basis of its size, we fitted regression models relating crab size to AFDM, ash content and DM for individuals of both crab species, collected in November 2015 and covering the entire size range found in the field. Collected crabs were stored in formalin and transported to the NIOZ Royal Netherlands Institute for Sea Research. Here, the width of each crab was measured to the nearest mm. Next, crabs were dried for three days at 55–60 °C in a ventilated oven, after which DM was obtained to the nearest 0.01 g. Subsequently the crabs were incinerated at 550 °C for two hours and the ash mass was obtained. AFDM was calculated as the DM minus the ash mass. Non-linear regression models (power function: $y = ax^b$; Table 7.1) were fitted using R-package gnls (R Development Core Team 2013). Crab plovers do not eat the carapaxes of large *Portunus*. Depredated carapaxes were collected and their DM, AFDM and ash was determined using the same methodology as mentioned above. Regression models (Table 7.1) relating crab width to empty carapaxes were made in the same way as the other regression models and were subtracted from the previous mentioned regression models to determine the true ingested flesh by crab plovers. We assume that the energy loss due to the formalin fixation is similar across species and size classes (Zwarts & Wanink 1993; Wetzel *et al.* 2005).

CM

In order to make predictions based on the CM, we calculated the profitability (e_i/h_i) of the prey in a series of feeding trials in which all three birds were offered differently sized prey items. We used prey items over the entire size range found in the field. Feeding trials were conducted during the morning to make sure birds had an empty stomach, so that they had the same motivation to eat. Furthermore, feeding trials were conducted on single birds to make sure that interference did not affect our results. All trial were filmed (Canon VIXIA HG21). To establish the profitability (e_i/h_i) of crabs, we first calculated the energy content (e_i) using the AFDM of each prey item offered, calculated by using the equations in Table 7.1. The handling time (h_i) was measured from the moment of attacking the prey till the moment of swallowing the prey. Pauses during handling were excluded from the handling time. We analysed the video's using 'The Observer' package (v. 5.0, Noldus Information Technology). Profitability was then calculated by dividing AFDM (e_i) by handling time (h_i). Linear mixed-effect models with crab width against profitability were fitted to test for a relation between profitability and crab width. We used crab width as a fixed effect and bird as a random effect. To compare the profitability between prey species we also used a linear mixed-effect model with crab species as a fixed effect and bird as a random effect. To fit the profitability versus size curves we used power functions: ($y = ax^b$), using R-package gnls (R Development Core Team 2013).

Table 7.1. AFDM (mg) versus crab width (mm), ash mass (mg) versus crab width (mm), DM (mg) versus crab width (mm) and handling time versus crab width (mm) for both crab species. For *Portunus* we also determined the carapax AFDM (mg), ash mass (mg) and DM (mg) versus crab width (mm).

model	*Macrophthalmus*	*Portunus*
AFDM ~ Size	$y = 4.05e\text{-}02x^{2.76}$	$y = 4.20e\text{-}02x^{2.53}$
Carapax AFDM ~ Size	-	$y = 8.89e\text{-}02x^{1.97}$
Ash ~ Size	$y = 3.66e\text{-}02x^{2.78}$	$y = 1.90e\text{-}02x^{2.65}$
Carapax ash ~ Size	-	$y = 1.58e\text{-}02x^{2.58}$
DM ~ Size	$y = 7.19e\text{-}02x^{2.80}$	$y = 5.96e\text{-}02x^{2.58}$
Carapax DM ~ Size	-	$y = 4.13e\text{-}02x^{2.44}$
Handling ~ Size	$y = 0.19x^{0.91}$	$y = 0.003x^{2.72}$

DRM

To make predictions based on the DRM, we first experimentally determined whether ash (undigestible part of the prey), AFDM (digestible part of the prey) or DM (undigestible + digestible part of the prey) is the ballast mass that sets a digestive constraint in crab plovers, following the same procedure as van Gils *et al.* (2003). We assumed that the rate at which digestively constrained crab plovers can process the ballast mass of a prey will be constant across prey types (van Gils *et al.* 2005b). This means that if the ballast mass of a prey item is double compared to the ballast mass of another prey item, the long term numerical intake rate on the prey item with the high ballast mass will be twice as low as the long term numerical intake rate on the prey item with the low ballast mass (van Gils *et al.* 2003). The rate at which prey can be consumed is given by the formula: $y = \frac{1}{x}c$ (where y is numerical intake rate (IR); x is DM, AFDM or ash content of the prey; and c is digestive constraint) (van Gils *et al.* 2003).

MAXIMUM-INTAKE EXPERIMENT

To determine the digestive constraint of crab plovers we offered the captive birds *ad libitum* food, being either *Macrophthalmus*, small sized *Portunus* or large sized *Portunus*. Each feeding trial lasted two hours and was repeated once, so we conducted (3 birds × 3 diets × 2 repetitions) 18 feeding trials in total. Three feeding trials were excluded because of camera failure. Trials were filmed (GoPro4) and intake was scored using 'The Observer' package (v. 5.0, Noldus Information Technology). Cumulative intake (# prey items) was plotted versus time (minutes) to estimate the long-term intake rate (slope). We estimated long-term intake rate (IR) using the slope between the point of first saturation (last crab ingestion before first digestive break) and the end point (last crab ingestion observed) of a feeding trial (Zwarts *et al.* 1996b; Zwarts *et al.* 1996a). The first saturation point was the point where crab plovers had not eaten for more than seven minutes which we interpreted as a digestive pause. We also inspected this graphically to confirm that the starting point was correct. IR of all the trials was then plotted versus average DM, AFDM and ash content of the crabs that were eaten during the experiment. A line was fitted using a linear mixed-effect model on log-transformed data with bird as a random effect. We tested whether the slope of this model differed significantly from –1, because a slope of –1 implies that there is a fixed amount of ballast mass, coined c, a stomach can process per unit of time (van Gils *et al.* 2003). This follows mathematically when log-transforming the formula: $y = \frac{1}{x}c$. We did this for DM, AFDM and ash content to determine what constrains the food intake of crab plovers (the one that does not differ from –1).

THE DIGESTIVE RATE MODEL

To parameterize the digestive rate model (DRM) we used the prey characteristics of both prey species. We plotted profitability (e_i/h_i) of both species versus ballast intake (k_i/h_i) (van Gils *et al.* 2005b). In addition, we plotted the digestive constraint. For k_i we used ash content (g), because that is what constrains the food intake of crab plovers (see Results).

Dichotomous prey choice experiment

Crab plovers were offered two different prey items in two separated trays (Fig. 7.1). Prey species were randomly assigned to different sides (left/right). Crab plovers were brought into the experimental aviary on the opposite side of the trays to make sure they could see both prey items when walking towards the trays before making a choice. We conducted several trials per bird, but all on different days. Trials were conducted during the morning when birds had not eaten for the whole night to make sure their stomach was empty. We offered each bird three combinations: *Macrophthalmus* versus small *Portunus* (18 trials), *Macrophthalmus* versus large *Portunus* (17 trials) and small *Portunus* versus large *Portunus* (18 trials). For crab characteristics of the crabs offered see Table 7.2. To test prey preference, we used the dichotomous prey test (Van der Meer 1992). We used a generalized linear model with prey choice as our response variable and the different prey types as our predictor variables. A quasibinomial model was used and the cardinal preference rank was calculated for each prey type. The cardinal preference rank of large *Portunus* was set to zero (no SE) as we compared *Macrophthalmus* and small *Portunus* to large *Portunus*.

Cafeteria experiment

Because prey choice might differ depending on the internal state (fullness of the stomach) of the crab plovers, we offered them *ad libitum* food of all three prey types, i.e. *Macrophthalmus*

Figure 7.1. Crab plover facing two different prey items in two separated trays. The left tray contains a small *Portunus* and the right tray a *Macrophthalmus*.

(on average 17 crabs), small *Portunus* (on average 9 crabs) and large *Portunus* (4 crabs), with each prey type in a separated tray. For crab characteristic of the crabs offered see Table 7.3. Each feeding trial lasted approximately two hours and was filmed to determine the exact moments of ingestion in time (GoPro4). From these videos the cumulative numeric intake was scored using 'The Observer' package (v. 5.0, Noldus Information Technology). We also scored which prey type was ingested. After each feeding trial we counted the crabs that were left to calculate the number of crabs the crab plover had eaten. Two of the three birds were used (the third was not used because of time limitation) on which we both conducted two feeding trials, so we had four trials in total. Trials were conducted on four different days and for each bird there was a day in between each trial. Birds that entered the trials had not eaten for at least four hours to make sure their stomach was empty. For the purpose of this study, two trials could not be used because in trial 3 the crab plover had eaten all Macropthalmus before reaching its digestive constraint and in trial 4 the crab plover stopped eating after the camera failed. This left us with two successful trials on two different birds. Trial 2 suffered from unfortunate camera failure after 15 minutes. Within this time period the experimental bird had reached its digestive constraint, and by counting the crabs that were left at the end of the trial we could calculate the number of crabs that were eaten after the camera failed. These crabs were included in the results but we do not know when these crabs were eaten and in which order.

Results

Feeding behaviour

As anticipated, the crab plovers swallowed the *Macrophthalmus* always whole, while *Portunus* was always stripped from the carapax, legs and pincers, and only the flesh was eaten.

CM

Macrophthalmus had a higher profitability than *Portunus* (df = 96, t-value = –14.81, P < 0.001; Fig. 7.2C) which was mainly caused by the short handling times on *Macrophthalmus*. Handling times were much larger for *Portunus* ranging from 50 to 500 seconds versus 2 to 5 seconds for *Macrophthalmus* (Fig. 7.2B). So following the CM crab plover should always choose the more profitable *Macrophthalmus*. We found a positive exponential relation between profitability and crab size in *Macrophthalmus* (df = 24, t-value = 3.59, P = 0.002). Crab size did not affect profitability in *Portunus* (df = 68, t-value = 0.13, P = 0.897).

Table 7.2. Crab characteristic of the crabs offered in the dichotomous prey choice experiment. The number of crabs offered (n) as well as the average crab size (± SD) is shown. Average (± SD) AFDM (mg), handling time (s) and ash (mg) was calculated based on the crab sizes of each individual crab using the formulas in Table 7.1. Average (± SD) profitability (e_i/h_i) was calculated by dividing AFDM (mg) by handling time (s) for each individual crab. Average (± SD) digestive quality (e_i/k_i) was calculated by dividing AFDM (mg) by ash (mg) for each individual crab.

	n	**Size** (mm)	**AFDM** (mg)	**Handling time** (s)	**Profitability** (e_i/h_i)	**Ash** (mg)	**Digestive quality** (e_i/k_i)
Macrophthalmus	35	19.1 ± 2.4	145 ± 51	2.8 ± 0.3	50.75 ± 11.94	139 ± 50	1.04 ± 0.00
small *Portunus*	36	42.6 ± 4.0	420 ± 108	82.6 ± 21.2	5.08 ± 0.00	145 ± 38	2.90 ± 0.01
large *Portunus*	35	68.4 ± 5.2	1490 ± 314	297.1 ± 63.9	5.03 ± 0.02	534 ± 117	2.80 ± 0.02

Table 7.3. Crab characteristic of the crabs offered in the cafetaria experiment (2 trials). The number of crabs offered (n) as well as the average crab size (± SD) is shown. Average (± SD) AFDM (mg), handling time (s) and ash (mg) was calculated based on the crab sizes of each individual crab using the formulas in Table 7.1. Average (± SD) profitability (e_i/h_i) was calculated by dividing AFDM (mg) by handling time (s) for each individual crab. Average (± SD) digestive quality (e_i/k_i) was calculated by dividing AFDM (mg) by ash (mg) for each individual crab.

	n	**Size** (mm)	**AFDM** (mg)	**Handling time** (s)	**Profitability** (e_i/h_i)	**Ash** (mg)	**Digestive quality** (e_i/k_i)
Macrophthalmus	34	20.0 ± 2.3	162 ± 47	2.9 ± 0.3	54.79 ± 11.17	156 ± 46	1.04 ± 0.00
small *Portunus*	18	44.3 ± 4.3	470 ± 117	92.5 ± 22.9	5.08 ± 0.00	163 ± 41	2.89 ± 0.01
large *Portunus*	8	73.4 ± 5.5	1803 ± 357	360.4 ± 72.8	5.01 ± 0.02	650 ± 133	2.78 ± 0.02

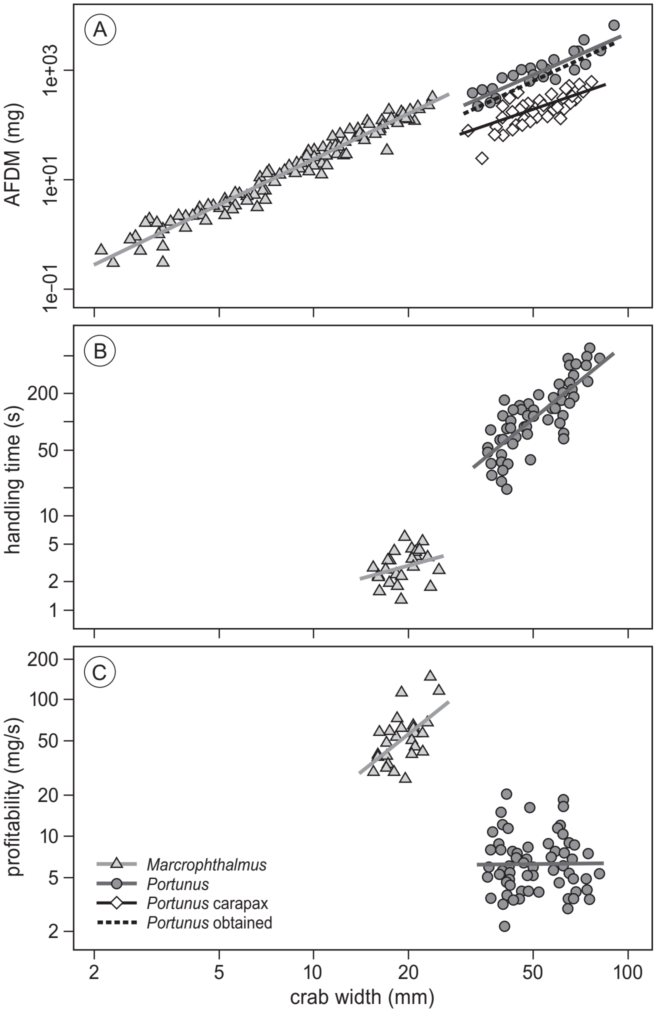

Figure 7.2. (A) AFDM (e_i) plotted versus crab width (mm) (note the logarithmic axes). Grey triangles represent *Macrophthalmus* and dark grey dots represents *Portunus*. Non-filled rhombs represent the amount of AFDM (e_i) that was left in depredated carapaxes of *Portunus*. The amount left in the carapaxes in terms of AFDM (e_i) was subtracted from the AFDM (e_i) of intact *Portunus*, yielding the amount of AFDM (e_i) obtained by crab plovers, superimposed with a black dotted line. For formulas see Table 7.1. (B) Handling time (h_i) plotted versus crab width (mm) (note the logarithmic axes). Handling time does not increase significantly with size for *Macrophthalmus* (superimposed with a light grey line), while for *Portunus* handling time significantly increases with size (superimposed with a dark grey line). For formulas see Table 7.1. (C) Profitability (AFDM (e_i) / handling time (h_i)) plotted versus crab width (mm) (note the logarithmic axes). Grey triangles represent *Macrophthalmus* and dark grey dots represent *Portunus*. Profitability significantly increases with size for *Macrophthalmus* ($y = 0.22x^{1.85}$; superimposed with a light grey line), while for *Portunus* profitability does not significantly increase with size ($y = 5.46x^{0.03}$; superimposed with a dark grey line).

DRM

MAXIMUM INTAKE EXPERIMENT

The slope of the relationship between the log-transformed IR and the different ballast weights was not significantly different from -1 for ash (slope = -0.94, p = 0.737; Fig. 7.3), marginally significantly different from –1 for DM (slope = –0.75, P = 0.053) and significantly different from –1 for AFDM (slope = –0.64, P = 0.004). This means that the variation in numerical intake rate between prey items can best be explained by the ash content of the prey: i.e. if a prey item contains twice as much ash compared to another prey item, the numerical intake rate on the prey item with the high ash content will be twice as low as the numerical intake rate on the prey item with the low ash content. Therefore, ash content (k_i) appears to constrain the long-term intake rate of crab plovers. Using the intercept of the obtained relationship ($^{10}\log(\mathrm{IR}) = -3.80 - 0.94 \times {}^{10}\log(\mathrm{ash})$), we found crab plovers to have a digestive constraint of ($10^{-3.80}$) 0.16 mg of ash per second.

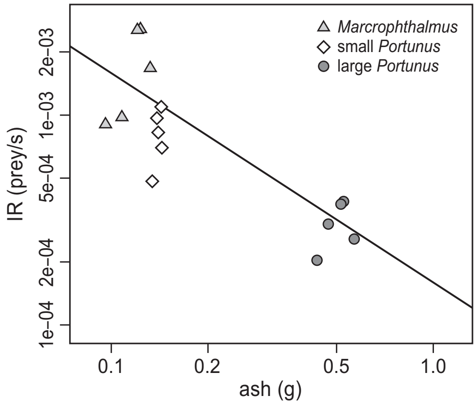

Figure 7.3. Intake rate (prey/s) plotted versus ash content of that prey (g/prey) in the *ad libitum* experiment. The line represents the relation: $^{10}\log(\mathrm{IR}) = -3.80 - {}^{10}\log(\mathrm{ash})$.

THE DIGESTIVE RATE MODEL

While *Macrophthalmus* had a higher profitability than *Portunus*, this was the other way around for digestive quality (slope (e_i/k_i)). We found the digestive constraint (c) to be on the left side of graph (see inset Fig. 7.4), which means that $k_i/h_i > c$ for all prey types. Thus, crab plovers that face a digestive constraint should always choose the better digestible *Portunus*.

Dichotomous prey choice experiment

Macrophthalmus was preferred over large *Portunus* (t-value = 3.480, P = 0.001; Fig. 7.5). Also small *Portunus* was preferred over large *Portunus* (t-value = 3.135, P = 0.003; Fig. 7.5). We found no difference in preference between *Macrophthalmus* and small *Portunus* (t-value = –0.587, P = 0.560; Fig. 7.5).

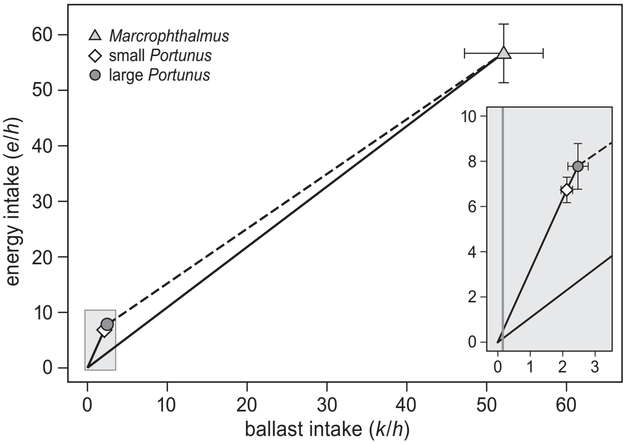

Figure 7.4. The digestive rate model. Energy intake rate (e_i/h_i) (mg/s) was plotted versus ballast (ash) intake rate (k_i/h_i) (mg/s) for both crab species. The grey triangle represents *Macrophthalmus* (n = 28), the non-filled rhomb represents small *Portunus* (n = 23) and the dark grey dot represents large *Portunus* (n = 43). Arrows represent the standard error of the mean. The inset gives a more detailed view of the *Portunus* size classes. The long solid black line represents the slope in terms of energy per ballast (e_i/k_i) for *Macrophthalmus*, whereas the short solid black line on the left represents the slope for *Portunus*. The solid grey line represents the digestive constraint (c) (0.16 mg/s ash). For both prey species $k_i/h_i > c$, which means that the highest long-term energy gain can be obtained by choosing the prey with the highest slope (in this case *Portunus*).

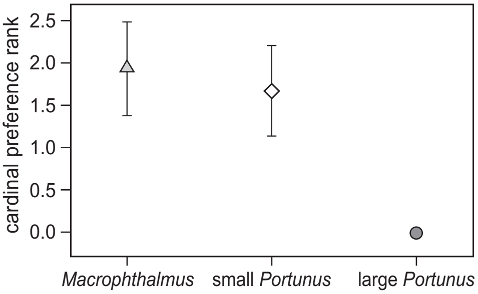

Figure 7.5. Dichotomous prey choice experiment. The cardinal preference rank is plotted against prey type. A higher cardinal preference rank (y-axis) indicates a higher preference over the other prey species. Arrows represent the standard error of the mean. Large *Portunus* is set to zero (no SE) as we compared *Macrophthalmus* and small *Portunus* to large *Portunus*. We found crab plovers to prefer *Macrophthalmus* over large *Portunus* (t-value = 3.480, P = 0.001). We also found crab plovers to prefer small *Portunus* over large *Portunus* (t-value = 3.135, P = 0.003). We found no difference in preference for *Macrophthalmus* versus small *Portunus* (t-value = –0.587, P = 0.560).

Cafeteria experiment

In both feeding trials, there was an initial preference for *Macrophthalmus*, i.e. in both feeding trials the crab plovers started eating a number of *Macrophthalmus*. The preference switched to *Portunus* in the course of the feeding trial after crab plovers had reached their digestive constraint (two out of two; Fig. 7.6). In the two trials that did not succeed we also observed the initial preference to be *Macrophthalmus*.

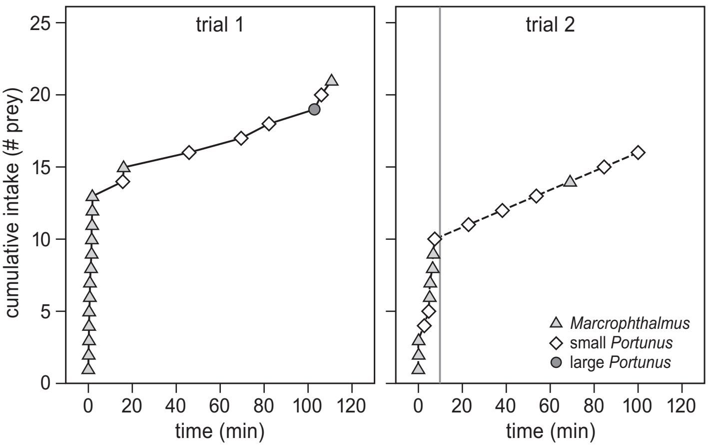

Figure 7.6. Cafeteria experiment. Cumulative intake (# prey) has been plotted on the y-axis and time (min) on the x-axis. Each point represents a crab that has been eaten. For trial 1 we obtained the whole video. For trial 2 the camera failed after some time. The vertical line represents the moment of camera failure. We know the number of crabs that were eaten after camera failure based on the number of crabs that were left after the feeding trials. These crabs have been plotted on the right side of the vertical line. Note that we do not know when these crabs were eaten and in which order. For simplicity, we plotted them in constant intervals to the end of the feeding trial. The birds had an initial preference for *Macrophthalmus*. In both trials the crab plover switched its prey choice from *Macrophthalmus* to small *Portunus* to the end of the feeding trial. The trials were conducted on two different birds.

Discussion

We found crab plovers to switch their prey preference depending on their stomach fullness. When offering crab plovers all prey types in *ad libitum* quantities, crab plovers switched their preference from the highly profitable *Macrophthalmus* to the high-quality *Portunus* after their stomach filled up to full capacity, which we assumed to be indicated by the observed breaks (Fig. 7.6). This suggests that crab plovers integrate their decisions over a relatively short time window. Hence, on an empty stomach they obeyed the CM, while they obeyed the DRM with a full stomach.

In addition, we also found that prey choice depends on the expected future prey items. When crab plovers with an empty stomach were offered two prey items only, they preferred *Macrophthalmus* over large *Portunus* (Fig. 7.5), which is according to the CM. However, when offering them *Macrophthalmus* and small *Portunus*, we did not find a preference for the more profitable *Macrophthalmus* (Fig. 7.5) which is against the predictions of the CM. This result differs from our cafeteria experiment, where we found that crab plovers with an empty stomach always choose *Macrophthalmus*. This discrepancy might be explained by the fact that in our dichotomous choice experiment we only offered two prey items. Crab plovers did not know what was coming after these two preys and might decide to take the one that yields the most energy first in spite of a longer handling time, i.e. the small *Portunus*, to minimize the risk of starvation (Houston & McNamara 1985; Kacelnik & Bateson 1996). This suggests that crab plovers anticipate future energy gains within a certain time-horizon and this might aid in shaping prey choice decisions.

Alternatively, the importance of the nutritional and toxic composition of the prey species might play a role. Stephens and Krebs (1) assumed that the diet of carnivorous animals mainly consists of prey with approximately the right balance of nutrients and that carnivorous animals make dietary decisions solely based on energy content, but recent studies showed some vertebrate and invertebrate predators to make dietary decisions based on macro-nutritional composition, rather than energy content (Simpson & Raubenheimer 2011; Machovsky-Capuska *et al.* 2016b; Machovsky-Capuska *et al.* 2016a). Also the presence of toxins in certain prey types can affect prey choice decisions of foragers (Oudman *et al.* 2014). The observed switch in prey choice could thus potentially also be explained by foragers aiming at achieving nutritional targets, or foragers being limited by toxic constraints. However, given that maximum intake rates in terms of ash were equal for both prey species, we don't expect one of our prey species to be toxic (Oudman *et al.* 2015). Furthermore, studies showing that carnivores balance their diet based on nutrients do not report sudden shifts, as we observed in crab plovers, but rather show a balanced mixed diet (Mayntz *et al.* 2009; Hewson-Hughes *et al.* 2011) or a switch over relatively long time periods, i.e. days or seasons, for instance to prepare for breeding (Molokwu *et al.* 2011). We thus believe that the observed diet switch in crab plovers is primarily driven by energy and shaped by stomach fullness. That crab plovers may encounter digestive problems can be expected as 47% (SD ± 8%) of *Macrophthalmus* consists of inorganic mass.

It is important to note that prey choice in the field may differ from our results, as conditions in the field differ from the conditions in our experiment. Problems in testing optimal prey choice in the field may arise because these models often fail when using mobile prey items, for example due to escape behaviour of prey (Sih & Christensen 2001). In our experiment, both species were readily available (same densities) and catchable (search time = 0), but this is certainly not true in the field where *Macrophthalmus* are known to escape into their burrows when a predator is near, which may be a much more effective escape behaviour than hiding in the sand near the surface like *Portunus* do. This may negatively affect searching efficiency on *Macrophthalmus*, which in turn potentially affects prey choice, especially when crab densities are low and/or when searching for *Macrophthalmus* and searching for *Portunus* are mutually exclusive. Furthermore, prey choice could differ in case crab plovers in the field are not energy maximisers, as assumed here, but instead are time minimisers (Bergman *et al.* 2001). I.e. if crab plovers aim to minimise time foraging (searching and handling) and take digestion for granted, we could expect that crab plovers should again switch to the more profitable prey, i.e. *Macrophthalmus*. In our experiment, the birds had lost weight during the pre-experimental period which might have turned them into energy maximisers in order to recover. Finally, in the field the optimal prey choice might also be affected by the interaction with the social environment, with other crab plovers foraging on crabs (Vahl *et al.* 2005). This can result in crab plovers preferring prey items with short handling times, i.e. *Macrophthalmus*, in order to minimize the chance for kleptoparasitism. It could also influence the searching time on *Macrophthalmus*, as the presence of a lot of crab plovers might make them escape into their burrows and as a result makes *Macrophthalmus* a less attractive prey. Detailed observations should give insight in which strategy is adopted by crab plovers in the field.

In conclusion, we show that under captive conditions, when crab plovers are in handling constrained circumstances, the CM predicts their prey choice well when offering *ad libitum* prey (initial phase in Fig. 7.6). However, when offering only two prey items, the CM only partially predicts prey choice, as time-horizon and anticipation effects come into play. When crab plovers become digestively constrained, the prey choice decisions are in line with the DRM (end phase in Fig. 7.6). Our results indicate that prey choice is not necessarily dependent on the CM (handling constraint) or the DRM (digestive constraint) alone, but is context dependent in terms of stomach fullness. This follows the predictions of Whelan and Brown (20) stating that food choice is dynamic and depends on an animal's digestive state. Based on our results it could be expected that stomach fullness is an important parameter for understanding prey choice. This has been shown in several experiments when offering differently sized prey items of the same species (Rechten *et al.* 1983; Gill & Hart 1998). Yet we could only find one study with experimental data (Molokwu *et al.* 2011) to substantiate, and one with field data (Verkuil *et al.* 2006) to suggest a switch of prey species based on stomach fullness as we found here. Thus, the generalization of how stomach content effects prey choice needs to be further studied.

That the stomach fullness affects prey choice might have serious implications when conducting prey choice experiments in captivity. Several laboratory studies have tested optimal diet theory on foragers having an empty stomach (Krebs *et al.* 1977; Bence & Murdoch 1986; van Gils *et al.* 2005b) or do not mention the context (i.e. stomach fullness) under which prey choice was tested (Labinger *et al.* 1991; Ball 1994). Optimal diet theory has sometimes failed (Sih & Christensen 2001), which, as we argue, could result from not taking into account the stomach fullness of a forager. Thus, precaution in terms of (changes in) stomach fullness should be taken when conducting lab experiments on prey choice decisions.

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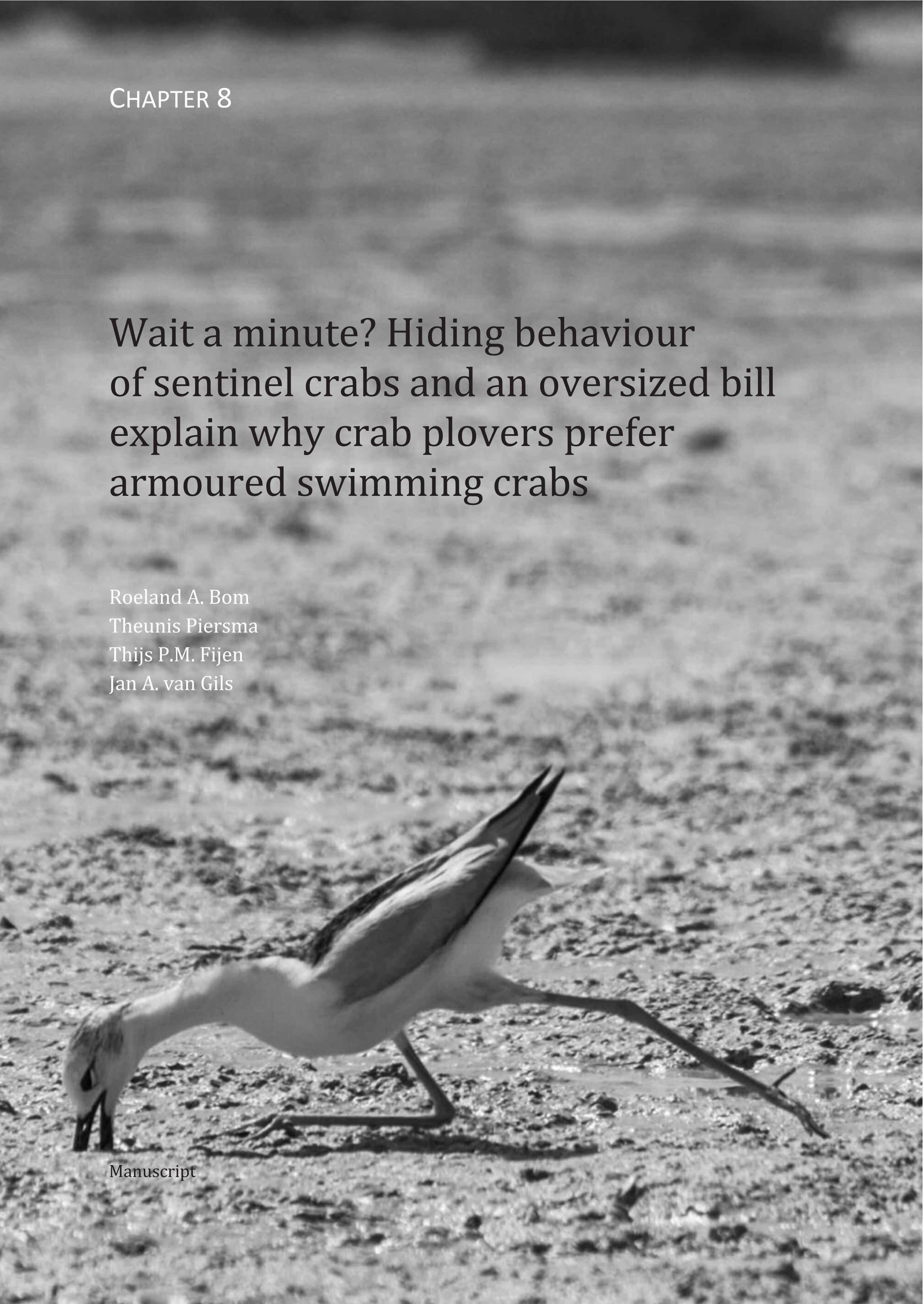

CHAPTER 8

Wait a minute? Hiding behaviour of sentinel crabs and an oversized bill explain why crab plovers prefer armoured swimming crabs

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Manuscript

Abstract

Along the shores of in the Indo-West Pacific region, a suite of shorebirds forage on burrowing crabs (superfamily Ocypodoidea) by waiting above the burrows for an occupant to re-emerge. The Indo-West Pacific is also the marine area with an intensely competitive fauna, where predator and prey species have evolved extravagant defence and attack mechanisms. A possible example is embodied by the endemic crab plover *Dromas ardeola*, a unique shorebird that eats burrow-hiding sentinel crabs as well as swimming crabs (family Portunus). In fact they were reported to only forage on swimming crabs, crabs with 'vast and powerful claws', and to ignore the much more abundant burrowing crabs. During four non-breeding seasons (2012–2015) we studied the trade-off made by crab plovers between the handling of swimming crabs and the waiting for sentinel crabs on the intertidal mudflats of Barr Al Hikman in the Sultanate of Oman. We demonstrate that crab plovers strongly preferred swimming crabs, and that diet composition depended exclusively on the densities of swimming crabs, i.e., crab plovers stopped waiting for sentinel crabs above threshold densities of swimming crabs even if sentinel crabs were abundant themselves. By modelling waiting time as part of the handling time (i.e. making it independent from prey densities) in a two-prey functional response model we could explain diet composition from an energy-maximization perspective. By means of state-space plots we conclude that the preference for swimming crabs emerges from a combined effect of the efficient handling of swimming crabs (by the crab plover) and hiding (by sentinel crabs). Undoubtedly, the massive bill enables crab plovers to make the handling of swimming crabs so profitable. We speculate that the bill of the crab plover is an example of an attack mechanisms that evolved in the escalated environment of the Indo-Pacific.

Introduction

The Indo-West Pacific is a warm, large, productive and relatively stable environment, under which conditions predator and prey species had the chance to evolve relatively extravagant defence and attack mechanisms by means of co-evolution and escalation (Vermeij 2004). Currently the Indo-West Pacific is the key example of a marine area with an intensely competitive fauna (Vermeij & Dietl 2006). For instance, the Indo-West Pacific harbours molluscs with the hardest to crush shells and crabs with the strongest claws and shell-crushing abilities (Vermeij 1977b; Chapter 2). Along the shores of in the Indo-West Pacific region, most shorebirds forage on burrowing crabs (superfamily Ocypodoidea) by waiting above the burrows for an occupant to re-emerge. The endemic crab plover *Dromas ardeola* is an example of a species not only eating burrowing crabs, but also the armoured swimming crabs (family *Portunus*). In fact crab plovers were previously reported to only forage on swimming crabs, crabs with 'vast and powerful claws', and to ignore the much more abundant burrowing crabs (Swennen *et al.* 1987).

Many predators foraging on burrowing species play a 'battle of waits' with their prey (Hugie 2003). This happens when a predators waits above the burrow for the occupant to re-emerge. This behaviour is found in (shore)birds foraging on burrowing crabs and fish (Piersma 1986; Zwarts 1990; Hugie 2004; Katz *et al.* 2010), bullhead fish *Cottus gobio* foraging on caddis larvae (Johansson & Englund 1995) and various predators foraging on alpine lizards *Lacerta monticola* (Martín & López 2001). The costs and benefits of foraging on burrow-hiding prey have been analysed for single predator-prey interactions from the perspective of game theory (Hugie 2003, 2004) and optimal foraging (Katz *et al.* 2010). What has not been studied so far, is a general strategy to forage on burrow-hiding species in multiple prey situations, where additional trade-offs may become detectable.

Optimal foraging models may help us to understand how foragers trade of foraging on burrow-hiding prey against foraging on prey that does not hide. These models are built on the premise that foragers maximize energy their intake rate. The classic diet model makes predictions about prey selection on the basis of the energy gain per handling time (profitability) (Stephens & Krebs 1986). One of the most rigorous predictions of this model is that sometimes certain prey items should be dropped from the menu. An important tool to quantify this prediction is the functional response, which relates the intake rate of a forager to the available prey (Holling 1959). In most functional response models, foragers are assumed to spend their time either searching or handling (the time required to process a prey once it has been captured) (Holling 1959; Jeschke *et al.* 2002). This assumes that all encountered prey are captured without time delays. However this may not be the case in foragers that play a 'battle of waits', i.e. that spend time waiting between prey detection and prey capture. If there is time between prey detection and prey capture, an 'identification' period should be added within the models as part of the handling time (Holling 1959) and for instance applied by (Zwarts & Esselink 1989; Fryxell *et al.* 2007), under the assumption that this time is independent from prey densities.

On the intertidal mudflats of Barr Al Hikman in the Sultanate of Oman a suite of shorebirds (e.g. Terek sanpipers *Xenus cinereus*, Eurasian curlews *Numenius arquata*, greater sand plovers *Charadrius leschenaultia*, grey plovers *Pluvialis squatarola* crab plovers *Dromas ardeola* (Fig.

8.1A, Chapter 2 and unpublished data) forage on burrowing species, mainly sentinel crabs of the genus *Macrophthalmus* and sand-bubbler crabs of the genus *Scopimera*. Sentinel crabs hide for considerable time when they see a predator approaching (Fig. 8.1C), and predators foraging these crabs often play the 'battle of waits'. Other crabs are also abundant in this coastal ecosystem, mainly swimming crabs of the genus *Portunus* (Chapter 3). However, there is only one species of shorebird that eat burrowing crabs as well as the armoured swimming crabs, and this is the crab plover; a large shorebird with an exceptionally massive bill (Fig. 8.1B). We studied the trade-off by between foraging on hiding sentinel crabs and fighty swimming crabs during 2012–2015. We found that crab plover prefer swimming crabs and consider this result in light of the escalated environment of the Indo-West Pacific.

Methods

Study area & crab plovers

Our study site is Barr Al Hikman in the Sultanate of Oman (20.6° N, 58.4° E). Barr Al Hikman harbours extensive intertidal mudflats that are flooded twice per lunar day (Chapter 10). The area is an important wintering area for many shorebirds (Chapter 5), Among them is the crab plover; a large-sized shorebird that winters along the shores of the Indian Ocean (Chapter 11). The present study relies on data collected in 2012–2015 in a study area of approximately 2 by 3 km (Chapter 3). Crab plovers forage within this area mainly on three crab species: burrow-hiding sentinel crabs of the genus *Macrophthalmus*, and the swimming crabs *Thalamita poissonii* and *Portunus segnis* (hereafter: *Thalamita* and *Portunus* and collectively referred to as 'swimming crabs').

Most sentinel crabs are caught using a stand-and-wait foraging technique (Fig. 8.1B & 8.2). The stand-and-wait mode of crab plovers can be distinct, with crab plovers waiting up to 10 minutes above a burrow. More often crab plovers adopt a subtle waiting technique by taking short pauses while walking at a low pace (here defined as less than 0.5 steps per second) through a patch with sentinel crabs (a waiting behaviour also described by Zwarts 1985; Hugie 2004). A small amount of sentinels crabs are caught using a walk-and-attack (defined here as more than 0.5 and less than 1 step per second) or run-and-attack (more than one step per second) foraging technique. The swimming crabs are mostly caught using a tactile search technique (Fig. 8.1). In addition, swimming crabs are also caught using a walk-and-attack foraging technique or a stand-and-wait mode. We refer to this latter technique as passive search (Fig. 8.1). Large swimming crabs (*Portunus* with a carapax width larger than approximately 30 mm) are opened prior to consumption. All other crabs are swallowed whole (Chapter 7). Sentinel crabs and swimming crabs have overlapping ranges (Chapter 3) and we cannot exclude that crab plovers can search for both species at the same time (see discussion).

Crab plover diet

We studied the diet of crab plovers during four subsequent non-breeding periods: November-December 2012, December 2013, November-December 2014 and November 2015. Within these periods we filmed foraging crab plovers during daytime low tide using a camera (Canon

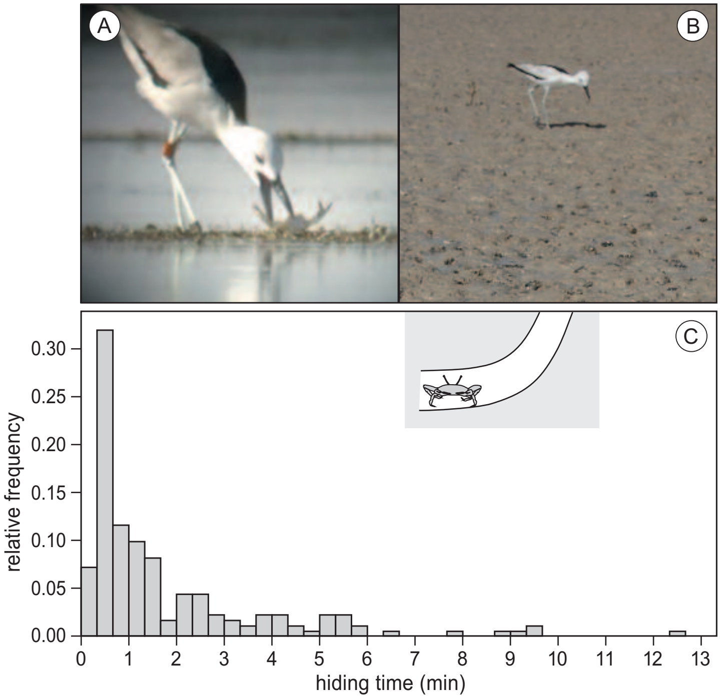


Figure 8.1. (A) Video still showing a colour ringed crab plover handling a swimming crab (B) A crab plover waiting above burrows for hiding crabs to re-emerge. Note the large number of foraging burrowing crabs in the foreground. (C) The distribution of hiding times in burrowing crabs observed after a simulated predator approach or attack (Appendix A8.1).

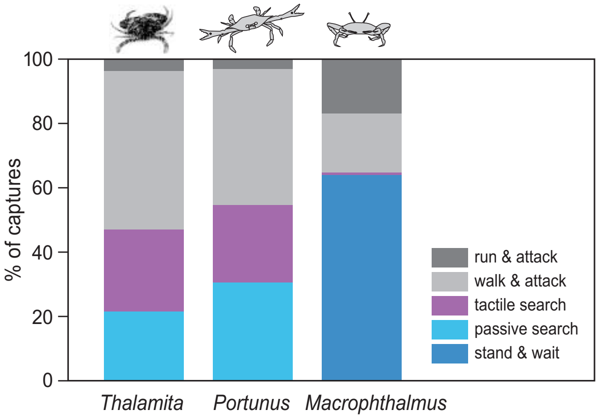


Figure 8.2. Observed feeding modes of crab plovers just prior to successful prey capture. Data is based on prey captures observed on video and includes 192 captures on *Thalamita*, 151 captures on *Portunus* and 142 captures on *Macropthalmus*. Bar plots show percentage of prey captures averaged per individual crab plover.

VIXIA HG21) mounted on a 20-60× telescope (Swarovski ATS 80HD). Many crab plovers carried individually-unique combinations of colour rings (Chapter 6), and only colour-ringed birds were filmed. Birds were filmed for as long as possible. As crab plover tend to stay close to the waterline, we could film individual birds up to 4 hours with the higher low tides, whereas during the lower low tides birds often flew off within 15 minutes. For the interest of this study, we only included footage collected within the 4 hours around low tide, which is roughly the period in which sentinel crabs emerge from their burrow (Evans *et al.* 2010). The total duration of the footage used was 65 hours in 2012 (28 unique birds), 12 hours in 2013 (20 birds), 12 hours in 2014 (19 birds) and 4 hours in 2016 (12 birds).

After each field visit, the behaviour of each filmed bird was analysed with OBSERVER XT software (v. 5.0, Noldus Information Technology). The recorded behaviour included: standing, stepping, tactile searching, prey attack, handling of prey, flying, preening, interaction with other birds and provisioning of young. Handling was defined as the time between prey capture and prey ingestion minus the time spend resting in between. Whenever possible, we also determined the prey species. Small species (probably mostly small shrimp-like crustaceans) often remained unidentified, whereas larger prey could always be identified up to the group level (crabs, fish, shrimp), and in the case of crabs mostly at the level of species (*Thalamita* and *Portunus*) or genus (*Macrophthalmus*). The percentage of prey items that remained unidentified was 20% in 2012, 8% in 2013, 11% in 2014 and 3% in 2015. The percentage of prey items that could be identified as crabs but not up to the species level was 6% in 2012, 3% in 2013, 0% in 2014 and 0% in 2015.

For each captured prey item we estimated prey size (carapax width) relative to crab plover bill size, in classes of 10%. When we filmed colour-ringed birds with known bill size, the estimated percentage could be multiplied by bill size to arrive at prey size in mm. For some individuals ringed in 2008, bill size was not available for which we used the mean bill size of crab plovers caught at Barr Al Hikman (58.8 mm) instead. To validate our prey size estimation, we compared the (positive) relation between estimated crab size and handling time with the (positive) relation between known crab size and handling time measured on captive crab plovers at Barr Al Hikman (on sentinel crabs and large, i.e. > 30 mm, *Portunus* only; Chapter 7). Linear mixed-effect models with individual (colour-ringed) bird as a random effect and location (lab or field) as fixed effect showed no significant difference in the relation between handling and crabs size of sentinel crabs (df = 17, t-value = –0.566, P = 0.58) and *Portunus* > 30 mm (df = 11, t-value = –0.872, P = 0.40). This suggests that our size estimation of crabs captured in the field does not differ substantially from the true crab size.

To express the diet composition on the basis of energy content, we estimated the energy content of each captured prey. We took ash-free dry mass (AFDM) as a measures of energy content (Zwarts & Wanink 1993). AFDM estimations of prey capture were based on non-linear regression models (power function: $y = ax^b$) relating AFDM to crab size (width), using data presented in Chapter 3 (Table 8.1 and Appendix Fig. A8.2). To calculate the AFDM for opened *Portunus* we used the relation between AFDM and crab width reported in Chapter 7 (Table 8.1 and Appendix Fig. A8.2). To calculate AFDM for shrimp we used the regression of shrimps in Barr Al Hikman derived in Chapter 2, and for fish a regression of gobies *Pomatoschistus* $y = (3.3e{-}3x^{3.4})*0.17$ (unpublished data). We first calculated for each individual bird per winter the diet composition as the percentages of different prey in the diet in terms of AFDM, and then averaged these values per winter to calculate the mean diet composition of crab plovers per winter. Non-linear relationships to calculate AFDM are given in Table 8.2.

All statistical calculations were carried out with the R software (R Development Core Team 2013). The package *gnls* was used for non-linear regression models.

Crab availability

In the analysis below we make extensively use of density estimates of *Macrophthalmus* and swimming crabs in the area. These density estimates are based on sediment samples taken on a spatial grid during the same period as we made diet observations on the crab plovers (Table 8.1). All present observations on crab plovers were taken within 1 km distance of this grid. Extensive sampling in 2012 covering the entire zone in which observations were made showed that there was no substantial difference in crab densities within the sampled grid and the area to which the observations extended. For further details on the sample procedure we refer to Chapter 3. We assume that all the sampled crabs are available to crab plovers. Some *Portunus* move in and out the intertidal area with the tidal flow, but visual assessments of these crabs suggest that their numbers are negligible compared to the number of swimming crabs that remain on the mudflats (Chapter 3).

Table 8.1. Numerical and biomass densities of the different crab species present in the study area across the four study years. Mean values are derived from Chapter 3. The last column gives information on the crab size of the sampled crabs (all years lumped).

	numerical density (#/m^2)				**biomass density** (g/m^2)				**width mean carapace** (range) (mm)
	2012	2013	2014	2015	2012	2013	2014	2015	
Thalamita	6.65	4.03	0.93	32.28	0.18	0.09	0.02	0.64	7.5 (2.5 – 25.2)
Portunus	0.70	0.19	0.00	0.19	0.07	0.01	0.00	0.11	22.6 (13.1 – 44.7)
Macrophthalmus	7.70	17.84	8.40	20.42	0.38	0.89	0.32	0.58	11.8 (1.6 – 25.1)

Table 8.2. Non-linear relationship relating crab size (mm) to AFDM (mg), handling time (s) and profitability (e/h and e/[h+w]) (mg/s) for *Macrophthalmus*, *Thalamita* and *Portunus* (swallowed whole and opened). Not all non-linear regression models were used for the presented study, but are shown for completeness. Mean values are given for non-significant regression models. See Appendix Fig. A8.2 for plotted values and statistics.

	Macrophthalmus	*Thalamita*	*Portunus* whole	*Portunus* open
AFDM ~ size	$y = 8.67e\text{-}2\ x^{2.50}$	$y = 3.49e\text{-}2\ x^{2.96}$	$y = 1.83e\text{-}1\ x^{2.24}$	$y = 1.2e\text{-}2\ x^{2.79*}$
handling ~ size	$y = 0.44\ x^{0.73}$	$y = 0.18\ x^{1.45}$	$y = 3.26\ x^{0.80}$	$y = 0.71\ x^{1.40*}$
profitability (e/h) ~ size	$y = 3.05e\text{-}1\ x^{1.73}$	$y = 7.28e\text{-}2\ x^{2.16}$	$y = 8.86e\text{-}1\ x^{1.05}$	$y = 9.27$
profitability (e/(h+w)) ~ size	$y = 7.11e\text{-}4\ x^{2.48}$			

Two-prey functional response model

To quantitatively predict and explain the diet choice in crab plovers, we developed a two-prey functional response model (Holling 1959) in which we modelled the energy intake rate on *Macrophthalmus* and swimming crabs. In this two-prey functional response model we modelled waiting time as part of the handling time. Actually, the assumption that waiting time is independent from densities, and thus should be modelled as part of the handling time and not of the search time, might be too simplistic. For instance, waiting time may vary through space and time if crabs vary their hiding time in relation to, for instance, predation pressure or conspecifics (Hugie 2004; Hedrick & Kortet 2006; Cooper & Frederick 2007), or if crab plovers at high crab densities can scan more burrows at the same time than at low densities. Therefore we also modelled waiting as part of the search phase and checked if this could better explain the observed diet (Appendix Fig. A8.3).

In case waiting time is modelled as part of the handling phase, Holling's functional response model (Holling 1959) on energy intake rate Y on two prey items labelled *s* (swimming crab) and *m* (*Macrophthalmus*), can be written as:

$$Y = \frac{a_s X_s e_s + a_m X_m e_m}{1 + a_s X_s h_s + a_m X_m (h_m + w_m)} \quad (1)$$

where a is the area of discovery or searching efficiency (in cm^2/s), X the available numerical prey density, e the average energy gained per prey (in mg AFDM), h the average handling time per prey (in seconds) and w_m the average waiting time per ingested prey (also in seconds). Under some circumstances, Y can be maximized by not accepting every prey that is encountered.

The classic diet model (Stephens & Krebs 1986) ranks prey on the basis of profitability (e/h). Crab plovers are predicted to exclusively select one prey and neglect the other prey when the energy intake rate on either of the crabs alone exceeds the profitability of the other prey type, i.e, in case of swimming crabs when:

$$\frac{a_s X_s e_s}{1 + a_s X_s h_s} > \frac{e_m}{h_m + w_m} \quad (2)$$

and in case of *Macrophthalmus* when:

$$\frac{a_m X_m e_m}{1 + a_m X_m (h_m + w_m)} > \frac{e_s}{h_s} \quad (3)$$

Note that in (2) we extended the concept of profitability by adding the waiting time as part of the handling time. For the ease of the story we will refer to this as the profitability. All models assume that searching, handling and waiting are mutually exclusive, and that encounters with crabs are random.

If the intake rate on one crab alone does not exceed the profitability of the other crab, crab plovers should accept both prey types in its diet. In case of a mixed diet, the relative proportion of each crab in the diet can be calculated from the expression relating energy intake rate on either of the crabs alone when foraging on both crabs at the same time. The energy intake rate on swimming crabs ($IR_{swim.both}$ in mg AFDM/s) while foraging on both crabs at the same time is given by:

$$IR_{swim.both} = \frac{a_s\, X_s\, e_s}{1 + a_s\, X_s\, h_s + a_m\, X_m\, (h_m + w_m)} \tag{4}$$

Likewise, the energy intake rate on *Macrophthalmus* $IR_{mac.both}$ in mg AFDM/s) when foraging on both crabs at the same time equals:

$$IR_{mac.both} = \frac{a_m\, X_m\, e_s}{1 + a_s\, X_s\, h_s + a_m\, X_m\, (h_m + w_m)} \tag{5}$$

The proportion of swimming crabs in the diet equals $IR_{swim.both}/IR_{both}$ and the proportion of *Macrophthalmus* in the diet equals $IR_{mac.both}/IR_{both}$.

Parameterization

Handling time: h_s and h_m were estimated by taking the mean of all handling times recorded for swimming crabs and *Macrophthalmus* respectively.

Energy content: e_s and e_m was calculated as the mean AFDM (in mg) of respectively swimming crabs and *Macrophthalmus* sampled in the area (Chapter 3).

Waiting time: The average waiting time per ingested *Macrophthalmus* was estimated by calculating the time waiting between two consecutive prey captures of *Macrophthalmus*. Thus, waiting was calculated as the total time spend waiting per ingested prey item, to acknowledge that time is wasted on not-consumed prey (Meire & Ervynck 1986). Crab plovers were assumed to be waiting when standing motionless (and not resting) or when they were walking at a pace of less than 0.5 steps per seconds. In total, we identified 84 successive captures of *Macrophthalmus* in 11 individuals. We averaged the average waiting time per ingested *Macrophthalmus* for each individual crab plover. Ultimate waiting time *h* was calculated as the average waiting time per ingested *Macrophthalmus* across all individuals.

Searching efficiency: a_s and a_m can be calculated from the average search time between two successive prey with known prey densities, because (5) and (6) can be rewritten as (Holling 1959):

$$a_s = \frac{1}{T_s X_s} \tag{6}$$

and

$$a_m = \frac{1}{T_m X_m} \tag{7}$$

where T is search time in seconds between two prey encounters. Ideally, T_s and T_m should be estimated under controlled conditions (Stephens & Krebs 1986; Duijns *et al.* 2015). However, as this is practically impossible with crab plovers, we estimated both parameters based on successive prey captures of free-ranging crab plovers. Successive prey captures also included instances in which searching was 'interrupted' by the capture of prey items other than crabs (shrimp and fish). As the estimated searching efficiency will be lower than the actual search efficiency in case birds are at their digestive constraint (Duijns *et al.* 2015) we only included successive prey captures of actively foraging crab plovers (i.e. all behaviour other than waiting, resting, preening, attack, handling, flying, interaction with other birds and provisioning).

In total, we identified 160 successive swimming crab captures in 27 individual crab plovers and 84 successive M*acrophthalmus* captures in 11 individual crab plovers. We calculated a for each successive prey capture, estimating X as the year dependent average numerical crab density. Next, to correct for individual variation in searching efficiency, we calculated the mean search time per individual bird. We averaged the average searching efficiency for each individual crab plover. Ultimate searching efficiency was calculated as the searching efficiency across all individuals.

Parameter values used in the two-prey functional response model are given in Table 8.3. Details of relationships that were used to estimate profitability are given in Table 8.1, Table 8.3 and Appendix Fig. A8.2. Large *Portunus* opened prior to consumption were left out of all analysis as they were not present in the grid samples in the years they were observed to be consumed.

Table 8.3. Empirical values of the two-prey functional response model parameters. Values show means ± standard deviations.

	a (cm^2/s)	***e*** (mg afdm)	***h*** (s)	***w*** (s)
swimming crabs	51 ± 98	44 ± 51	25.4 ± 50.8	
Macrophthalmus	296 ± 21	48 ± 45	3.5 ± 2.6	125 ± 32

Data analysis

PROFITABILITY

For conception purposes we first plotted the profitability for each species based on the crabs available in the field (Chapter 3) and of the crabs taken by crab plovers. To this end we fitted non-linear regression models (power function: $y = ax^b$) relating profitability (expressed as the conventional profitability e/h, and as $e/[h + w]$) to crab size (Table 8.2). A generalized linear model (GLM) was used to test if the available crabs differed in (log) profitability. A similar model was fitted on the crabs taken by crab plovers, with individual as a random effect (GLMM). A Tukey HSD test was used for post-hoc comparison. GLMMs were fitted using the *lmer* function in the r package *nlme*. Inspection of residual plots did not reveal deviations from normality.

DIET COMPOSITION

We used the two-prey functional response model to predict diet composition as a function of swimming crab densities X_S by fixing *Macrophthalmus* densities at 14 crabs per m^2, which equals the average *Macrophthalmus* densities in the area (Table 8.1). Likewise, diet composition as a function of *Macrophthalmus* densities X_m was predicted by fixing swimming crab densities at 11 crabs m^2, which equals the average density estimates of swimming crabs in the area (Table 8.1). We compared the predicted diet with the observed diet.

PREY PREFERENCE

We further used the two-prey functional response model to calculate prey preference using Ivlev's electivity index (Jacobs 1974). For a given prey species, the index compares its relative fraction in the diet (F_{diet}) with its relative fraction available (F_{avb}) in the following manner:

$$I = \frac{F_{diet} - F_{avb}}{F_{diet} + F_{avb}} \tag{8}$$

Hence, I ranges from −1 to 1, with $I > 0$ indicating preference and $I < 0$ indicating aversion. The available food supply (F_{avb}) was obtained from sediment samples taken on a spatial grid during the crab plover study period (Table 8.1). We compared the predicted prey preference with the observed prey preference.

Results

Crab plover diet

The diet of crab plovers at Barr Al Hikman consisted mainly of *Thalamita* (n = 192), *Portunus* (n = 151, Fig. 8.3) and *Macrophthalmus* (total captures n = 142). Swimming crabs were included every winter, whereas *Macrophthalmus* was included in the diet primarily in the winters of 2013 and 2014 (Fig. 8.3). Shrimp (n = 51) and fish (n = 23) contributed little to the diet.

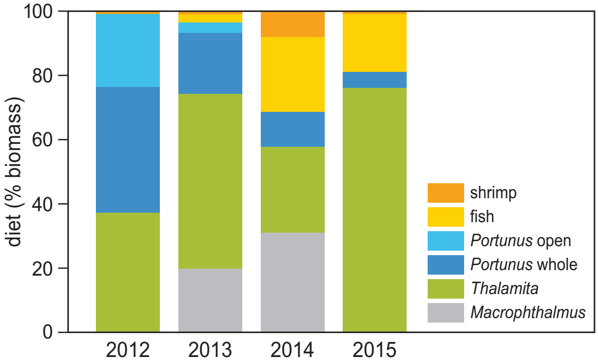


Figure 8.3. Diet of crab plovers on the basis of biomass across four subsequent winters. The data show average diet composition pooled for all individuals.

Two-prey functional response model

PROFITABILITY

Estimated profitability of the crabs available in the field was highest on *Macrophthalmus* (*e*/*h*) and *Portunus*, with *Thalamita* and *Macrophthalmus* (*e*/[*w* + *h*]) being successively less energetically profitable (Fig. 8.4A). These differences were significant (Fig. 8.4A, df = 1269 $t_{24.798}$ $P < 0.001$). Post-hoc test showed no difference between *Macrophthalmus* (*e*/*h*) and *Portunus* ($Z_{1.410}$ $P = 0.46$), whereas the estimated profitability on all other available crab species differed significantly from each other (all $P < 0.001$). Estimated profitability of the crabs taken by the crab plover were largely in line with the crabs available in the field. *Macrophthalmus* (*e*/*h*) and *Thalamita* had the highest profitability, with *Portunus* and *Macrophthalmus* (*e*/[*w* + *h*]) being successively less energetically profitable (Fig. 8.4B). Also the expected profitability on the crabs taken by crab plovers differed significantly between crab species (Fig. 8.4B, df = 549 $t_{28.565}$ $P < 0.001$). Post-hoc test showed no difference between *Macrophthalmus* (*e*/*h*) and *Thalamita* ($Z_{-1.095}$ $P = 0.69$) and *Portunus* and *Thalamita* ($Z_{-2.376}$ $P = 0.08$) whereas the profitability on all other crabs species differed significantly from each other (all $P < 0.001$).

PREDICTED VS OBSERVED DIET COMPOSITION

At average densities of *Macrophthalmus*, energy intake is maximized by adopting a mixed diet when swimming crab densities are below 3 crabs m^{-2} (Fig. 8.5A). Above this threshold, energy intake rate is maximized by foraging exclusively on swimming crabs. Variation in densities of *Macrophthalmus* has little effect on the expected diet composition as the searching efficiency on *Macrophthalmus* was found to be high (Fig. 8.5B, Table 8.3). At average densities of swimming crabs, energy intake is maximized by exclusively adopting a diet of swimming crabs (not plotted)

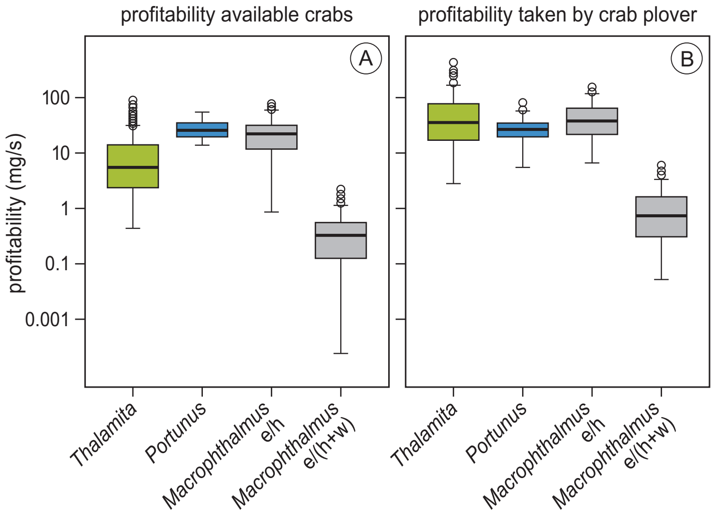


Figure 8.4. Expected profitability of (A) available crabs in the field and (B) those taken by crab plovers. Profitability of *Macrophthalmus* is calculated as the conventional *e*/*h* and as *e*/(*h* + *w*). Figures show data lumped across all four years of study.

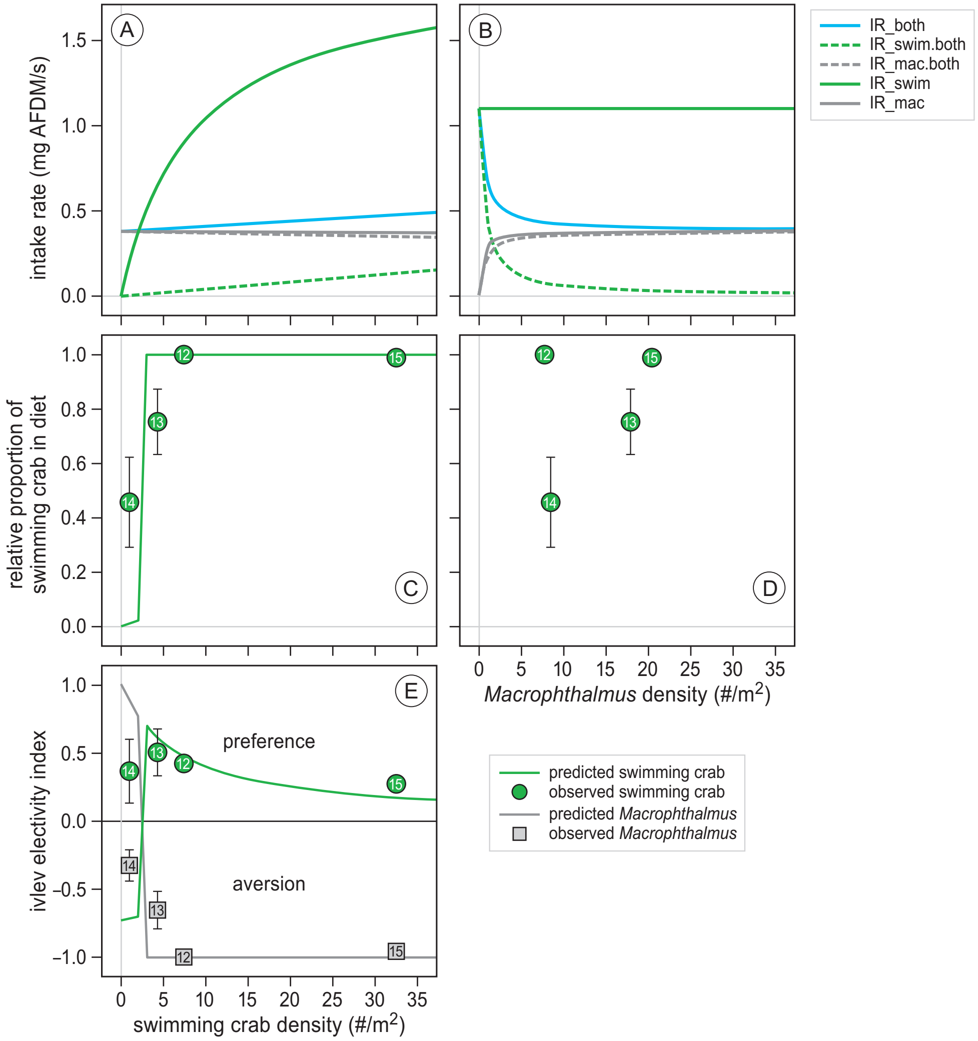


Figure 8.5. (A) Predicted energy intake rate of crab plovers in relation to swimming crab densities under fixed densities of *Macrophthalmus*. Shown are the predicted total energy intake rate when always accepting both crabs (blue line), which is the sum of the predicted energy intake rate on *Macrophthalmus* (dotted grey line) and swimming crabs (dotted green line). The energy intake rate when accepting either of the crabs is also given for *Macrophthalmus* (grey line) and swimming crabs (green line) are shown. (B) Shows similar curves for the energy intake rate in relation to *Macrophthalmus* densities under fixed densities of swimming crabs. (C) The observed proportion of swimming crabs and *Macrophthalmus* in the diet plotted against observed swimming crab densities. The line shows the predicted relative proportion of swimming crabs based on the functional response model shown in (A). (D) Observed proportion of swimming crabs and *Macrophthalmus* in the diet plotted against observed *Macrophthalmus* densities. Values in (C) and (D) show yearly averages calculated as the mean of individual averages. (E) Observed prey preference (Ivlev electivity index) as a function of swimming densities. Values larger than 0 indicate a preference. Lines show the predicted preference based on the predicted intake rate calculated in (A). In all graphs error bars denote standard errors and express among individual variability.

When swimming crab densities were above 7 crabs m^{-2}, crab plover diets were found to exclusively contain swimming crabs (relative to *Macrophthalmus*) (Fig. 8.5C). In the two years that swimming crab densities were below 7 crabs m^{-2}, the proportion of swimming crabs in the diet of crab plovers decreased with decreasing swimming crab densities (Fig. 8.5C). In the two years that *Macrophthalmus* was included, densities of *Macrophthalmus* were relatively low in one year and relatively high in the other year (Fig. 8.5D).

PREDICTED VS OBSERVED PREFERENCE

Based on the predictions and observations detailed above we concluded that the diet of crab plovers is closely related to the densities of swimming crabs and not to the densities of *Macrophthalmus*. Accordingly we calculated the prey preference in relation to densities of swimming crabs only. Based on the functional response models we predicted that crab plovers should almost always positively select swimming crabs under the range of observed swimming crab densities. Only when swimming crab densities are below densities of 3 crabs per m^2 crab plovers should negatively select swimming crabs (Fig. 8.5E).The observed Ivlev values closely matched the predicted values, except that swimming crabs were still positively selected under swimming crab densities below 3 crabs per m^2 (Fig. 8.5E).

Discussion

In all years of study crab plovers preferred swimming crabs, including the armoured and fighty species, while the often more numerous and powerless sentinel crabs (*Macrophthalmus*) were mostly ignored. Indeed, the diet of crab plovers appeared to be closely correlated to the abundance of swimming crabs and not to the abundance of sentinel crabs. We could explain the preference for swimming crabs from an optimality perspective, as crab plovers in most years maximized their energy intake rate by exclusively foraging on swimming crabs. This is because the energy gained per handling time of swimming crabs exceeds the energy gain per handling *and* waiting time on sentinel crabs. The observed preference for swimming crabs thus emerges from efficient handling of swimming crabs by the crab plover and long enough hiding by sentinel crabs.

Based on the two-prey functional response model we predicted that crab plovers should drop sentinel crabs from the diet at relatively low swimming crab densities. This was exactly what we observed (Fig. 8.6C & 8.6D). It is important to note that we could only explain the exclusion of sentinel crabs from the menu if waiting was modelled as part of the handling phase, and not if it was modelled as part of the searching phase (Appendix Fig. A8.3) – as is sometimes done for foragers that spend time between prey detection and capture (McPhee *et al.* 2011). The congruence suggests that our assumption that waiting time is independent of prey densities is justified.

Ideally, the importance of handling of swimming crabs by crab plovers and hiding in burrowing crabs is substantiated with experiments in which both handling and hiding are manipulated. Indeed, an experiment with captive crab plovers showed that the hiding behaviour of burrowing crab is essential to explain the preference for swimming crabs as captive

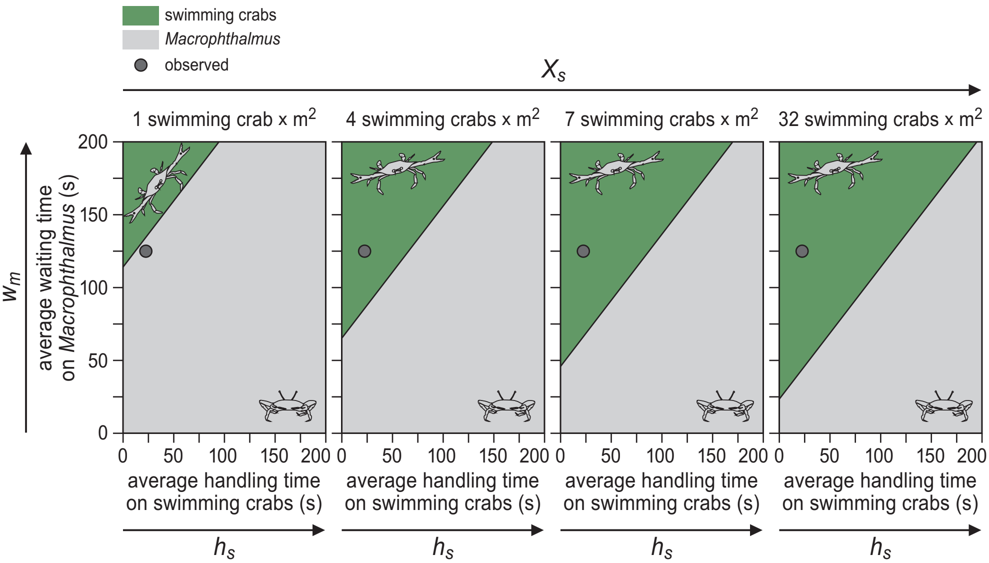


Figure 8.6. State space plots showing the predicted diet of crab plovers under a range of waiting times on Macrophthalmus and handling times on swimming crabs. Graphs are based on the assumption that search time on Macrophthalmus is negligible. Hence for each point we assumed a swimming crab exclusive diet when

$$\frac{a_s X_s e_s}{1 + a_s X_s h_s} > \frac{e_m}{h_m + w_m}$$

by varying h_s and w_m(and leaving the other parameters equal). For X_s we used densities of 1, 4, 7 and 32 swimming crab densities as observed in 2014, 2013, 2012 and 2015 respectively. The point shows the observed average value for waiting time and handling time.

crab plovers (with an empty stomach) offered *ad libitum* prey preferred burrowing crabs over large swimming crabs (Chapter 7), exactly what is to be expected from an energy maximizing point of view when both crabs are readily available. As it is practically challenging to experimentally manipulate handling time in swimming crabs, we 'manipulated' handling times in a state space model and calculated the expected diet composition in relation to variation in waiting time (under the realistic assumption that search time on *Macrophthalmus* is negligible) for each of the observed swimming crab densities (Fig. 8.6). These graphs shows the effectiveness of handling (in crab plovers) and hiding (in *Macrophthalmus*) as it is predicted that crab plovers would change their diet only if handling or waiting would be at least two times shorter than observed under most densities of swimming crabs.

In our experiments with captive crab plovers we observed that plovers with a full stomach switched their preference from *Macrophthalmus* to large swimming crabs (that were opened prior to consumption) (Chapter 7). This switch was attributed to the high digestive quality of large swimming crabs. The small swimming crabs that dominate the diet of free-ranging crab plovers have an equal or lower digestive quality than *Macrophthalmus* (Appendix Fig. A8.4), so we argue that stomach fullness cannot explain the observed preference for small swimming crabs in free-ranging crab plovers. The experiments also suggested that crab plovers in our study area and in winter do not select their diet on the basis of nutrients or toxins (Chapter 7). This further justifies that we took an energy maximization approach to explain the crab plover diet. One issue that we did not include are the usually higher energetic costs associated with active foraging compared to sit-and-wait foragers (Higginson & Ruxton 2015). We suggests that the accelerometers now available can provide detailed information on this issue (Elliott *et al.* 2013; Chapter 9).

Although the two-prey functional response model captured the observed drop of burrowing crabs from the diet, it did not capture the diet at low densities of swimming crabs. At low densities of swimming crabs the model predicted an almost complete switch (cf. Murdoch 1969) from swimming crabs to burrowing crabs, whereas we observed crab plovers to take more swimming crabs than predicted (Fig. 8.5C). Presumable this is a result from spatiotemporal variation in crab availability, not covered with our average density estimates. That crab plovers included more swimming crabs than predicted further suggests that crab plovers have a high preference for swimming crabs.

Crab plovers are endemic to the shores of the Indo-West Pacific biogeographical region (Chapter 11). In agreement with our study, the species was reported in several areas to only forage on swimming crabs with ‘vast and powerful claws’ and to ignore the much more abundant burrowing crabs (Swennen *et al.* 1987). Undoubtedly, the massive bill of the crab plover enables the species to handle swimming crabs efficiently and allows the species to mostly ignore the much-easier-to-handle, but hiding, burrowing crabs burrowing crabs. Other shorebird species within our study area lack the heavy bill, and are predetermined to wait for burrowing crabs. The beach thick-knee *Esacus magnirostris*, which is not closely related to the crab plover (Pereira & Baker 2010), is the only other shorebird with a similarly heavy bill (Rands 1996). Like crab plovers, beach thick-knees are endemic to the Indo-West Pacific region and includes armed crabs in their diet (Mellish & Rohweder 2012). We speculate that this is no coincidence and propose that the seemingly oversized bills of crab plovers and beach thick-knees provides an example of convergent evolution evolved in similarly ‘escalated’ environments (Vermeij and Dietl 2006).

Appendix A8

A8.1. Hiding times burrowing crabs

Hiding times in burrowing crabs can be easily measured as burrowing crabs are known to respond strongly and reliably to simple dummies (Hemmi & Pfeil 2010). In a 'hiding-time experiment' we initiated hiding times in *Macrophthalmus* by approaching foraging crabs with a dummy oystercatcher *Haematopus ostralegus* (a similar-sized bird as a crab plover). The dummy was tied to a nylon rope between two poles 12 meters apart at a height of 20 cm. A camera was placed above the crabs to record crab behaviour (see Fig A8.1).

Appendix A8.1. Set up of the hiding time experiment. For a video of a simulated attack see: https://www.youtube.com/watch?v=xDDvAwAbfAs

Attacks and approaches were simulated by pulling the dummy towards the crabs that were filmed. After each simulated attack the dummy was quickly pulled back. To mimic the various speed at which crab plovers were observed to walk while foraging we simulated attacks and approaches either at a "fast" or "slow" speed, which corresponded with a speed of 1.55 (SD ±0.40) m s^{-1} and 0.29 (SD ±0.077) m s^{-1} respectively (speed was known as the attacks were filmed with a second camera from which we measured the time it took to cover 12 m). To mimic the different time intervals at which *Macrophthalmus* crabs are 'disturbed' under 'real' conditions attacks were simulated at different intervals of either 1.25, 2.5, 5 or 10 minutes. The attack speed and the frequency of attack were chosen randomly prior to the simulations. The experiment was repeated on five consecutive days, (24–03–2011 and 28–03–2011). Experiments where conducted at typical *Macrophthalmus* patches within our study area at about 1 km from the shore. Densities of *Macrophthalmus* burrows at the study location were about 40 crabs m^{-2}. Between days slightly different locations were chosen. After the experiment we measured how long the crabs that burrowed right under the endpoint of the dummy remained in their burrow after a simulated attack using the OBSERVER XT software (v. 5.0, Noldus Information Technology). Within days, multiple hiding times were recorded per individual.

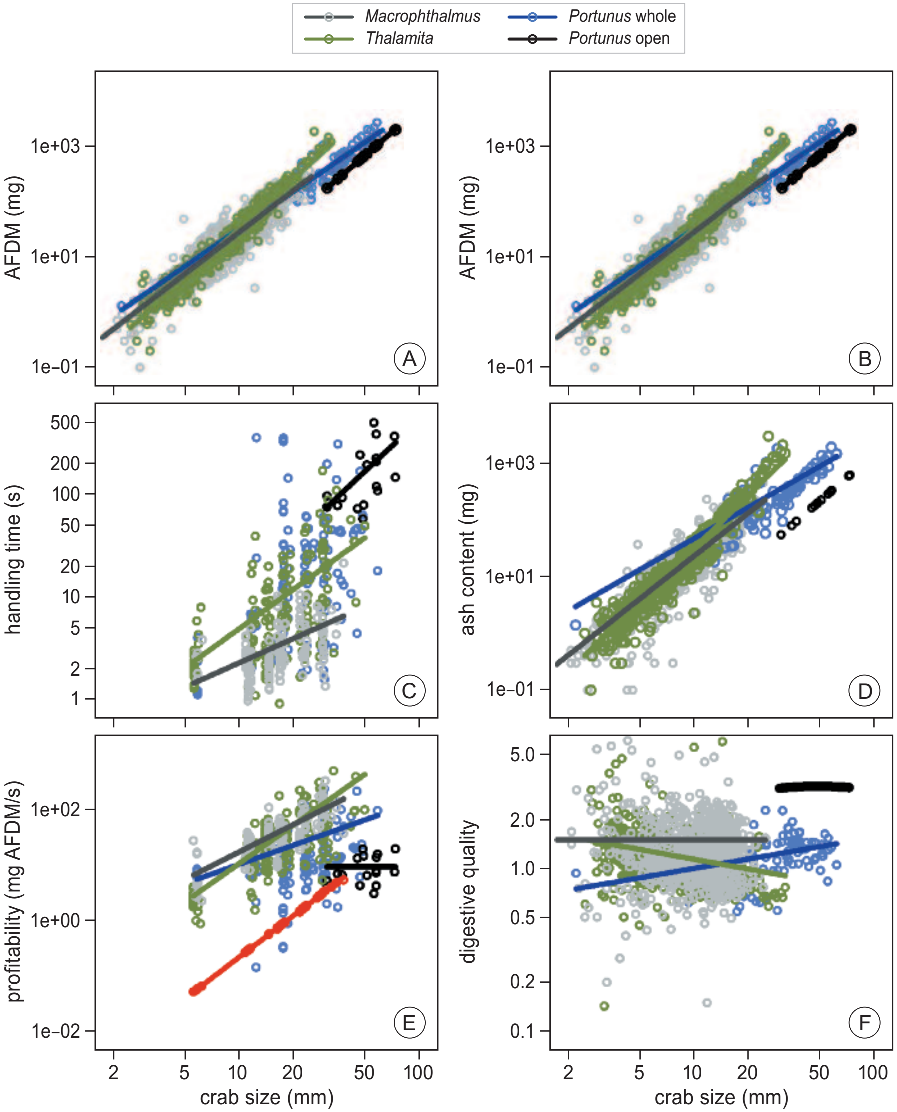
The distribution of observed hiding times followed a log-normal distribution (Fig. 8.1). The median hiding time measured was 56 s (n = 173 in 20 individuals) and ranged from 3 to 749 seconds (Fig. 8.1). Based on the distribution of hiding times we calculated the average expected waiting time before a crab emerges from its burrow based on the scenario that an observer (for instance a crab plover) has a fixed maximum waiting time*. The average waiting time before a crab emerges (w_m) for a fixed maximum waiting time equals:

$$w_m = \frac{p_{suc}\, w_{suc} + (1 - p_{suc})\, w_{max}}{p_{suc}} \tag{1}$$

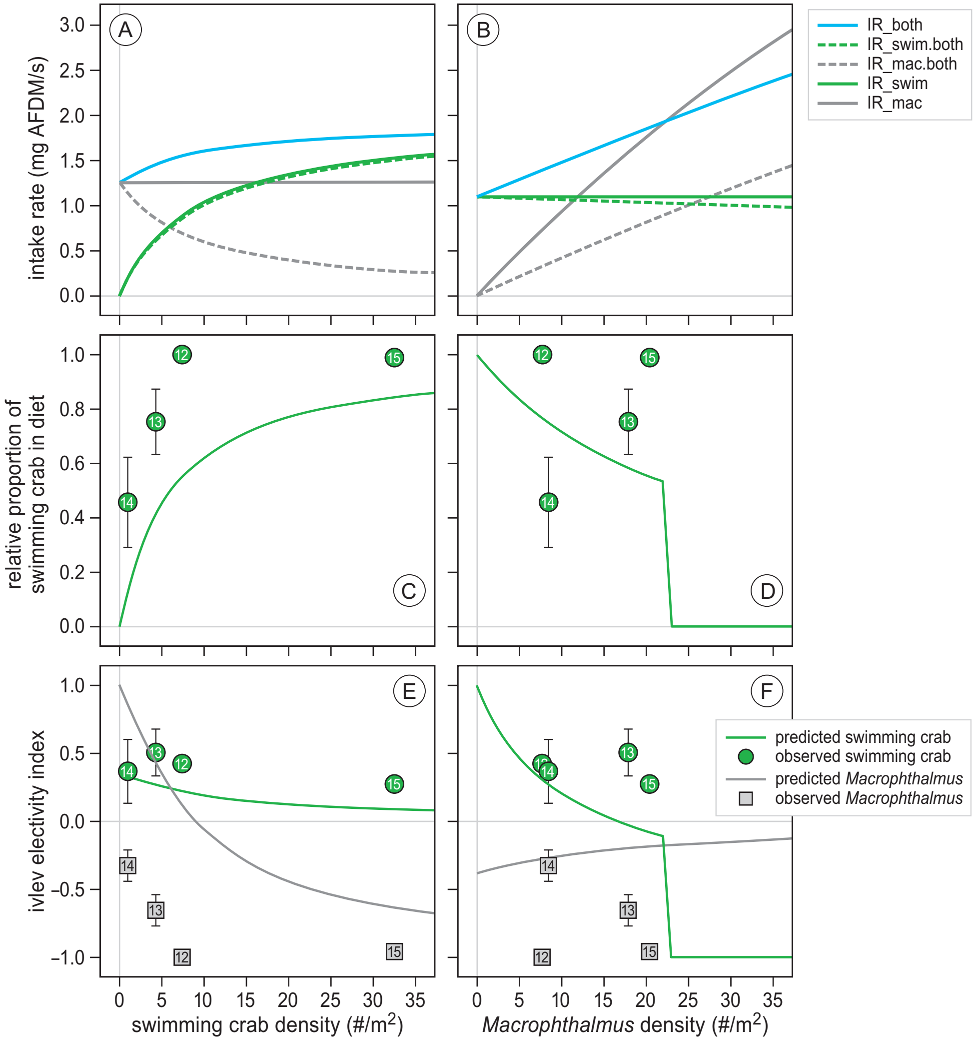
where p_{suc} is the proportion of successful waiting times, w_{suc} the average time until success, and w_{max} the maximum waiting time. This yields an optimal maximum waiting time of 100 s. 69 % of the crabs have a hiding time shorter than 100s. The average hiding time of these crabs is 44 s. Hence, when adopting a maximum waiting time of 100 seconds w_m = (0.69×44 + 0.31×100)/0.69 = 89 s.

It can be expected that crab plovers do not always capture a crab when outwaiting it. The capture probability of attacks after a stand-and-wait event was 0.29 ± 0.24 (mean ± SD of individual capture success). Thus, by taking capture success into account, the average waiting time before capture is 89/0.29 = 307 s. Crab plovers were observed to wait on average 125 s prior to prey capture. We suggest that the difference between calculated and observed waiting time indicates that crab plovers can wait above multiple burrows at the same time.

*note that such a strategy is not evolutionary stable (Hugie 2003).

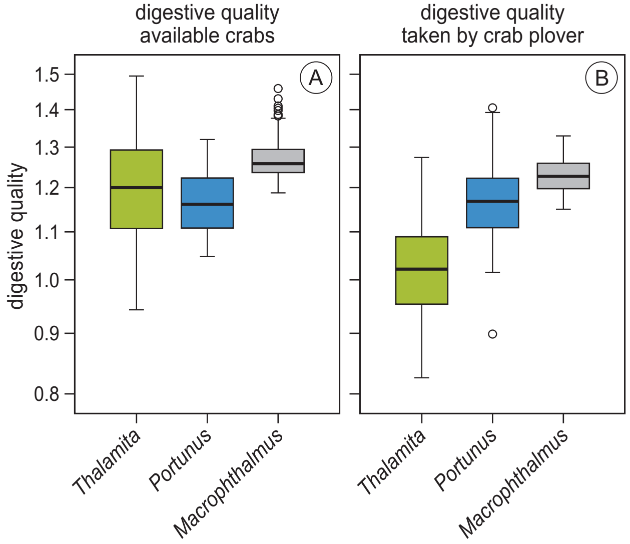


Appendix A8.2. Crab size (carapace width) plotted against (A,B) AFDM, (C) handling time, (D), ash content, (E) profitability and (F) digestive quality. Note the red line in (E) showing the profitability of *Macrophthalmus* when expressed as $e/(h + w)$. Equations of the relations are given in Table 8.2 in the manuscript.



Appendix A8.3.

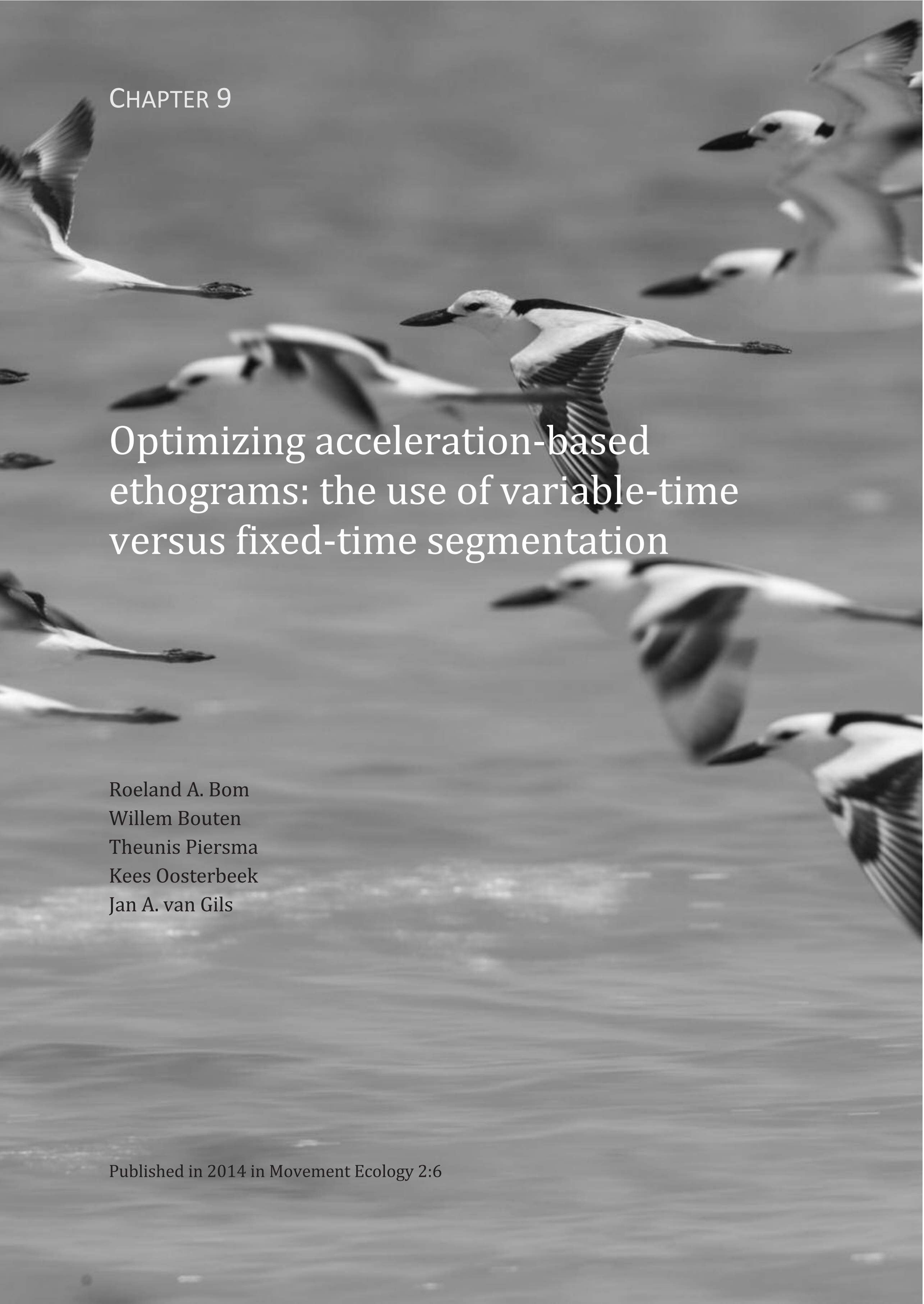
We developed a two-prey functional response model similar to the one presented in the manuscript, but modelled waiting as part of the search phase instead handling phase. The equations for this exercise are identical to those used in the two-prey functional response model developed in the manuscript, except that waiting was deleted from the equations. Furthermore, the parameter value for a_m, the searching efficiency on *Macrophthalmus*, was calculated by assuming that all time between two consecutive prey captures is spend searching. This yielded a searching efficiency a_m of 20.72 cm^2/s (SD ± 14.70). The results of this model are plotted below, analogues to Fig. 8.5. Fig (A) and (B) show that this model predicts a mixed diet under almost all densities of crabs, as the energy intake rate on both crabs (blue line) is in general higher than the energy intake rate on either of the crabs alone (solid grey and green line). This also means that diet composition would depend both on densities of swimming crabs (C) and *Macrophthalmus* (D). Likewise, the preference for the preference (Ivlev) plots in (E) and (F) shows a relation with the densities of both crabs. For many cases, the observed died composition (C & D) and preference (E & F) does not much with the predicted composition and preference. As the model in which waiting time was modelled as part of the handling time had a much better fit with the observed data we conclude that that model is a much better model describing our observations.



Appendix A8.3.

To make sure that crab plovers did not select their prey on the basis of digestive quality we calculated the digestive ballast mass for each studied prey species. Ash content of the prey was used as a measure of digestible ballast mass as ash content was found to constrain food intake in crab plovers (Chapter 7). Non-linear models relating ash content to crab size were fitted on the data collected in Chapter 3 to calculate ash (Appendix Fig. A8.3). Based on this model we calculated the digestive quality of (A) the crabs available and (B) taken by the crab plovers.

The digestive quality of the available crabs differed significantly between crab species (GLM, df = 851 $t_{28.081}$ $P < 0.001$). *Macrophthalmus* had the highest digestive quality (Fig. A8.4a). Post hoc tests showed that *Macrophthalmus* and *Thalamita* ($Z_{-11.675}$ $P < 0.001$) and *Macrophthalmus* and *Portunus* ($Z_{-4.023}$ $P < 0.001$) differed from each other whereas *Thalamita* and *Portunus* ($Z_{-1.055}$ $P = 0.51$) did not. Also the digestive quality of the crabs taken by the crab plover differed significantly between crab species (df = 408 $t_{16.79}$ $P < 0.001$). *Macrophthalmus* had the highest digestive quality and *Portunus* and *Thalamita* were successively lower in digestive quality (Fig. A8.4b). Post hoc tests showed that the digestive quality of all crabs taken by crab plovers differed from each other (all $P < 0.001$).



CHAPTER 9

Optimizing acceleration-based ethograms: the use of variable-time versus fixed-time segmentation

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Abstract

Animal-borne accelerometers measure body orientation and movement and can thus be used to classify animal behaviour. To univocally and automatically analyse the large volume of data generated, we need classification models. An important step in the process of classification is the segmentation of acceleration data, i.e. the assignment of the boundaries between different behavioural classes in a time series. So far, analysts have worked with fixed-time segments, but this may weaken the strength of the derived classification models because transitions of behaviour do not necessarily coincide with boundaries of the segments. Here we develop random forest automated supervised classification models either built on variable-time segments generated with a so-called ‘change-point model’, or on fixed-time segments, and compare for eight behavioural classes the classification performance. The approach makes use of acceleration data measured in eight free-ranging crab plovers *Dromas ardeola*. Useful classification was achieved by both the variable-time and fixed-time approach for flying (89% vs. 91%, respectively), walking (88% vs. 87%) and body care (68% vs. 72%). By using the variable-time segment approach, significant gains in classification performance were obtained for inactive behaviours (95% vs. 92%) and for two major foraging activities, i.e. handling (84% vs. 77%) and searching (78% vs. 67%). Attacking a prey and pecking were never accurately classified by either method. Acceleration-based behavioural classification can be optimized using a variable-time segmentation approach. After implementing variable-time segments to our sample data, we achieved useful levels of classification performance for almost all behavioural classes. This enables behaviour, including motion, to be set in known spatial contexts, and the measurement of behavioural time-budgets of free-living birds with unprecedented coverage and precision. The methods developed here can be easily adopted in other studies, but we emphasize that for each species and set of questions, the presented string of work steps should be run through.

Introduction

In trying to achieve a deeper understanding of the functions of, and the mechanisms underlying, animal movement, it helps to know the details of movement in relation to relevant behaviours, especially in well-known field contexts (Nathan *et al.* 2008). This requires (1) the technology to measure movements (Ropert-Coudert & Wilson 2005; Rutz & Hays 2009) and (2) a classification of behaviours, including different types of movement behaviour (Nathan *et al.* 2012), a 'movement ethogram' as it were. With technology now going far beyond binoculars and notebooks, combinations of animal-borne GPS and tri-axial accelerometer devices present us with a solution to study the whereabouts and behaviour of animals on a precise and near-continuous basis (Bouten *et al.* 2013). GPS receivers fix their location, while acceleration data can be used to classify animal behaviour (Shepard *et al.* 2008).

Two types of classification approaches can be used to identify behavioural modes in acceleration data. Unsupervised classification algorithms are needed when information on the behaviour is not known at the start of the modelling (Sakamoto *et al.* 2009) and after the exercise is done, behaviour is classified based on expert knowledge. Supervised classification algorithms can be built on a labelled dataset (Nathan *et al.* 2012) and the behaviour classification is a direct outcome of the model. A protocol for obtaining acceleration-based behavioural classification with supervised machine learning algorithms has been outlined previously (Nathan *et al.* 2012; Shamoun-Baranes *et al.* 2012) (summarized with adjustments in Fig. 9.1). The approach has a data collection, a data processing, a modelling, and a model application part. The data collection part consists of acquiring acceleration data and gaining information on the behaviour of the animal on which the accelerometer is mounted. The data processing part consists of dividing the acceleration data into segments, and of assigning a behaviour class to each segment. The modelling part consists of calculating and selecting summary statistics that describe the data and of building the classification model. Finally, in the model application part the model is used to classify behaviour for all the collected data.

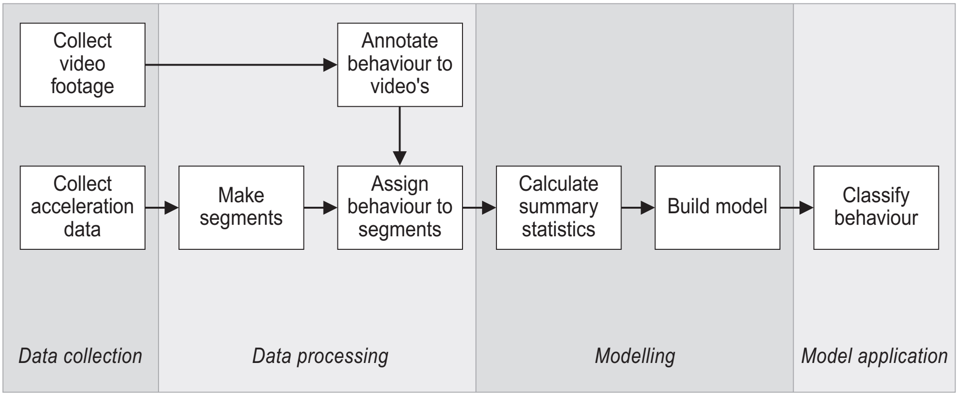


Figure 9.1. The eight step protocol for obtaining acceleration-based supervised behavioural classification that was followed during our study.

Figure 9.2. A crab plover carrying the UvA-BiTS tracker. The arrows represent the tree-axial acceleration that is measured by the device.

A tricky part in this approach is the segmentation. So far, most, if not all studies aiming to obtain acceleration-based behavioural classification (Ravi *et al.* 2005; Watanabe *et al.* 2005; Lagarde *et al.* 2008; Martiskainen *et al.* 2009; Staudenmayer *et al.* 2009; Nathan *et al.* 2012; Shamoun-Baranes *et al.* 2012; Nishizawa *et al.* 2013) used fixed-time segments (e.g. of 1 second) as input for classification models. Fixed-time segments may well limit the classification power of the resulting models as they typically can consist of 'contaminated' acceleration data that represent two behavioural classes. To overcome this problem the idea of using variable-length segments has been proposed (Nathan *et al.* 2012) but never fully examinated.

In this paper we develop a supervised classification model built on both variable-time and fixed-time segment lengths using acceleration data of free-ranging crab plovers *Dromas ardeola* (Fig. 9.2) moving around and foraging during low tide on the tropical intertidal mudflats of Barr al Hikman in the Sultanate of Oman, and compare the resulting classification performances of both approaches.

Methods

An eight step protocol for obtaining acceleration-based behavioural classification is summarized in Fig. 9.1. Below we follow the workflow step by step, illustrated with the collected crab plover data and by emphasizing the data segmentation part.

Data collection

ACCELERATION DATA

In March 2011, November 2011 and November 2012, respectively 3, 11, and 8 adult crab plovers were fitted with the UvA Bird Tracking System (Bouten *et al.* 2013) (Fig. 9.2). All birds were caught with mist nets at night. The tracked crab plovers weighed an average of 375 g (SD ± 25 g), mean weight of the trackers and their attachments was 15.1 g (SD ± 0.5 g), so on average the birds had to cope with 4% added mass. The tracking device was solar powered and included a GPS receiver and a tri-axial accelerometer which measured acceleration in three directions: surge (X), sway (Y) and heave (Z). Each direction was measured at 20 Hz. All tracking devices were calibrated to convert the three components of the acceleration data in G-force (1 G = 9.8 m s^{-2}). When tags were within reach of the antenna network, both the interval at which the GPS measures as well as the interval and duration at which the accelerometer measures could be changed. During daylight and low tide, trackers were set to measure positions at either 15 or 30 s intervals. Position fixes were always followed by 200 measurements of acceleration (thus, since acceleration is measured at 20 Hz, for a duration of 10 s).

VIDEO FOOTAGE

In November and December 2011 and 2012, during daylight low tides, the intertidal mudflats were searched for tracked birds and whenever a bird was encountered, we filmed it through a 20–60× spotting telescope (Swarovski ATS 80HD) using a Canon VIXIA HG21 camera. We obtained video material on eight birds.

Data processing

BEHAVIOUR ANNOTATION TO VIDEOS

We designed an ethogram of eight behaviours (Table 9.1) and assigned behaviours to acceleration data that could be synchronised with the collected video material using the UvA-BiTS annotation tool (http://staff.science.uva.nl/~bredeweg/pdf/BSc/20102011/DeBakker). The tool will soon be available as a web service (www.UvA-BiTS.nl/virtual-lab). We could synchronise 919 bouts of acceleration data of 10 s each with video recordings and in a total of 2,668 instances a class of behaviour was assigned (Table 9.1).

Table 9.1. Ethogram of the behavioural classes of crab plovers distinguished on the video recording and the number of assignments per tracked bird.

Behavioural class	Description	# of observations per tracked bird								Total
		#446	#642	#672	#674	#675	#676	#680	#682	
Attack	fast forwards prey attack, typically followed after a period of waiting	1	3	1	6	0	0	0	26	37
body care	cleaning and arranging feathers	21	0	0	18	3	23	0	2	67
Fly	flying	4	0	0	7	0	0	0	8	19
Handle	preparing prey for ingestion, usually crabs are stripped on the ground	53	6	1	19	12	3	0	75	169
Inactive	all inactive behaviours, sit, sleep, stand, sit on tarsus, lurk	207	24	56	257	70	77	6	480	1177
Peck	pecking, similar to attack, but more downwards and slower	17	0	0	11	2	8	0	9	47
Search	the bill is used to sense prey, similar to, but less irregular than handling	56	0	14	31	47	35	0	116	299
Walk	moving legs forwards	124	16	45	213	60	59	5	331	853

SEGMENTATION

As introduced, we make both variable- and fixed-time segments in our acceleration data and subsequently complete the classification procedure (Fig. 9.1) for either approach. Variable-time segments were made using the change-point model framework. This framework provides a method for detecting multiple change points in a sequence, for instance a time series. The models work by evaluating at every possible split point the distribution of a parameter (e.g. mean, variance or both) using a two-sample test statistic(Ross 2013). A change point, or in our case a segment boundary, is detected when a set threshold is exceeded. Within the R environment (R Development Core Team 2013), a change-point model is implemented in the 'cpm' package (Ross 2013) that provides the function 'processStream'. This function uses a test statistics and the parameters 'ARL_0' and 'startup' (explained below) to detect sequential changes in a time series. Inspection of the acceleration bouts showed that the *x* signal responds most strongly to a behavioural change by changes in the mean and variance, so here we make segments based on changes in the *x* signal. To do so we used the Generalized Likelihood Ratio (GLR) test statistics which detect both mean and variance changes in a Gaussian sequence. Parameter ARL_0 corresponds to the average number of observations before a false positive occurs. As we had no expectations, for ARL_0 we used the values of 500 (the default value), 5,000 and 50,000 (the maximum value allowed) and tested the resulting classification performance for each value (see below). The parameter *startup* indicates the number of observations after which monitoring begins. The default and minimum value was set at 20, which in our case corresponds with 1 second as acceleration was measured at 20 Hz. As we noticed that

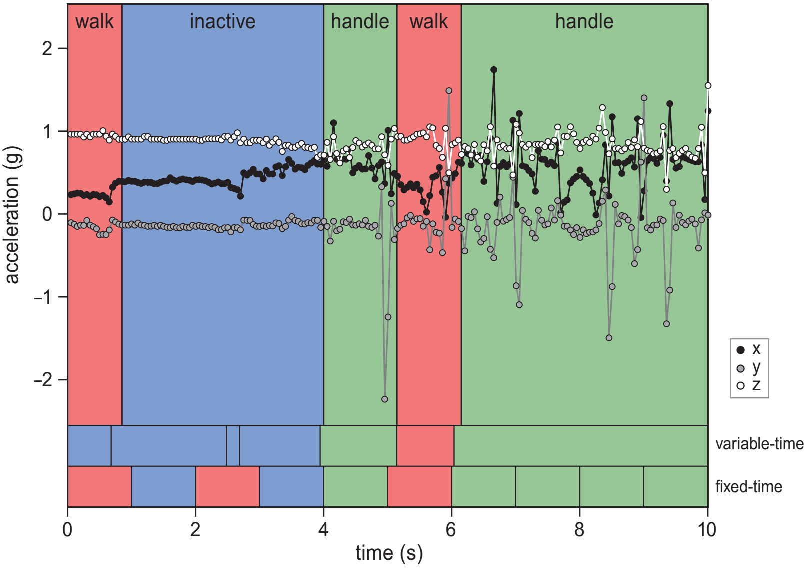


Figure 9.3. Example of 10 seconds acceleration data. The top diagram shows the tri-axial accelerometer data at 20 Hz and in colour the observed behavioural classes. The variable-time row shows the boundaries of the variable time segments (ARL_0 = 50,000) and the classified behavioural class. The fixed-time row shows the boundaries of the fixed time segments (1 sec) and the classified behavioural class. The background colours are unique per behaviour.

crab plovers can change their behaviour within 0.25 seconds, we do not increase the value of *startup*. Fixed-time segments were made of different lengths, i.e. 0.5, 1, 2 and 3 s.

BEHAVIOUR ASSIGNMENT TO SEGMENTS

Each segment was assigned to a behavioural class (Table 9.1) that, according to the video annotation, made up most of that segment. Fig. 9.3 shows an example of 10 seconds of acceleration data with variable-time segments (ARL_0 = 50,000) and fixed-time segments (fixed at 1 second), with both the assigned and classified behaviour.

Modelling

SUMMARY STATISTICS

We calculated summary statistics to characterise the acceleration data within a segment and we used them as features for machine learning. The following were calculated: mean, standard deviation, maximum value, minimum value, skewness, kurtosis, dominant power spectrum, frequency at the dominant power spectrum (Hz), trend, dynamic body acceleration and the overall dynamic body acceleration (ODBA) (Nathan *et al.* 2012; Shamoun-Baranes *et al.* 2012). Summary statistics were calculated for the *x*, *y* and *z* separately except for the ODBA, which was calculated by taking the sum of the dynamic parts of the three dimensions together. Thus, a total of 31 summary statistics were calculated. The R package 'moments' (Komsta & Novomestky 2012) was used to calculate the kurtosis and skewness.

MODEL BUILDING

The number of behavioural assignments for attack, fly and peck, and to a lesser extent body care, handle and search, were low. We up-sampled the number of observations of attack, fly and peck by a factor six, and of body care, handle and search by a factor two. To this end we used the Synthetic Minority Over-sampling Technique (implemented in the SMOTE function, R package 'DMwR'), which creates synthetic instances of the minority class using nearest neighbours (Torgo 2010). For the actual model building part, we applied the random forest supervised algorithm to the selected summary statistics using the R package 'randomForest' (Liaw & Wiener 2002) (default settings used). It was concluded in another study that this method yields the best performance compared to linear discriminant analysis, support vector machines, classification and regression trees and artificial neural networks (Nathan *et al.* 2012). Using a resampling procedure, we randomly split the data into two subsamples: 70% of the data was used to train the model and behaviour was classified for the remaining 30% of the data. This classified behaviour was then linked to every single record of acceleration. The classification performance was defined as the number of acceleration records with identical observed and classified behaviour divided by the total number of acceleration records. This procedure was repeated 1,000 times and for each behavioural mode the mean and 95% confidence intervals of the classification performance were calculated. For both approaches we identified settings that yielded the highest classification performance, and used these for further comparisons between the two approaches. For behaviours for which the 95% confidence intervals did not completely overlap, i.e. search, handle and inactive, we compared sample means of the variable-time and the fixed-time approach, using data generated by the resampling procedure. For each behaviour, we calculated the Z-statistic and p-value under the null hypothesis that the means do not differ (i.e. a two-tailed Z-test). The data were logit-transformed to meet the normality assumption.

Model application

BEHAVIOUR CLASSIFICATION

As an example we show the movement ethogram and the hourly % of time devoted to each classified behaviour of crab plover #674 on 20th November 2012, starting 5 hours before, and ending 5 hours after low tide, using the variable-time segmentation approach (ARL_0 is 50,000).

Results

Useful classification was achieved by both approaches, but the variable-time segmentation approach considerably outperformed the fixed-time approach for several classes of behaviour (Table 9.2). The best classification performance for the variable-time segmentation was established when parameter ARL_0 was set to its maximum value of 50,000. For most behaviours, the best classification performance for the fixed-time approach was obtained when segments were fixed to 1 second. Thus, comparing the variable-time and fixed-time segmentation approach for the settings for which the classification performance was highest (Fig. 9.4.), inactive behaviours (95% vs. 92%), flying (89% vs. 91%), walking (88% vs. 87%), handling (84% vs. 77%), searching (78% vs. 67%) and body care (68% vs. 72%) were reasonably classified with both approaches, and peck (15% vs. 4%) and attack (2% vs. 1%) were never very accurately classified. Compared with the fixed-time segmentation approach, the variable-time segmentation approach yielded a significant higher classification performance for inactive behaviours ($Z = 3.12$, $P < 0.01$), handling ($Z = 1.50$, $P < 0.01$) and searching ($Z = 2.00$, $P < 0.01$).

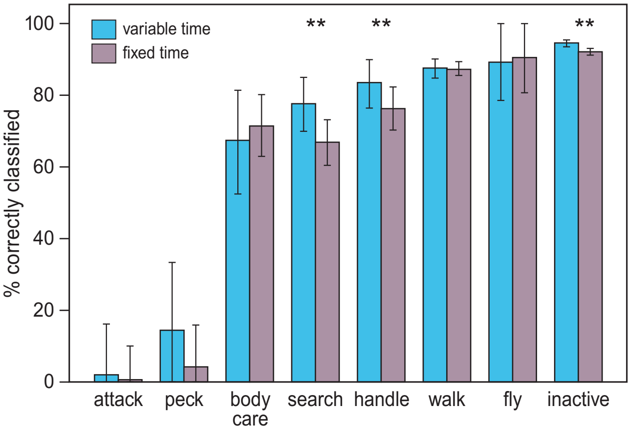


Figure 9.4. Results of the variable-time and fixed-time approach with the settings that yielded highest classification performance. The mean classifications performance and 95% confidence intervals are shown. Significant differences in classification approaches between methods are indicitated on top of the behavioural classes.

Table 9.2. Classification performance (mean percentage and 95% confidence intervals) of the variable-time segmentation approach for different values of ARL_0 (upper three rows) and of the fixed-time segmentation approach for different fixed segment lengths (lower four rows).

Segmentation	**ARL_0**	**Fixed length** (s)	**Attack** (%)	**Body care** (%)	**Fly** (%)	**Handle** (%)	**Inactive** (%)	**Peck** (%)	**Search** (%)	**Walk** (%)
Variable-time	500		5.0 (0–24.1)	65.9 (50.3–78.0)	89.8 (55.6–100)	77.6 (70.5–84.4)	94.5 (93.5–95.4)	13.5 (0–28.6)	74.5 (67.0–81.6)	87.6 (85.2–89.7)
	5,000		2.8 (0–17.5)	64.4 (47.3–77.7)	87.8 (52.7–100)	80.3 (73.0–86.7)	94.8 (93.8–95.7)	17.2 (0–33.5)	77.1 (69.2–84.8)	87.8 (84.9–90.2)
	50,000		2.2 (0–16.2)	67.6 (52.4–81.4)	89.4 (47.7–100)	83.7 (76.3–90.1)	94.7 (93.6–95.6)	14.5 (0–33.6)	77.7 (69.8–85.3)	87.8 (84.8–90.3)
Fixed-time		0.5	7.3 (0–21.9)	64.6 (57.2–71.3)	87.6 (78.3–95.7)	70.4 (65.6–75.3)	93.9 (93.0–94.8)	0.4 (0–5.2)	66.3 (60.9–71.8)	88.5 (86.7–90.1)
		1	0.7 (0–10.2)	71.6 (62.8–80.3)	90.8 (80.8–100)	76.5 (70.1–82.4)	92.2 (91.0–93.3)	4.1 (0–16.0)	67.0 (60.4–73.2)	87.4 (85.4–89.5)
		2		62.7 (49.6–75.6)	90.8 (77.9–100)	76.6 (68.5–84.2)	88.2 (86.3–89.8)		61.8 (53.2–68.9)	82.5 (79.6–85.5)
		3		50.4 (35.0–66.0)	95.0 (83.7–100)	73.0 (62.9–81.8)	85.0 (82.8–87.3)		46.9 (37.5–56.5)	80.8 (76.6–84.5)

Fig. 9.5 shows the ‘movement ethogram’ of crab plover #674 during a single tide on 20 November 2012. This example starts around 04 o’clock when the crab plover is inactive at its shoreline roost. With the ebbing tide, the bird goes to the mudflat where it moves between and within distinct areas, which we here call patches. Between patches the bird travels by flight. Within patches the crab plover mainly walks and is inactive and occasionally is searching for, or handling a prey. The example ends in the early afternoon when the water has reached the beach and the crab plover starts to be more inactive. The time budget in Fig. 9.6 suggests that off the mudflats crab plovers are mainly inactive and sometimes walk.

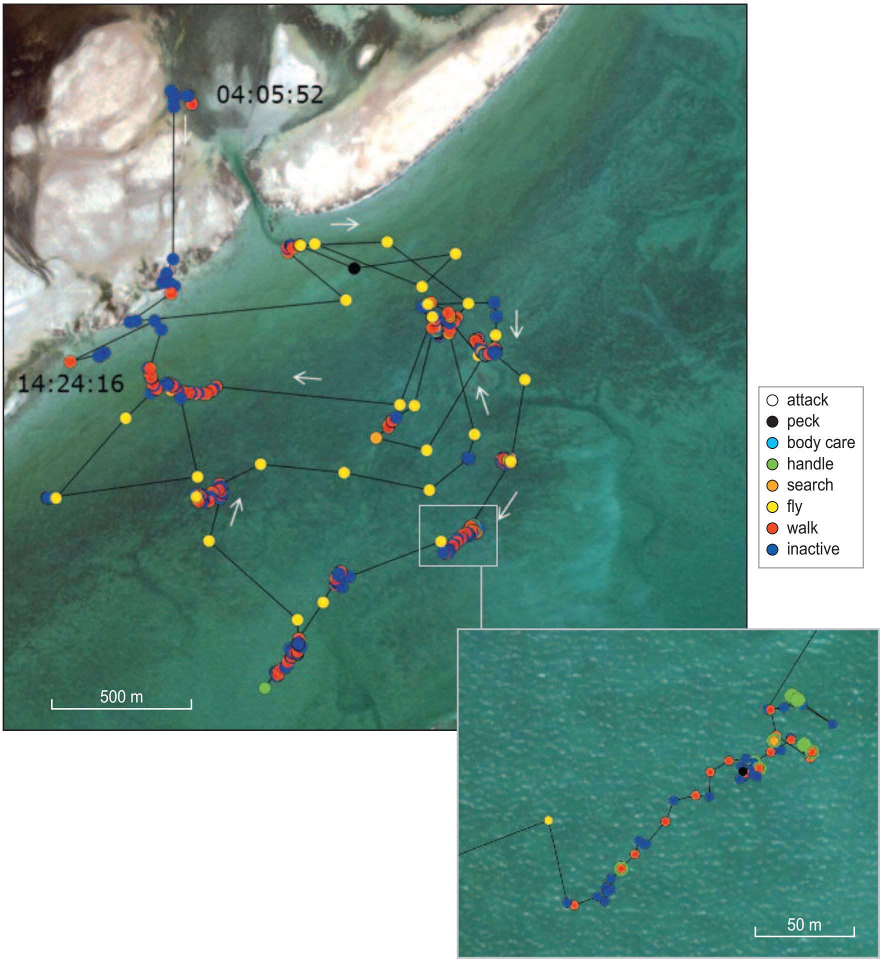


Figure 9.5. Movements of crab plover #674 during a single low tide on 20 November 2012. The time between points is, in general, 30 seconds during low water and 10 minutes during high water. Lines connect subsequent measured positions. After each measured position, acceleration was measured during 10 seconds. Acceleration-based behaviour classification was done using the variable-time segmentation approach. In the enlargement, the point size of handling is slightly larger for visual reasons. The hourly time budget for this example is shown in Fig. 9.6.

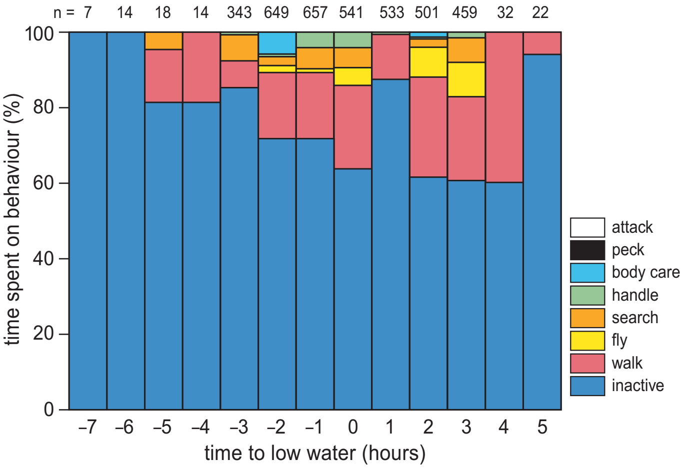


Figure 9.6. Hourly time budget constructed from accelerometer data for crab plover #674 during a single low tide on 20 November 2012, using the variable-time segmentation approach. N-values refer to the number of segments. Behaviours are ranked from least to most occurring.

Discussion

Variable-time segmentation for acceleration based behaviour classification

We explored the use of variable-time segments and fixed-time segments for developing acceleration-based behavioural classification. By implementing variable-time segments to our data, very useful levels of classification performance were achieved for almost all behavioural classes, levels that were not always achieved by using fixed-time segments. Especially, the implementation of variable-time segments enabled us to satisfactorily raise the classification performance of two behaviours that may look similar in nature; i.e. handle and search (Table 9.1). These are behavioural classes we are particularly interested in from an ecological point of view (see below).

Given our results we think that other studies developing acceleration-based behavioural classification models will likely raise their classification performance when using the variable-time segmentation approach. Yet, we also realise that the extent to which this is true will depend on the kind of acceleration data that is available, on the studied species and on the aim of the study. The variable-time segmentation approach will be of limited use when few acceleration records are available (i.e. < 20), or impossible when the acceleration data are already summarized by the manufacturer (Grünewälder *et al.* 2012). Also, studies on animals that have short sequences of vigorous behaviours (certainly true for crab plovers that are typical ambush predators which rapidly attack their prey after relatively long motionless waiting bouts) will benefit more from variable-time segmentation than studies that use data collected on animals that have long-lasting behaviours that are slow by nature, e.g. cows (Martiskainen *et al.* 2009). Similarly, variable-time segmentation is probably not needed when the aim of the study is to classify only obviously distinct behaviours such as inactive versus active.

Application

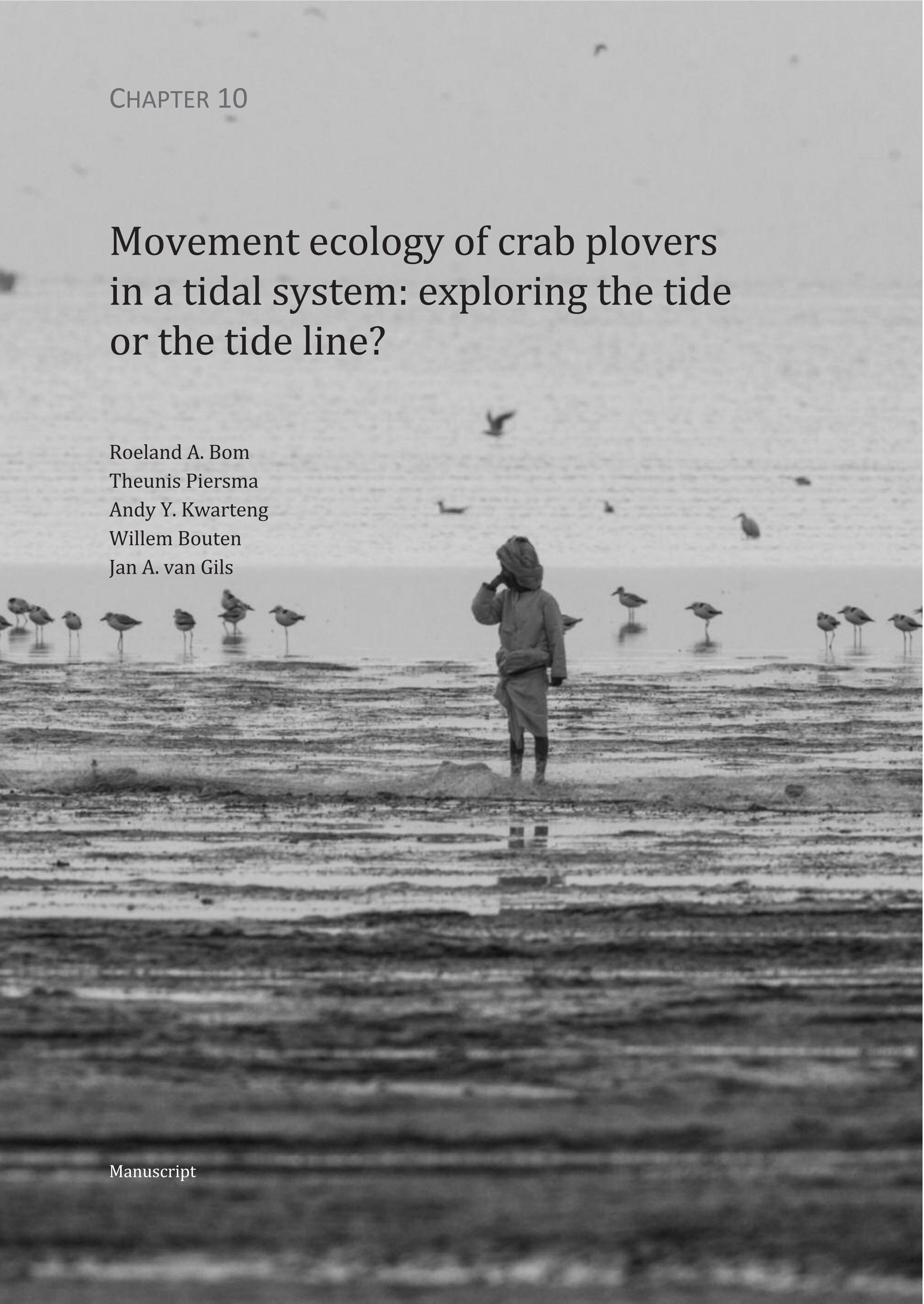
The present calibration study enables us to study spatial distributions in relation to the behaviour of free-living crab plovers during their non-breeding season at unseasonable hours and inaccessible sites with exceptional coverage and precision. For instance, we can emphasize when and where crab plovers are inactive, when they are searching for prey and how often they handle prey, day and night (crab plover forage during low tide, day and night), predict the sizes of prey ingested (handling time in crab plovers is log-linear related with the size of the crab that is ingested (Chapter 7 & 8), estimate the (relative) energy expenditure of different behavioural classes (Halsey *et al.* 2009) and, since crab plovers fly between foraging sites (Fig. 9.5) and since accelerometers indirectly measure wing-beat frequency while flying, we could potentially measure the increase of body mass before and after foraging (Sato *et al.* 2008). As crab plovers travel between patches by flight we can also identify patch giving-up decisions (Brown 1988). Together with field experiments measuring digestive constraints of crab plovers (Chapter 7), we can analyse if, where and when prey intake of crab plovers is constrained by searching, handling and or digestive breaks. Furthermore, search and handling are the key input behaviours to the quantification of the relationship between predator intake and prey densities, the 'functional response' (Holling 1959), which is the first step in mechanistically understanding the spatial distribution of (foraging) animals (van der Meer & Ens 1997; Moreau *et al.* 2009).

Concluding remarks

Techniques to analyse acceleration data are beginning to appear in the ecological literature. A growing number of studies has developed supervised classification algorithms that satisfyingly classify behavioural modes of the studied individuals (see introduction), for other individuals of the same species (Moreau *et al.* 2009) and even classify behaviour beyond the species level (Campbell *et al.* 2013). Outperforming the resolution of more traditional telemetry (e.g. van Gils *et al.* 2006; Dwyer *et al.* 2012), especially when accelerometers are combined with GPS sensors, the new methods have great potential for movement ecology. Nevertheless, acceleration-based behavioural classifications have not been successful to classify all behavioural categories accurately (e.g. Shamoun-Baranes *et al.* 2012; Nishizawa *et al.* 2013; our study). In our case, the low classification performance for some behaviours was probably due to a low sample size, but also due to the short-lasting nature of the behaviour (this is true for both attack and peck) and of the acceleration-signal being very similar to other behaviours. Thus, future studies are challenged to come up with techniques that can identify such hard-to-distinguish behaviours. These techniques may involve optimization of either of the essential steps in the presented workflow (Fig. 9.1). Our contribution to optimize acceleration-based behavioural classification was to include a variable-time segmentation of the acceleration data. The inclusion of the variable-time segmentation enabled us develop a model that could classify several behavioural modes in crab plovers at satisfying levels. By combining the behaviour classifications with simultaneously measured location data, we were able to make 'movement ethograms' on a near-continuous basis with coverage and precision that are unprecedented in the field of movement ecology.

Acknowledgements

All the work was done under the permission of the Ministry of Environment and Climate Affairs, Sultanate of Oman. We are very grateful to its Director-General, Mr Ali al-Kiyumi, for making all the necessary arrangements during our work in Oman. This work could not have been done without the help of Symen Deuzeman and all other people that took part in the fieldwork. We thank two anonymous reviewers for their comments, Allert Bijleveld for valuable discussions and Merijn de Bakker for good help while annotating the videos. Our bird behavioural studies are supported by the UvA-BiTS virtual lab on the Dutch national e-infrastructure, built with support of LifeWatch, the Netherlands eScience Center, SURFsara and SURFfoundation. RAB and JAvG are financially supported by NWO (ALW Open Programme grant 821.01.001 awarded to JAvG).



CHAPTER 10

Movement ecology of crab plovers in a tidal system: exploring the tide or the tide line?

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Manuscript

Abstract

Foragers exploiting intertidal resources face challenges related to the non-alignment of daily and tidal rhythms and with resource availability varying in complex ways. Some avian foragers have been shown to distribute themselves as a function of the extent of the exposed intertidal, whereas other concentrate foraging around the moving tidal edge. Here we study how crab plovers *Dromas ardeola* deal with these tide-specific time and space problems: do they use entire exposed intertidal space or do they follow the tideline? We used GPS- and accelerometer tracking data, obtained on 11 crab plovers in the intertidal of Barr Al Hikman, Sultanate of Oman. Movement patterns cycled in concert with the tidal cycle of 12.4 hours. Birds were away from the roost to actively forage during periods of 8–10 hours centred around low tide. Crab plovers almost always remained close to the water line, presumably because the swimming crabs, their preferred prey, were most active and abundant in and close to the tide line. Birds remained longer at sites where they were shown with accelerometers to handle prey. This suggests that crab plovers exhibit area-restricted search, the expected behaviour for birds foraging on prey showing spatial autocorrelation. Between tides, birds followed the waterline, but with little respect to precise location, as at a grain size of 200 m they hardly revisited sites between consecutive tides. This 'opportunistic' spatial behaviour is expected for birds exploiting resources which are unpredictably distributed, suggesting that swimming crabs move with the waterline but at unpredictable locations. Our study gives an intimate picture of the timing and space use of crab plovers and how they are closely linked with the tide. In this species, most if not all foraging decisions of crab plovers are moulded by a moving waterline.

Introduction

Intertidal areas offer an interesting arena for the study of movement ecology as foraging animals need to solve common time and space problems with intriguing rhythmic features (Bulla *et al.* 2017). To start with, because tidal waters rise twice per lunar day and alternately cover and uncover the intertidal area (de la Iglesia & Johnson 2013), the intertidal resources are unavailable during part of the day (van Gils *et al.* 2006). Because the lunar day last 12.4 hours, the availability changes in time with respect to the circadian rhythm. Thus, animals foraging within the dynamic intertidal areas should schedule their behaviour with the interacting environmental rhythms (Leiva *et al.* 2016; Bulla *et al.* 2017).

In addition to timing-related issues, intertidal foragers should schedule their space use such that they acquire their daily energetic demands. Tidal foragers in search for invertebrate prey items, depending on the prey items they aim to exploit, should concentrate their movements around the moving tide line or extend their movements to exposed or covered mudflats (Both *et al.* 2003; Granadeiro *et al.* 2006). The more sedentary intertidal resources remain hidden under the surface, whereas more mobile prey items are most active in the waterline or move in and out the intertidal area with the tidal flow (Rosa *et al.* 2007; Cardoso *et al.* 2010). On top of that, invertebrate prey are often patchily distributed (Kraan *et al.* 2009). Theory and empirical work shows that foragers exploiting patchily distributed prey items should stay and search longer in the places where resources are abundant and should not spend too much time at sites where there are few resources (Benhamou 1992; Nolet & Mooij 2002; Fryxell *et al.* 2008). In the tidal area the decision to leave a place may also be affected by the incoming or outgoing tide, as over time places become unavailable or places with possible better feeding opportunities become available.

Another movement-related issue is to revisit previously visited areas (Bracis *et al.* 2018). Tidal foragers face this issue multiple times per day, as they are pushed out of the intertidal area with the tidal flow. The degree of animals to return to an area is predicted to decrease as the temporal autocorrelation of resources increases (Switzer 1993; Mueller & Fagan 2008). The temporal predictability of sessile prey such as molluscs and polychaetes may be high between tides, whereas the temporal predictability of mobile resources (e.g. shrimps, crabs and fish) may be lower. But, adding complexity, in tidal areas opportunities to revisit previously visited places are often hampered by the tidal rhythm, as the low tides show different levels because the moon's gravitational pull is added to that of the sun.

Traditionally, visual studies on animals foraging in the intertidal area have been confined to daytime and to relatively small spatial areas (e.g.Zwarts & Esselink 1989) as it is difficult to study animals during the night and when they move out of sight at low tides (but see for instance Hulscher 1976; Piersma *et al.* 1993c). With the onset of GPS and accelerometer tracking technology, it has now become possible to study the space use and the behaviour of individual animals in great detail by day and night, during high and low tide (Shamoun-Baranes *et al.* 2012). Yet, only a few studies have used tracking data to explore how animals schedule their space use and behaviour in complex intertidal systems (van Gils *et al.* 2006; Bijleveld *et al.* 2016; Bulla *et al.* 2017; Dokter *et al.* 2017).

Here we used tracking data to study the spatiotemporal movements and behaviour of crab plovers *Dromas ardeola* foraging on the intertidal mudflats of Barr Al Hikman in the Sultanate of Oman. We amalgamated the challenges that crab plovers face in the dynamic intertidal zone into four questions: (1) when do they forage? (2) do they follow the tide line or do they exploit the mudflats? (3) when do they leave a site? and (4) how often do they revisit previously used sites? Crab plovers are enigmatic shorebirds that breed and winter in tidal areas (De Marchi *et al.* 2015a), primarily foraging on crabs (Rands 1996). In our study area crab plovers forage on mobile swimming crabs or on more sedentary burrow-hiding sentinel crabs (Chapter 8). Weighing about 375 g, crab plovers can carry state-of-the-art GPS- and accelerometer trackers (www.UvA-BiTS.nl; Bouten *et al.* 2013). A previous study (Chapter 9) developed an ethogram of crab plovers based on the classification of accelerometer data.

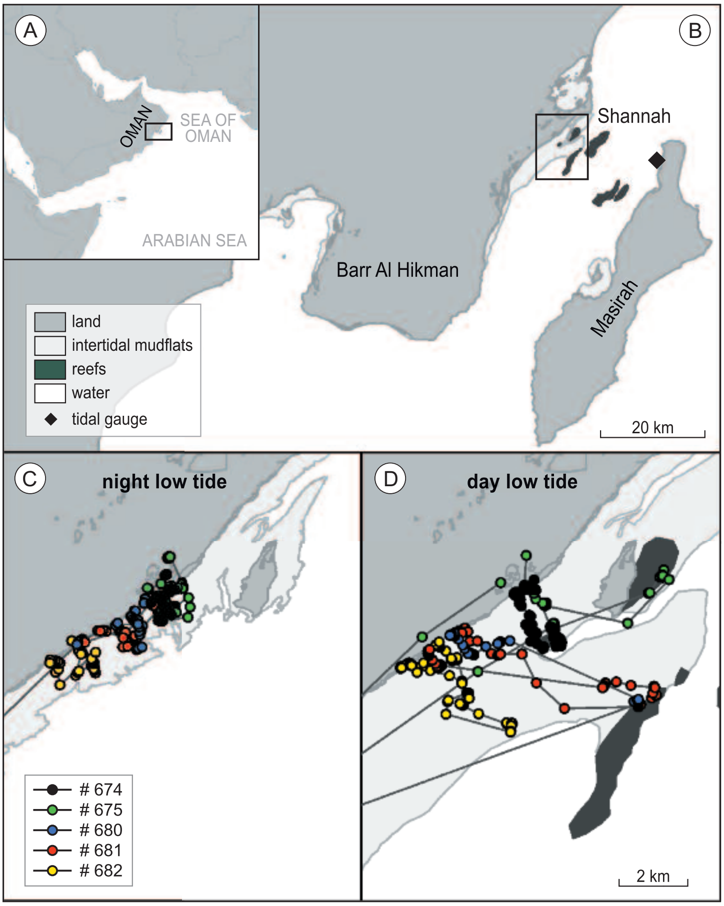


Figure 10.1. (A) The Arabian Peninsula with the location of Barr Al Hikman in the red square. (B) The Barr Al Hikman Peninsula with the intertidal mudflats, reefs and the tidal gauge at Masirah. The red square shows the area depicted in (C) and (D) in which we show (C) the tracking data collected during the first low tide on 1 December 2012, 05:07 with a minimum water level of 1.7 m and in (D) the tracking data collected during the second low tide on 1 December 2012, 17.12 with a minimum water level of 0.7 m.

Methods and Materials

Study system

Barr Al Hikman is a peninsula of approximately 1400 km^2 in the Sultanate of Oman (20.6°N, 58.4°E) (Fig. 10.1A and B). The peninsula is bounded by intertidal mudflats of about 190 km^2. The tidal cycle in the area consists of a mixture of diurnal and semidiurnal tides (Fig. 10.2A, based on a tide gauge at the nearby (25 km) island of Masirah; predicted data from http://www.ukho.gov.uk/Easytide/easytide/, observed data from https://uhslc.soest.hawaii.edu/data/?rq#uh113a). For this study we made observations in the time period 19 November – 31 December 2012 and 18 November – 31 December 2014. Lomb-Scargle periodograms (Lomb, 1985), which determine cycles in time series, showed that for each tide the water level at each second next low tide was more alike than the water level at the next low tide (Fig. 10.2). Furthermore, tides showed recurrent pattern in water level after about 26–32 tides. At a shorter time scale the water level exhibited a clear 12.4 hours and 24 hour rhythm (Fig. 10.2B). The predicted and observed water level at low tide ranged from 0.1 m to 1.9 m (Fig. 10.2A, 10.3A). During the night, defined as the period between sunset and sunrise, the water level of the low tides were significantly higher in the period of observations (Fig. 10.3B, linear model (lm), df = 16, t = 6.820, $P < 0.001$). We confined our observations to the area south-east of Shannah (Fig. 10.1C and 10.1D) in which the size of the exposed intertidal mudflats is related to the water level (Fig. 10.3C, lm, df = 6, t = 12.03, $P < 0.001$, based on a bathymetry map presented in Chapter 3).

Barr Al Hikman is renowned for its abundant birdlife (Chapter 5). For the crab plover, a species that is endemic to the Indo-West Pacific, the area is the most important wintering ground (Chapter 6). About 8,000 individuals can be found in the area between November and March (Chapter 5).

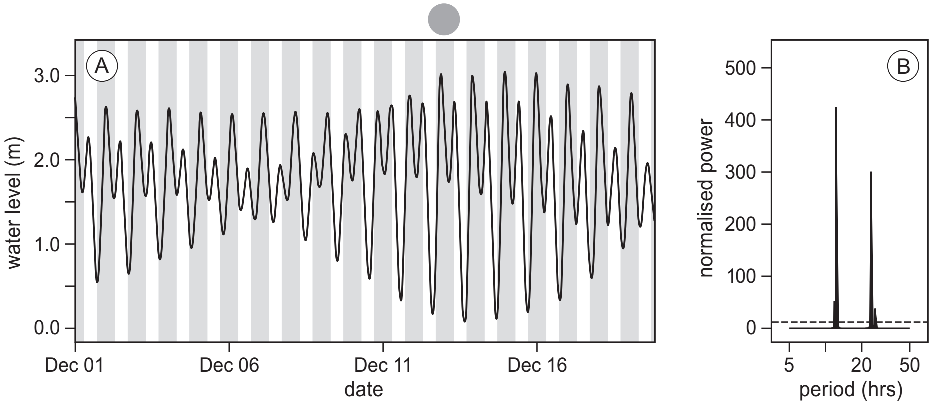


Figure 10.2. (A) Example of the tidal rhythm at Barr Al Hikman for a 18-day period during the study period in 2012. Shaded envelops indicate nights. New moon was on 13 December. Data is based on measured water levels at Hilf, Masirah Island (B) Lomb–Scargle periodogram of the water level shows a distinct peak at 12.4 hours and at 24.0 hours. The dotted horizontal line shows the border above which peaks are considered significant.

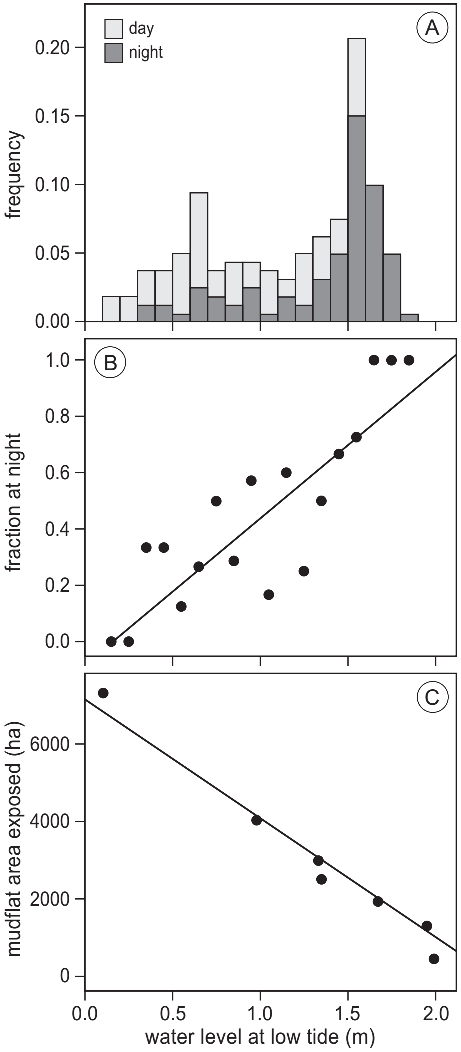


Figure 10.3. (A). Frequency distribution of water level at low tide during the period of observation, with dark bars showing night low tides and light-grey bars showing day low tides. From this figure the fraction of low tides occurring at night was calculated and shown in (B) The water level at low tide is in general higher during the night than during the day. (C). During neapish low tides significantly less mudflats area is exposed . The exposed area was calculated for the east coast of Shannah and based on 6 satellite images.

Tracking details

Crab plovers were caught with mist nets at night. In November 2012 and November 2014 respectively 8 (4 males, 4 females) and 10 (7 males, 3 females) adult crab plovers were fitted with UvA BiTS trackers (Bouten *et al.* 2013) using a full-body harness made of 6 mm wide Teflon strings and weighing about 2 g. In addition, all birds received a unique combination of colour rings (Chapter 6). Birds were released within 20–40 min after capture. The tracked crab plovers weighed an average of 380 g (SD ± 38 g) in 2012 and 367 (SD ± 41 g) in 2014. The mean weight of the trackers and their attachments was 15.1 g (SD ± 0.5 g) in 2012 and 9.8 gram (SD ± 0.1 g) in 2014. This means that on average the birds had to cope with 3–4 % added mass. In 2012, five of the eight tracked birds stayed within the study area. Two other moved within two days out of the study area to the south of the Barr Al Hikman Peninsula and to Masirah Island. Connection with another bird was lost after a day. In 2014, seven of the 10 birds tracked in 2014 stayed within the study area, of which one stopped working after two days. The number of obtained tracks per tide type per year are given in Table 10.1. All tracked birds that stayed within the study area were regularly observed and behaved as their conspecifics. Crab plover provision their offspring throughout the first winter (De Sanctis *et al.* 2005) and two of the tracked birds in 2014 (#2008 and #2118) were regularly observed feeding a first winter bird. Three of the 8 birds tracked in 2012 were observed in 2013, of which we observed one in 2014. Four of the 10 birds tracked in 2014 were observed in 2015. The area was not visited in 2016. Apparent survival of colour-ringed crab plovers in the area was estimated at 90% (Chapter 6). Four of the seven trackers resighted after a year were still working, but we could not collect enough data to analyse movement details for any individual in more than one year.

The tracking device is solar-powered and includes a GPS receiver and a tri-axial accelerometer which measured acceleration in surge (X), sway (Y) and heave (Z) at 20 Hz. Tracking data is downloaded via a wireless network, which can also be used to upload new sampling schemes. The trackers were set to record position at an interval of 10 minutes. When possible, the trackers were set to sample at a high interval of either 15 or 30 s intervals for about 4 hours around day-time low tide. When battery voltage was low, the trackers stopped recording. Position fixes were always followed by 10 seconds of acceleration measurements.

In crab plovers, acceleration measurements can be usefully transformed into five behaviours: body care, inactive, handle, tactile search, fly and walk (Chapter 9).

Timing of foraging movements

Non-foraging crab plovers aggregate on roosts, usually around high tide, were they remain mostly inactive (Chapter 6). Thus, to study how crab plovers schedule their timing of foraging

Table 10.1. Number of tides at which tracks were obtained from each tracked birds, the number of 'complete' tracks collected (defined as a track at which more than 90% of the 10 minute interval measurements were collected) and the number of tides during which high resolution measurements were obtained.

	2012					2014					
	#674	#675	#680	#681	#682	#2008	#2114	#2116	#2117	#2118	#2119
# of tides tracked	80	58	49	79	78	35	21	26	41	44	55
# of 'complete' tides	38	23	29	33	43	32	15	22	30	42	43
# of tides with high resolution data	26	27	20	25	20	8	9	11	10	19	22
# of tides between first and last tide	79	74	70	79	79	35	23	24	53	44	55

movement we analysed periodic patterns of distance to the roost and the amount of active behaviour using the Lomb-Scargle or least-squares periodogram method. The Lomb-Scargle method is an alternative to traditional Fourier analysis and is ideal for analysing tracking data as it can be used on unevenly sampled data (Péron *et al.* 2016). The roost was defined as any position on the mainland. The amount of active behaviour was defined as the percentage time spent on all behaviours except no-motion and body care, as measured with the acceleration based ethograms (Chapter 9). For computational convenience a dataset was created on a 10-minute interval. For tides in which higher resolution data was collected we created 10-minutes data by making bouts of 10 minutes in which we calculated the median position and the average percentage of all behaviour.

We found that the foraging movement of crab plovers followed a tidal as well as a circadian rhythm. In the night birds stayed closer to their roost and were less active. As the water level is in general higher during the night (see above) we studied if the foraging movements in the night were a result of the day-night cycle or of the water level. To this end we selected for each bird and per low-tide water level an equal number of day and night tides. Day tides where defined as tides with a low-tide time more than 2.5 hours prior to sunset or 2.5 hours after sunrise and a similar approach was used to define night times. Confining measurement to 2.5 hours around low tide, we calculated for each selected tide and per bird the average distance to the roost and the time spent inactive. We then compared whether any of these factors differed between day and night using linear mixed-effect models with individual as a random effect. All analyses were done using the R software (R Development Core Team 2013). Distance to roost was calculated using the *gDistance* function in the *rgeos* package, Lomb-Scargle periodograms using the *lsp* function in the *lomb* package and mixed-effect models using the *lme* function in the *nlme* package.

Following the waterline or exploring the exposed intertidal mudflats?

To study whether crab plovers followed the water line or explored the mudflats we calculated the distance to the waterline for each position. This was done by first extracting for each measurement the tidal height at that specific moment from the tide measurements at Masirah. As tidal measurements were available at an hourly basis we interpolated the tidal height using the *ftide* function in *TideHarmonics* package in the R software. We then calculated the position of water line, based on the bathymetry map available for the area (Chapter 3). This was possible because the bathymetry map gives a measure of elevation relative to the waterline. In our approach the waterline is given as a defined position of the waterline, whereas in reality the transition between exposed and flooded mudflats is not so stringent, especially with the ebbing tide. The calculations were done on the 10-minute interval data. Besides that we calculated the distance to the water for the real positions, we additionally calculated the distance to the water for a simulated bird exploring the mudflats, i.e. for each measured position we simulated a random location on mudflats that were exposed at that moment. We calculated the distance to the waterline using the *gDistance* function in the *rgeos* package in the R software. Negative distances indicates positions in the water and positive distances positions on exposed mudflats. As the bathymetry map did not cover the reefs found in the low tidal zone we excluded all locations on reefs.

Patch use

We studied if bird stayed longer at a place, further referred to as a patch, when successful. A patch was defined by the foraging animal's behavior (c.f. Kacelnik & Bernstein 1988); if a bird travelled more than 200 m in 10 min we assumed that it entered a new patch. Birds were assumed to be successful if they were found handling, indicated by the acceleration data. To exclude the possibility that birds stayed longer in a patch because it was handling, patch-residence time was calculated as the time spent in a patch minus the time spent handling in that patch. Because acceleration data was obtained for about 33% of the time, the exact total handling time in a patch could not be directly calculated. Therefore, we estimated the total time spent handling in a patch as the average time handling multiplied by the total residence time. We also checked if birds spent more time inactive in 'handling patches', for instance to digest food.

Furthermore we studied if the decision to leave a patch was related to a decrease in handling time (i.e. foraging success) and to the water level. For this latter analysis we divided each patch visit into two halves of equal duration and then calculated if birds handled more in the first part. We used the R package *recursive* to define patches and to calculate patch-residence time. Calculations of patch use were based on the high-resolution data (Table 10.1). To make sure that we included positions of foraging birds only we excluded all positions less than 200 m away from the roosts and positions where birds were flying. For the statistical analysis we calculated per bird the mean patch residence time for 'handling patches' and 'no-handling patches'. To explore possible cues that underlie the decision to leave a patch we analysed the relationship between patch-residence time and handling probability and the relationship between time spent inactive and handling probability with linear mixed models, using the R package *nlme*. Likewise we analysed if the distance to the waterline at patch departure differed between 'handling patches' and 'no handling patches', making a distinction between the ebbing tide and the flooding tide. Bird id was entered as random effect. Visual inspection of the residual plots revealed no deviations from normality.

Revisit rate

To study if birds revisit places in subsequent tides we calculated for each bird a revisit rate against the tidal time lag. For each tidal time lag x the revisit rate was calculated as the number of revisited places on tide $t + x$ divided by the number of visited places on tide t (hence a value of 1 would mean that all sites were revisited and a value of zero no revisits). To this end we used the *getRecursions* function in the R package *recursive* (Bracis *et al.* 2018). We used a circle with a radius of 200 m moving along the trajectory with 10-minute data. At each point, the number of trajectory segments entering and exiting the circle was counted to determine the number of revisits (Bracis *et al.* 2018). The studied spatial scale of 200 m matches with the scale at which we sampled the prey of the crab plover (Chapter 3). Smaller and larger radius (100 m to 1000 m) gave qualitatively similar results. Positions less than 200 m away from the roosts and positions where birds were flying were excluded. Only itineraries in which the tracker was on for more than 90% of the time were included (Table 10.1). To explore possible causes of individual differences in revisit rate we relate for each individual its mean revisit rate for the first 23 tides (the maximum time lag for bird #2114) to the mean distance travelled per tide (calculated as the sum of the distances between each point) using linear models. Likewise we related for each individual the mean revisit rate to the average time handling per tide (as a measure of absolute foraging success) and to the average time handling divided by the average time searching and walking (as a measure of relative foraging success) using linear models. Furthermore we tested if there was a difference in revisit rate between birds that were found provisioning and birds that were not seen provisioning (referred to as independent) using a one-way ANOVA.

Results

Timing of foraging movements

Lomb-Scargle periodograms showed a clear peak at 12.4 hours and 24 hours in the distance to the roost and active behaviour (Table 10.2). This means that crab plovers exhibit both a tidal and circadian foraging rhythm. Actograms (Fig. 10.4A and Appendix A10.1) and ethograms (Fig. 10.4B and Appendix A10.1) showed that the 12.4 peak is related to the tidal height, with birds going further from the roost (Fig. 10.5 and Appendix A10.2) and being less active around low tide. In the night, birds were closer to the roost and were less active than during the day (Fig. 10.4). In the subset of data in which we tested if the tendency to stay closer at the roost was related to the day-night cycle or to the water level we found no difference in distance to roost (t = –1.007048, df = 10, P = 0.34), and in activity t = –1.49654, df = 10, P = 0.14), suggesting that the differences in the day-night cycle are exclusively related to the tidal cycle, rather than to the light-dark cycle.

Table 10.2. Frequency values of the first and second peak measured with Lomb-Scargle periodograms. Values give medians and interquartile range calculated over estimates per individual.

	first peak (hrs)	**second peak** (hrs)
distance to roost	12.40 (12.38 – 12.44)	23.99 (23.91 – 24.07)
active behaviour	12.43 (12.41 – 12.45)	23.99 (23.90 – 24.08)

Following the waterline or exploring the mudflats?

Although there was considerable variation between individuals and between tides (Appendix A10.3), in general crab plovers stayed close to the waterline rather than exploiting the entire tidal flats at low tide (Fig. 10.5). With the outgoing tide birds lagged behind the waterline and with the incoming tide, around two hours after low tide, the water line took over the birds (Fig. 10.5).

Patch use

Birds stayed longer at patches where acceleration data showed that it has been handling (t = 15.904790, df = 10, P = 0, Fig. 10.6). The tendency of birds to stay longer at 'handling patches'

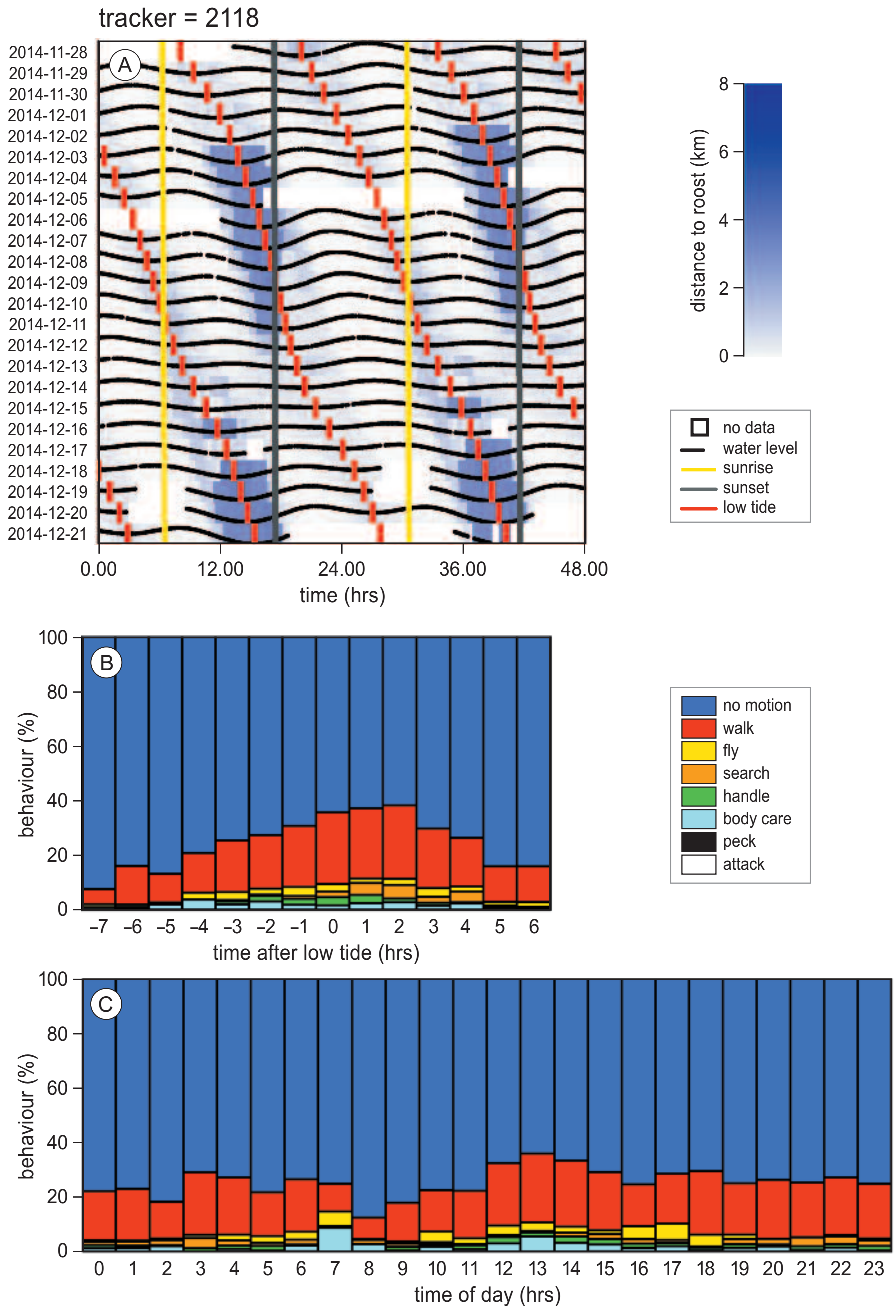


Figure 10.4. (A) Example of the actogram showing the distance to the roost over time (the darker the blue the further away) for the bird with tracker #2118. Note that between 2 and 11 December when the bird moved closer to the roost around sunset (timing of sunset given by dark-grey line). Ethograms showing the different behaviours of the same crab plover in relation to the time after low tide (B) and the time of the day (C). The data was pooled for all tides and hours respectively. See the actograms and ethograms for all studied birds in Appendix A10.1.

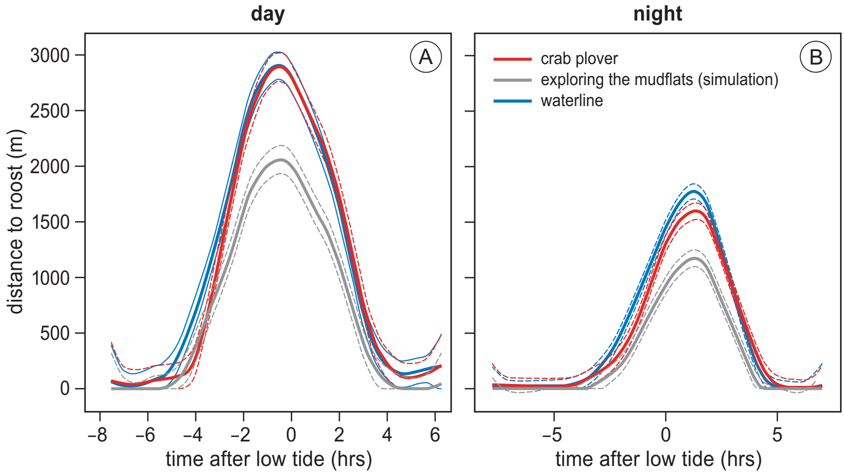


Figure 10.5. Summary of the movements of crab plovers in relation to the tidal cycle during (A) day and (B) night. The red lines show the distance to roost in relation to the time after low tide. The blue lines show the average distance to the waterline added to that of the distance to the roost, thus showing that birds before low tide move slightly behind the waterline and after low tide birds spent on average more time in the water. The grey line show a simulation of a bird randomly exploring the exposed mudflats. Solid lines are average lines interpolated with a loess smoother, dotted lines show 95% confidence intervals showing variation between individuals. See Appendix A10.2 & A10.3 for graphs on distance to the roost and distance to the waterline for individual birds.

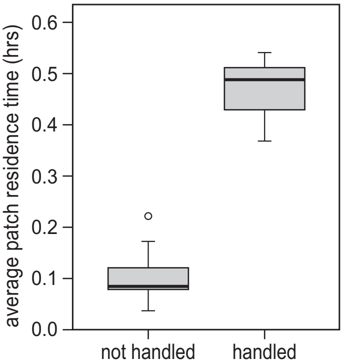


Figure 10.6. Average patch residence time on patches where birds did not and did handle prey items (according to acceleration data). Residence time was calculated by excluding the time spent handling so, the tendency to stay longer at a patch was not because of the time spent handling. Boxplots show variation in individual averages.

was not because birds spent more time inactive as there was no difference in the percentage of time inactive between ‘handling patches’ and ‘no-handling patches’ (t = –0.94974, df = 10, P = 0.3646). The average time spent handling was equally long in the first half within a patch compared to the second half (t = –0.2129012, df = 10, P = 0.2052). At the patch departure time, the distance to the waterline did not differ between ‘handling patches’ and ‘no handling patches’ neither at the ebbing tide, nor at the flooding tide (t = 0.1646353, df = 30, P = 0.87).

Revisit rate

In general the tracked birds revisited less than 20% of the places (Fig. 10.7A). The revisit rate decreased with increasing time lag between tides and approached 0 after around 50 tides. For the first 10 tides the revisit rate showed a clear zigzag pattern in relation to the time lag, meaning that the revisit rate was a higher at each second-next tide (Fig. 10.7A), which coincides with the mixed semi-diurnal tidal pattern (Fig. 10.2). In addition, the revisit rate showed a peak after about 30 tides, which coincide with the recurrent pattern in water level (Fig. 10.2). There was no relation between mean revisit rate and mean distance travelled per tide (F = 1.118, df = 1, P = 0.3180), the average time spent handling per tide (F = 2.668, df = 1, P = 0.1368) and the relative foraging success per tide (F = 2.068, df = 1, P = 0.1843). The two birds that were observed provisioning a juvenile bird had a significant higher revisit rate than independent birds (Fig. 10.7B, F = 9.606, df = 1, p = 0.0127).

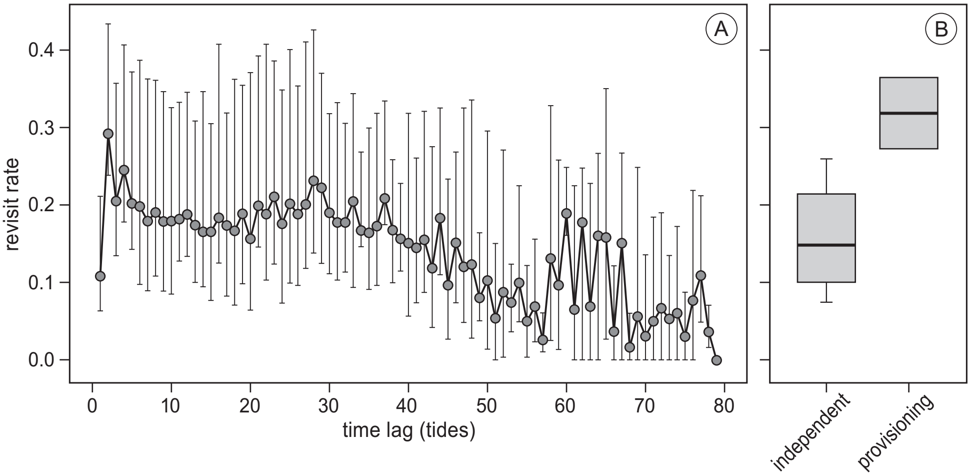


Figure 10.7. (A) Revisit rate as a function of time lag. Red points show the mean revisit rate calculated over individual mean. Error bars show 95% confidence intervals. The number of individuals included for each time lag can be obtained from Table 10.2. (B) Variation in revisit rate for birds that were observed to be independent and that were seen provisioning a first-winter bird. Boxplot show variation in mean individual revisit rate calculated over the first 23 tides.

Discussion

Our tracking data showed that all movements and behaviour of crab plovers within Barr Al Hikman was tightly structured by the tidal rhythm of 12.4 hours. As expected, crab plovers stayed close to the roost and remained inactive around high tide. During periods of 8-10 hours around low tide, crab plovers moved away from their roost and were actively foraging. Less expected, but clearly shown by our data, is that in addition to the tidal rhythm crab plovers exhibited a circadian rhythm of 24 hours, as birds stayed closer to the roost and were less active at night. Yet, the water level in the night tides are in general higher (Fig. 10.2A and 10.3B) and the analysis in which we compared day and night tides with similar water levels showed no differences in activity or distance to roost. This indicates that also the nocturnal movements of crab plovers are closely linked to the tidal cycle, rather than to the dark-light cycle.

Although the general conclusion is that movements of crab plovers are closely linked to the tidal cycle, it was obvious from the actograms that at some occasions the tracked birds strongly reacted to the nightfall when they moved closer to the roost. Inspection of the data shows that this movement was often from the reefs to the mudflats, suggesting that feeding opportunities interact with place and day and night. Furthermore, the behaviour of the tracked birds correlated with sunrise, when birds showed a peak in body care and flying (Fig. 10.4C and Appendix A10.1). The peak in flying, we assume, is a response to avian predators, notably marsh harriers *Circus aeruginosus*, which are mainly active at that time period.

Crab plovers almost always stayed close to the water line (Fig. 10.5). This indicates that they preferably foraged on prey that is active at or close to the waterline, as is the case in several other shorebirds (Both *et al.* 2003; Granadeiro *et al.* 2006; Piersma *et al.* 2017). Detailed observations on crab plovers in Barr Al Hikman, in a confined area up to 2 km from the coasts (i.e. roost), shows that crab plovers primarily forage on swimming crabs, and to a lesser extent on burrowing crabs, fish and shrimps (Chapter 8). Outside this area crab plovers could not be studied visually, but the tracking data suggests that crab plovers continued foraging on swimming crabs, fish and shrimps (and not on burrowing crabs), as these are the species that are active in or close to the waterline on occur throughout the entire tidal zone (Chapter 2, 3).

Accelerometer data indicated that birds, while following the waterline, stayed longer at ‘patches’ in which prey items were found (Fig. 10.6). In these ‘handling patches’ birds remained active, so the tendency to stay longer was not because of prey digestion. This suggests that crab plovers continued searching for prey at places where they have been successful: a behaviour known as area-restricted search (Smith 1974; Benhamou 1992). Area-restricted search has been documented before in shorebirds foraging in a tidal landscape (Dias *et al.* 2009; van Gils *et al.* 2015), and is beneficial for a forager when prey densities are spatially autocorrelated, which is found in many tidal resources (Kraan *et al.* 2009). Indeed, also swimming crabs, the preferred prey of crab plovers, show some degree of autocorrelation, but this differs between years (Appendix A10.2).

Our tracking data did not reveal the nitty-gritty details of what determines a crab plover to leave a patch. The time spent handling in a patch was equally long in the first half of the patch compared to the last half, suggesting that the decision to leave a patch was not because birds were less successful over time. We also did not find that birds left the ‘handling patches’ later with respect to the ingoing or outgoing tide, suggesting that the water level was also not the cue to leave a patch. Further research, perhaps a combination of tracking data and visual observations, is required to better understand what affects the decision to leave a patch.

While following the waterline, crab plovers did this rather ‘opportunistically’ as birds hardly revisited locations between consecutive tides (Fig. 10.7A). Theory predicts that the tendency of animals to revisit sites should increase as the temporal predictability of resource distributions increases (Switzer 1993; Mueller & Fagan 2008), and several tracking studies are in line with this prediction (Weimerskirch 2007; Fryxell *et al.* 2008). Also the ‘opportunistic’ behaviour of crab plovers may well be a result of an unpredictable food source, as swimming crabs tidally move with the waterline and therefore, between tides, the spatial predictability may be low (Chapter 3 and 8). Yet, there may be some temporal predictability in the prey, as birds tended to revisit sites more often in tides with a similar low-tide water level, indicated by (1) the zig-zag pattern in revisit rate (and matching with the mixed semi-diurnal tide, Fig. 10.2A) and (2) the tendency to revisit sites more often after about 30 tides (matching the lunar-driven recursive tidal pattern at Barr Al Hikman, Fig. 10.2A). Finally, we cannot exclude that the ‘opportunistic’ behaviour of the crab plovers is a result of food depletion, caused by crab plovers. However, given that the prey is active in the waterline and may well redistribute with every tide, we do not consider this a likely possibility.

The tendency to return to previously visited sites differed considerable between individuals (Fig. 10.7A). These differences likely reflect variation in the individual itself rather than variation in the environment because the studied crab plovers moved in the same area. Yet, for now we have little knowledge on the nature of individuality in crab plovers, and the number of tracked birds restrict extensive analysis at the individual level. Interestingly however, the two birds that were observed provisioning a first winter bird had the highest revisit rate of all birds (Fig. 10.7B). This was not a consequence of restricted mobility, which is sometimes found in animals that accompany their offspring (van Beest *et al.* 2011), as the total length travelled per tide did not show a relation with revisit rate. We speculate that the benefits of returning to the same area may be found in not losing each other.

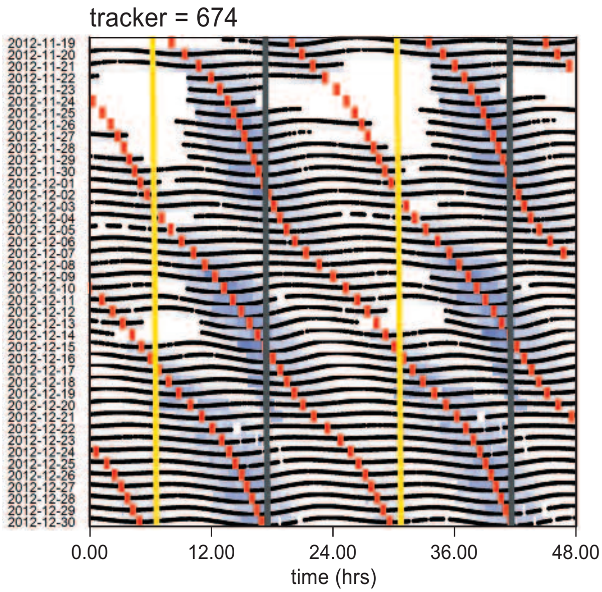
Finally, we acknowledge that we did not consider interactions with conspecifics or predators, whereas both are well known to affect space use in shorebirds (Both *et al.* 2003; Folmer & Piersma 2012; van den Hout *et al.* 2014). Indeed, the peak in flying behaviour in the sunrise hours, presumably in response to marsh harriers, shows that it is not only foraging that matters in the lives of crab plovers wintering at Barr Al Hikman. Furthermore, although crab plovers do not forage in closely aggregated groups, they do forage loosely together, and so a decision to stay or move may also be influenced by the foraging success of conspecifics (such as in red knots, Bijleveld *et al.* 2015b). Although all such factors may affect foraging decisions, we believe that with the current study we have taken a big step in unravelling the mechanisms that drive behaviour and space use of crab plovers, which may contribute to better understand of the movement ecology of tidally foraging shorebirds in general.

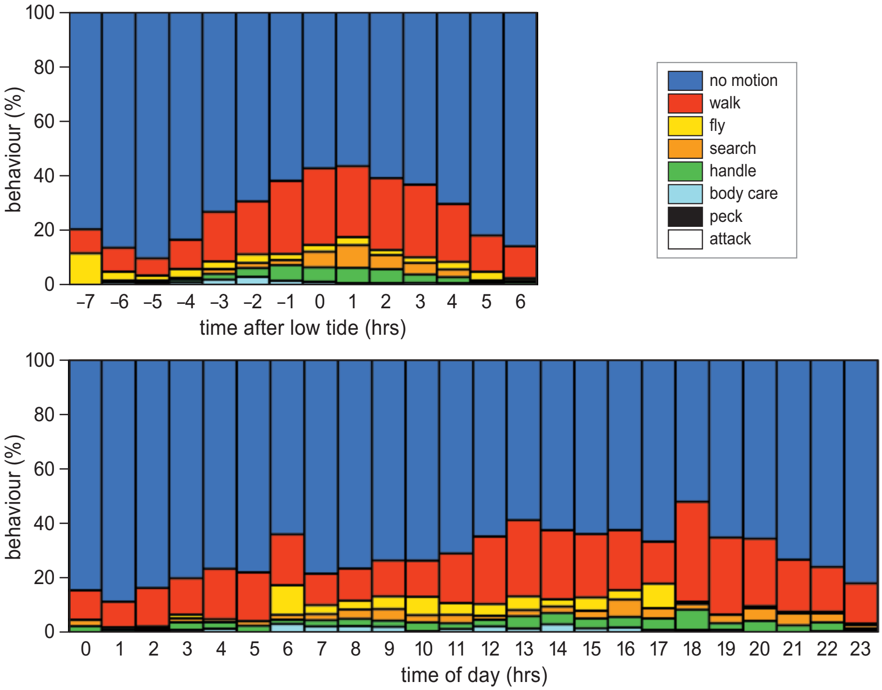
Acknowledgements

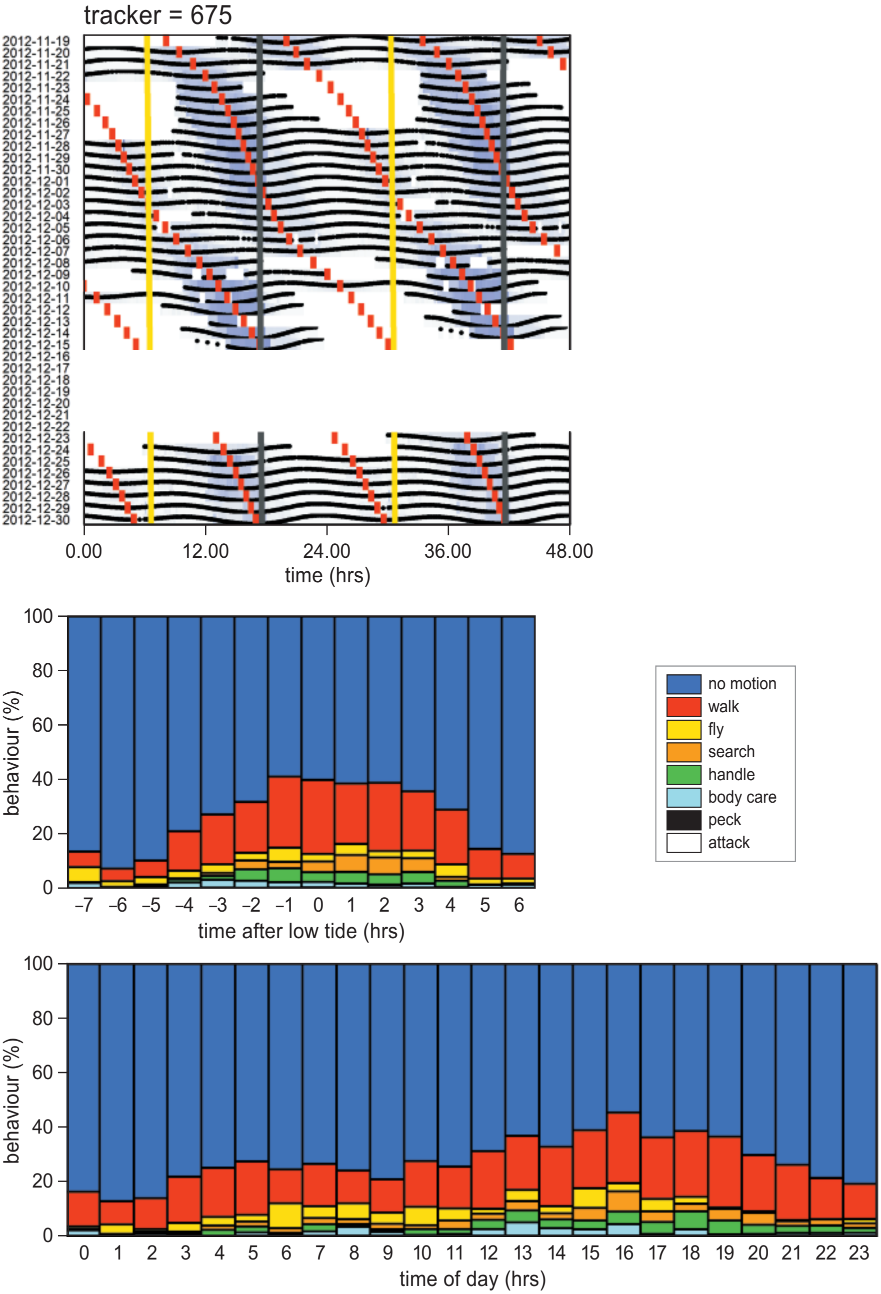
Many volunteers helped with catching and tracking of crab plovers. We especially thank Kees Oosterbeek and Symen Deuzeman for exciting times in the field. We thank Allert Bijleveld, Martin Bulla and Thomas Oudman for inspiring discussions. Our study was financially supported by the Research Council (TRC) of the Sultanate of Oman (ORG/EBR/12/002 grant awarded to AYK) and by NWO in the Netherlands (ALW Open Programme grant 821.01.001 awarded to JAvG). Catching, tagging and banding of crab plovers was carried out under permission of the Ministry of Environment and Climate Affairs, Sultanate of Oman. We are grateful to the assistant Director-General Ms. Thuraya Said Al-Sairiri and Director-General Mr Sulieman Al Akhzami for their assistance.

Appendix A10

A10.1 Actograms and ethograms for all tracked birds except for #2118 which was shown in the manuscript



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2012-12-27
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2012-12-29
2012-12-30
0.00
12.00
24.00
36.00
48.00
time (hrs)
behaviour (%)
100
80
60
40
20
0
–7 –6 –5 –4 –3 –2 –1 0 1 2 3 4 5 6
time after low tide (hrs)
no motion
walk
fly
search
handle
body care
peck
attack
behaviour (%)
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60
40
20
0
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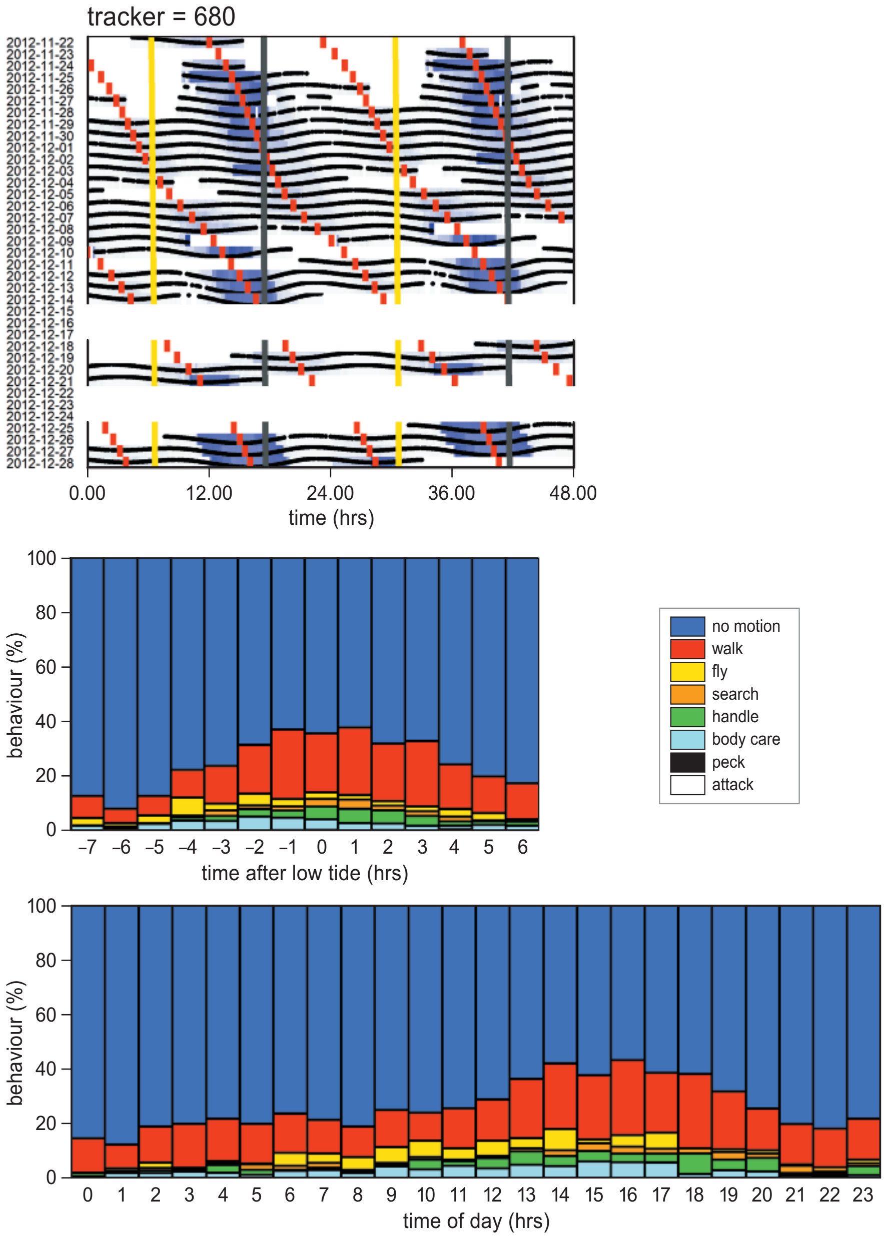
time of day (hrs)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2012-12-28
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48.00
time (hrs)
behaviour (%)
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40
20
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–6
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–3
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–1
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1
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5
6
time after low tide (hrs)
no motion
walk
fly
search
handle
body care
peck
attack
behaviour (%)
100
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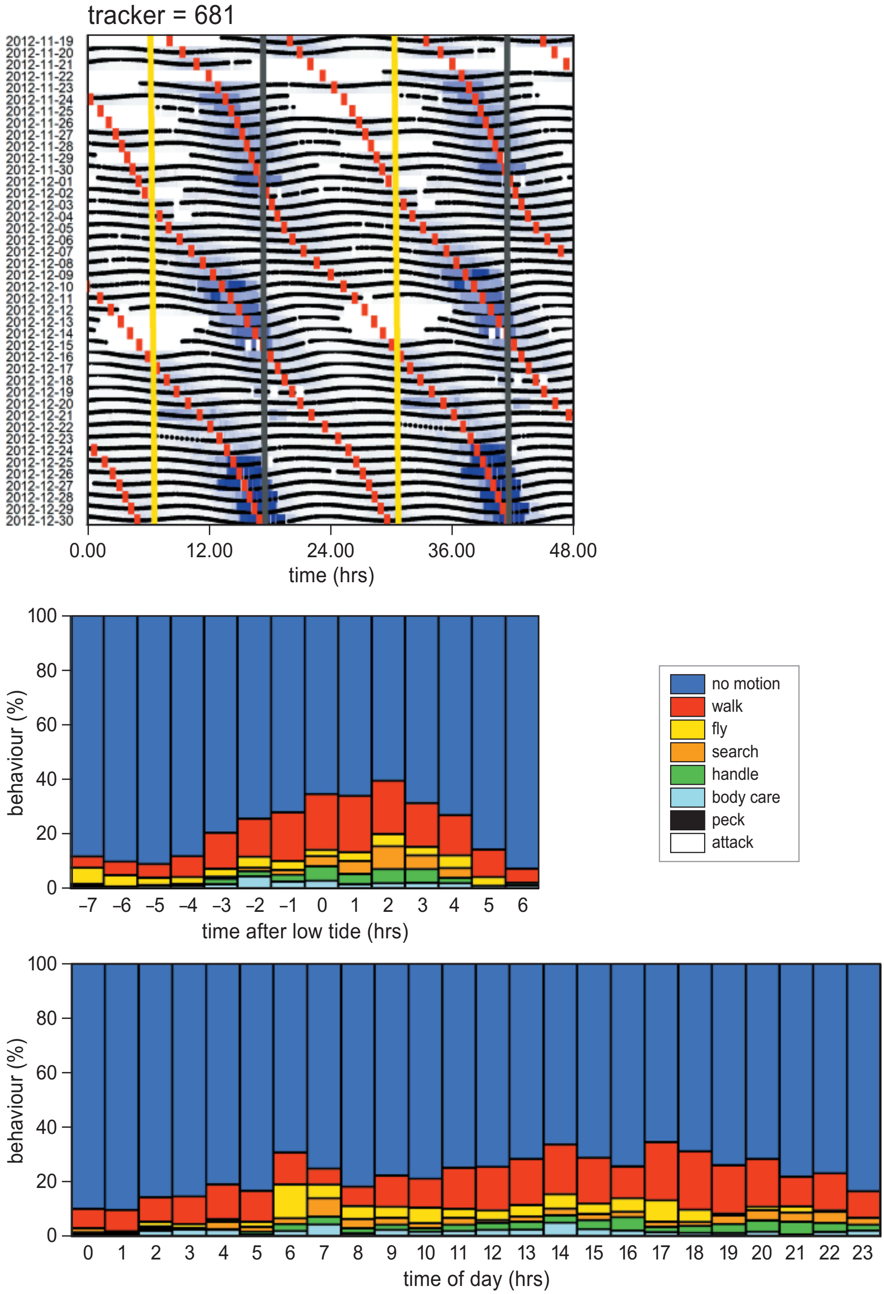
22
23
time of day (hrs)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2012-12-30
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time (hrs)
behaviour (%)
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time after low tide (hrs)
no motion
walk
fly
search
handle
body care
peck
attack
behaviour (%)
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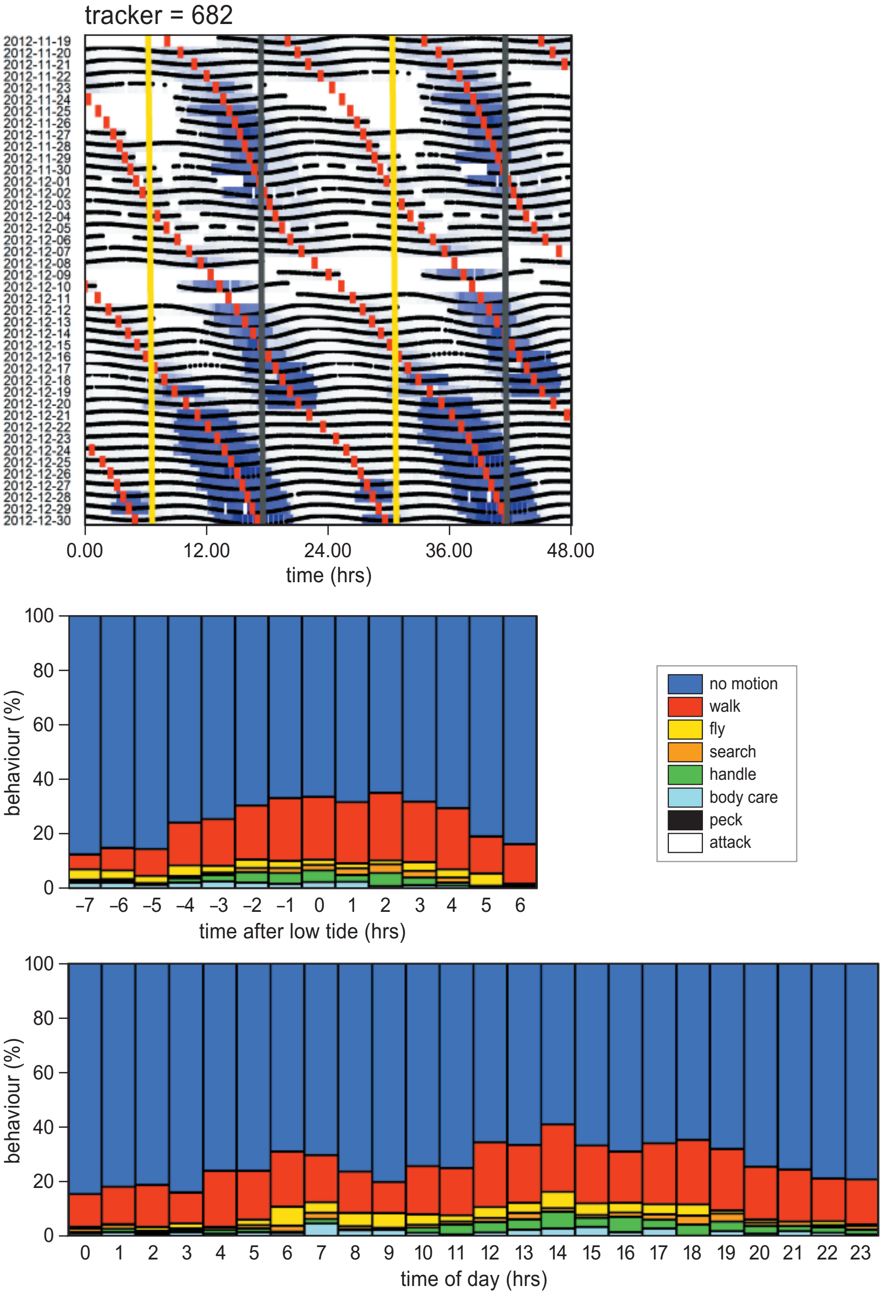
time of day (hrs)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time (hrs)
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behaviour (%)
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time after low tide (hrs)
no motion
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body care
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behaviour (%)
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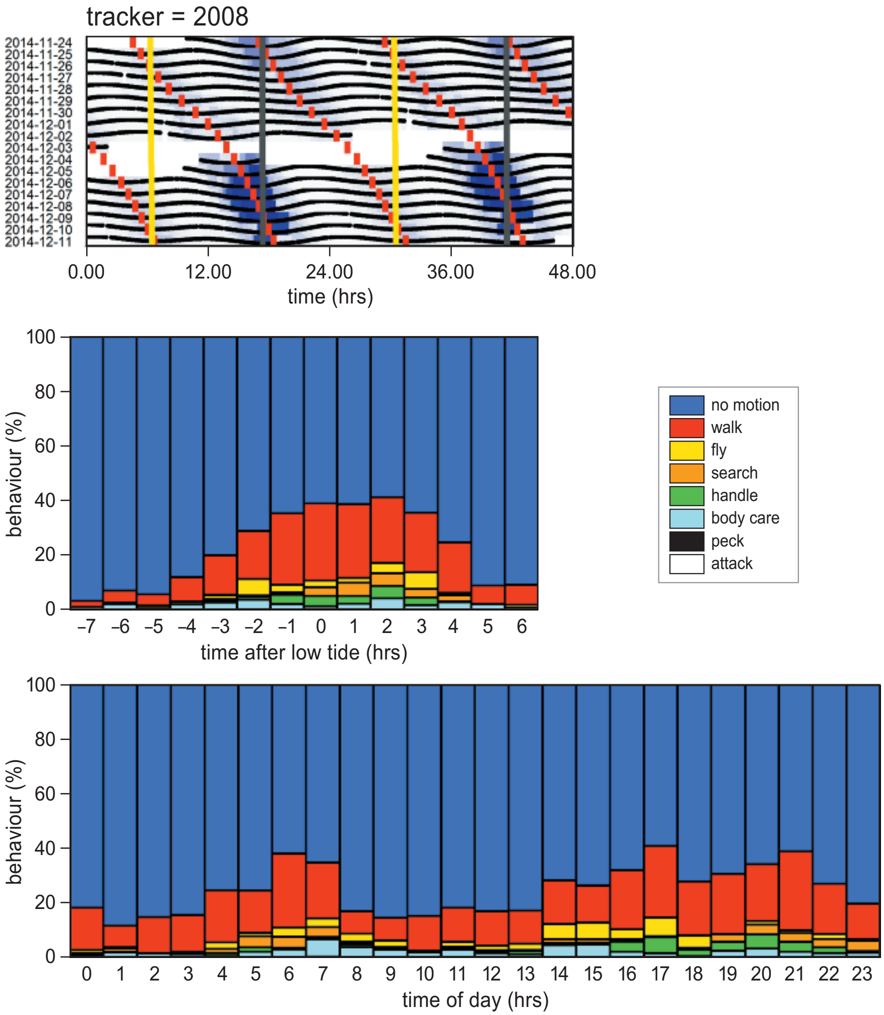
time of day (hrs)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time (hrs)
behaviour (%)
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time after low tide (hrs)
no motion
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search
handle
body care
peck
attack
behaviour (%)
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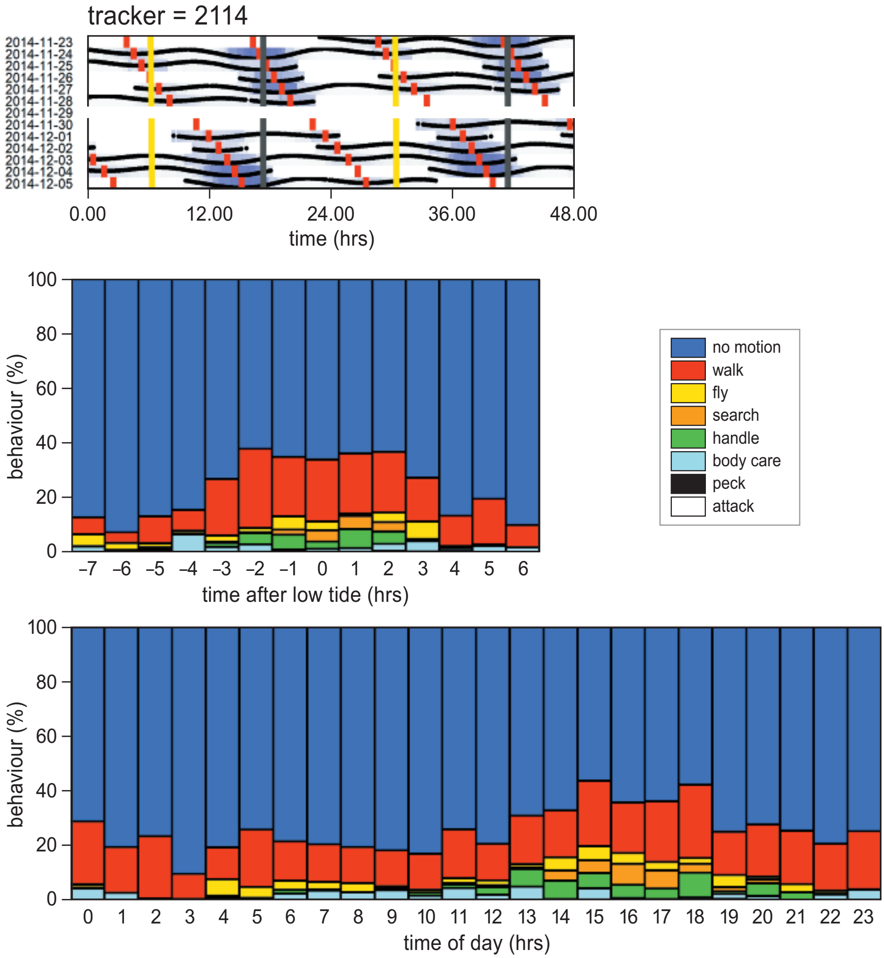
time of day (hrs)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time (hrs)
behaviour (%)
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time after low tide (hrs)
no motion
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search
handle
body care
peck
attack
behaviour (%)
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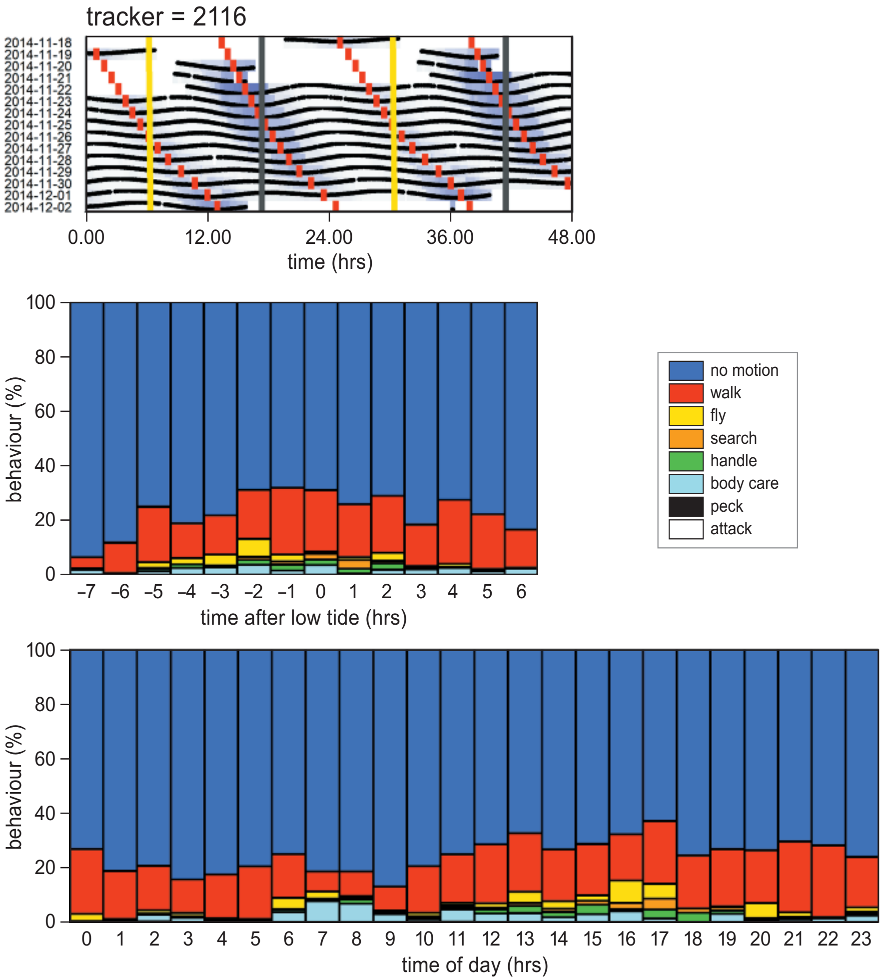
time of day (hrs)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time (hrs)
behaviour (%)
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time after low tide (hrs)
no motion
walk
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peck
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behaviour (%)
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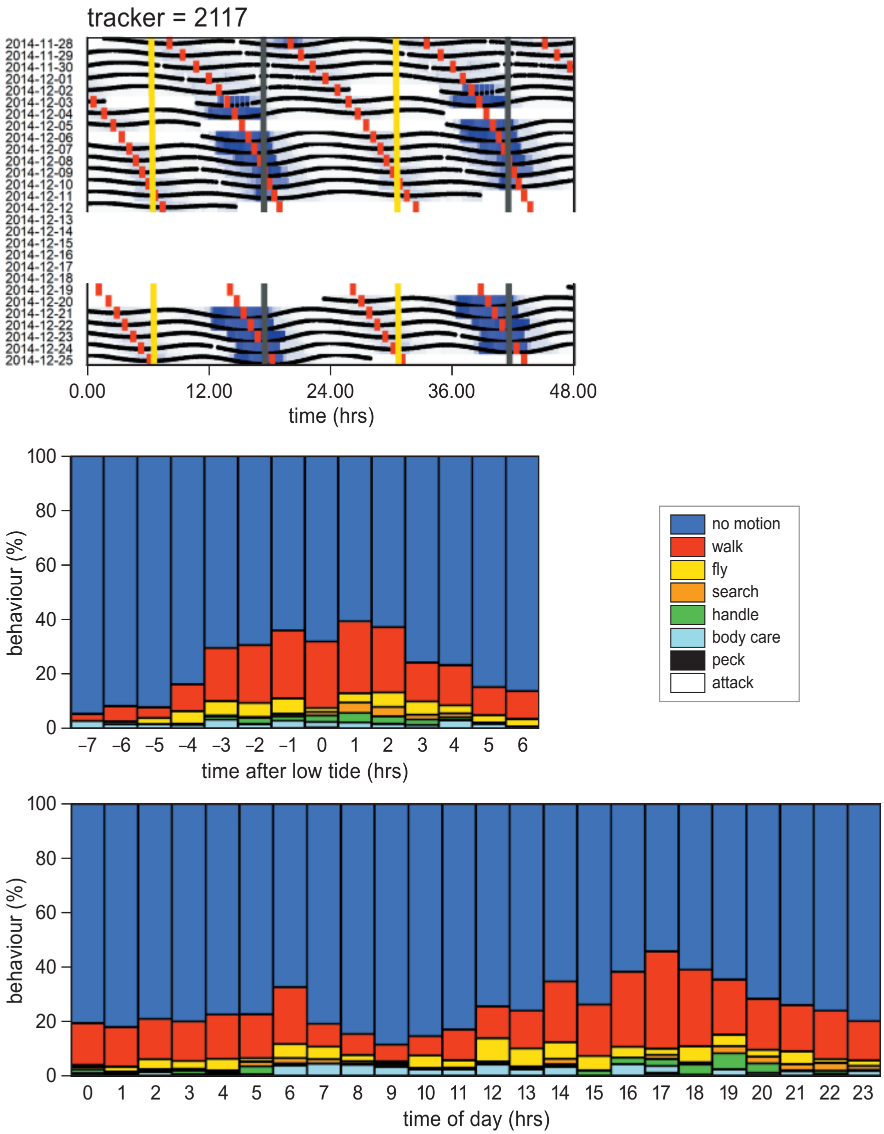
time of day (hrs)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time (hrs)
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time after low tide (hrs)
no motion
walk
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search
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body care
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attack
behaviour (%)
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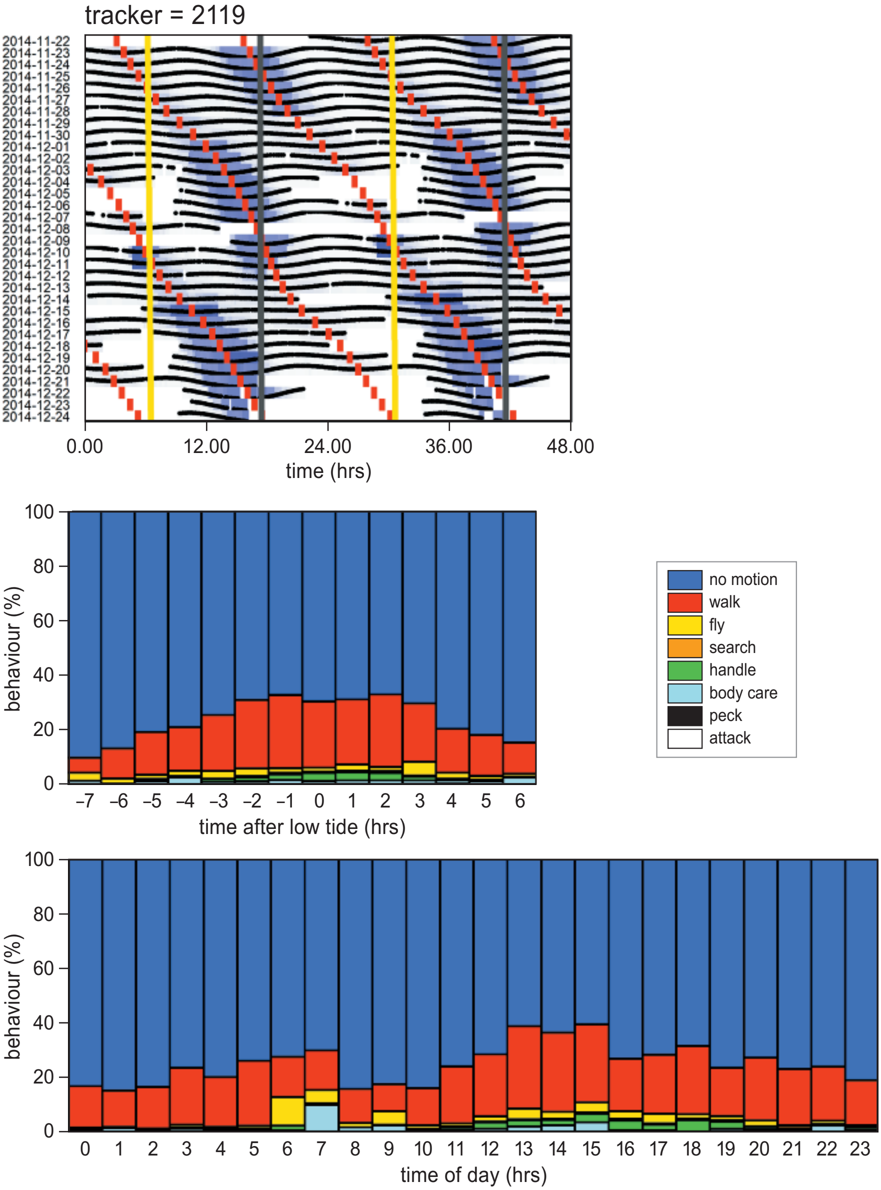
time of day (hrs)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48.00
time (hrs)
behaviour (%)
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−1
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6
time after low tide (hrs)
no motion
walk
fly
search
handle
body care
peck
attack
behaviour (%)
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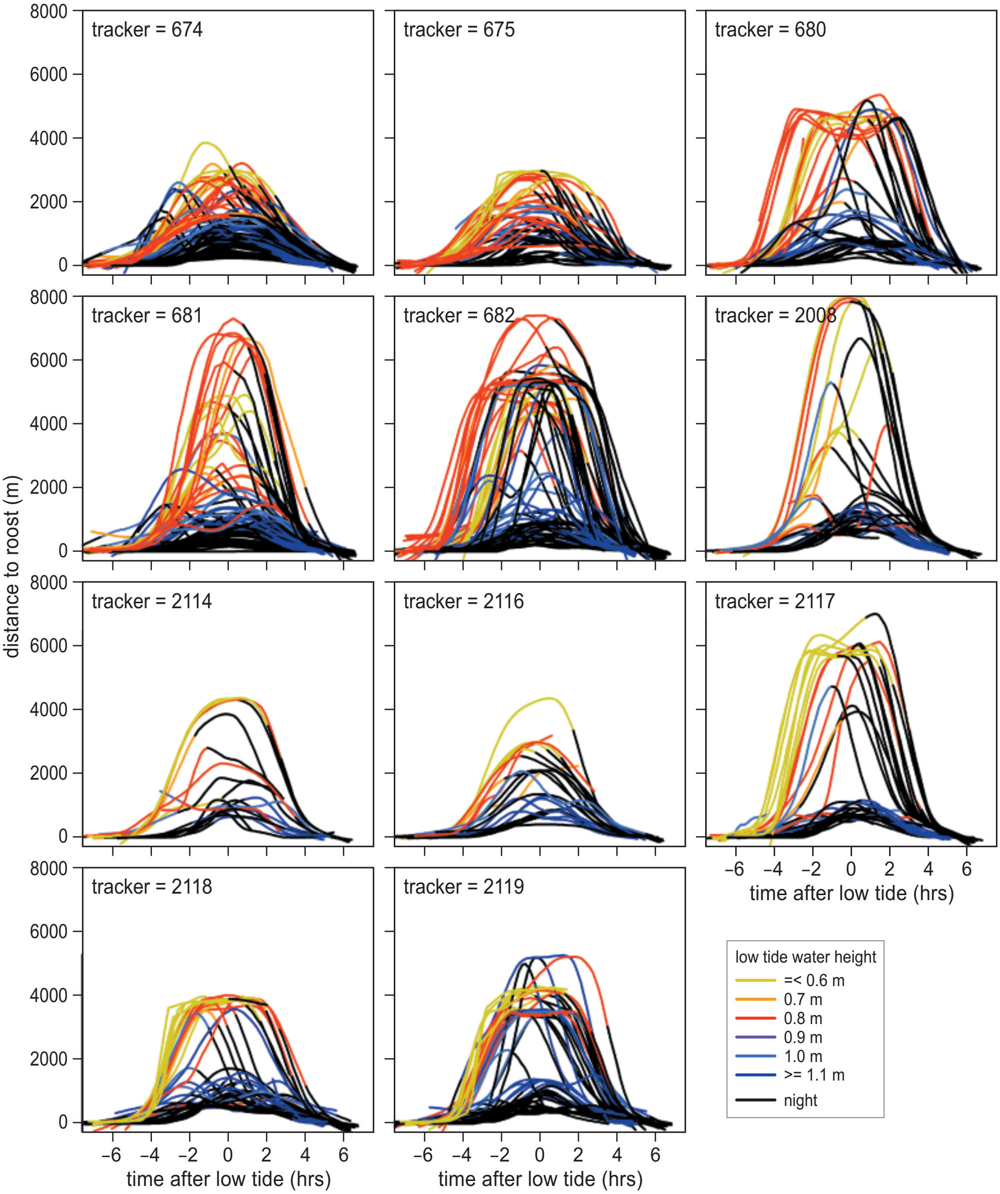
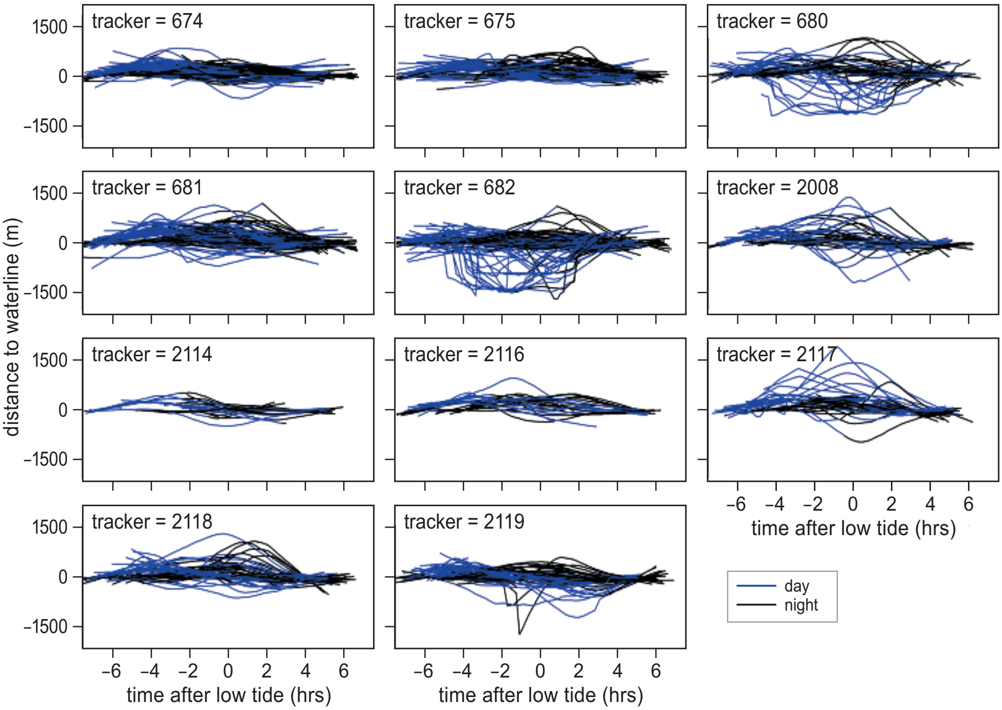
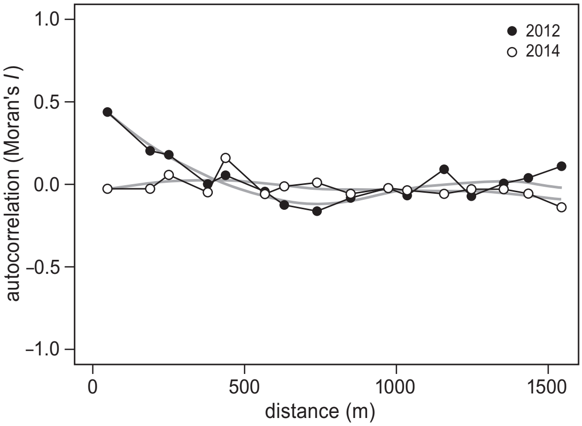
23
time of day (hrs)



Appendix A10.2. Individual variation in the distance to the roost in relation to the time to low tide, for all tracked tides. Lines are interpolated with a loess smoother.



Appendix A10.3. Individual variation in the distance to the waterline in relation to the time to low tide, for all tracked tides. Lines are interpolated with a loess smoother.



Appendix A10.4. Correlogram of numerical swimming crab density in the two years of tracking. Spatial autocorrelation was estimated by calculating Moran's *I* values, based on samples collected at a spatial grid of 200 m, plus additional random points (for details see Chapter 3). Because samples were collected over multiple days we cannot exclude that temporal factors affect the obtained spatial correlation. Yet, at short distances samples were taken on the same day and likely the obtained autocorrelation at distances smaller than 500 m reflects spatial autocorrelation only.

Box B

Migration of crab plovers wintering at Barr Al Hikman

Most crab plovers leave Barr Al Hikman in spring (Eriksen & Victor 2013). The migration and the breeding areas of crab plovers wintering at Barr Al Hikman was previously unknown. We obtained seven migration tracks from six GPS-tracked birds (see Chapter 9 and 10 for tracking details). All birds migrated to breeding areas in the extreme north-west corner of the Arabian/Persian Gulf. Three birds spent the summer at known breeding areas at Dara Island in the very south-west coast of Iran (Tayefeh *et al.* 2011). Three other birds spent the summer at breeding areas in Kuwait (Chapter 11), situated at less than 50 km distance from Dara Island. Six birds ringed at Barr Al Hikman were observed in the same breeding area in the same summer. Together, these two breeding areas host about one-third of the world population of crab plovers (Chapter 11). The local movements of the tracked birds in the breeding areas never concentrated around a single place for more than four weeks, suggesting that none of the tracking birds had a succesful breeding attempt. This may have been a conseqence of the tag, which is situated on the back of the bird and perhaps negatively affects the freedom of movement inside the burrow.

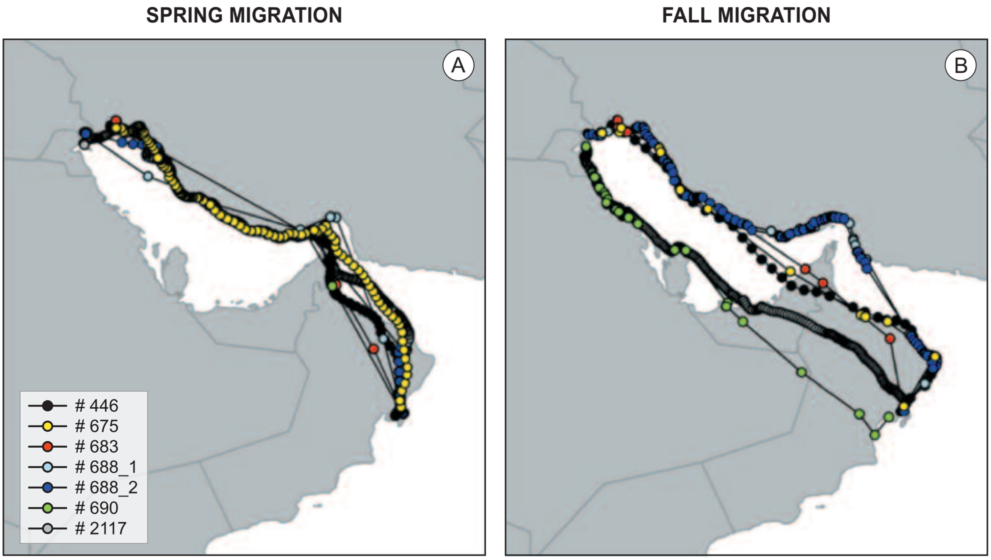


Figure B.1. (A) Spring migration routes of six tracked birds. (B) Fall migration routes for the same birds. Two full migrations were obtained from bird with tracker #688.

All tracked birds took a rather similar route during spring migration. After departing from Barr Al Hikman they migrated straight north, crossing the desert of the Wahiba Sands (Oman) and the Jebel Akhdar mountains (Oman) (Fig. B.1A). The highest recorded altitude was 1495 m, while flying over the mountains. After reaching the north coast of Oman, the birds closely followed the coastline of the Arabian/Persian Gulf further north and west until arrival al the breeding areas in Kuwait and Iran. Because the sampling interval differed between individuals (ranging from 10 minutes to 0.5 days), we cannot compare the distance travelled. The bird with the tracker having the smallest sampling interval, 10 minutes, travelled 2087 km on spring migration, which should be regarded as the minumum distance this bird travelled.

The route during fall migration was more variable among individuals. Four birds migrated along the northern coasts of the Arabian/Persian Gulf. Two other birds followed the southern coasts instead. These latter two birds crossed the empty quarter (the vast desert covering the border area of Saudi Arabia and Oman), flying for about 600 km over the desert. This latter behaviour is in line with one rare observation of a group of crab plovers flying over the middle of the Omani dessert (Mike Jennings pers. comm).

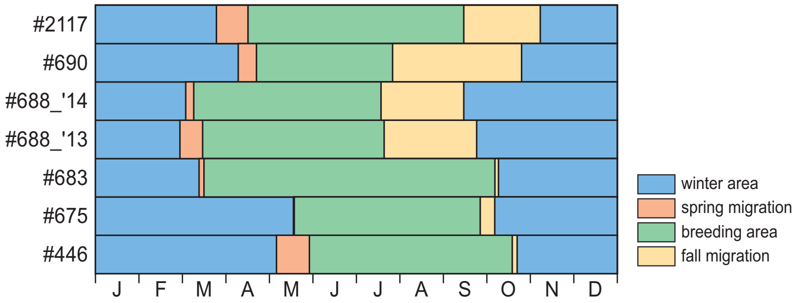


Figure B.2. Annual cycle of six tracked crab plover that winter at Barr al Hikman. Spring migration was defined as the period between departure from Barr Al Hikman and arrival at the breeding areas. Likewise, fall migration was defined as the period between departure from the breeding areas and arrival at Barr Al Hikman.

All tracked birds had several stopovers along the migration route. They usually departed in the early evening and migrated during the night until the early morning and then stopped. Presumably, they did this to avoid flying in the heat. Some birds showed longer stopover periods on both spring and fall migration. The number of days between departure from Barr Al Hikman and arrival at the breeding areas ranged between 3 and 24 days (Fig. B.2). The fall migration took between 3 and 91 days. In spring, the departure date at Barr Al Hikman was related to the arrival date at the breeding grounds, suggesting that crab plovers do not compensate for a late spring departure (Fig. B.3A). In fall there was no relation between the date of departure at the breeding areas and date of arrival at Barr Al Hikman. Early departing birds arrived in the wintering area around the same week as late departing birds (Fig. B.3B).

One bird was tracked for two subsequent years. The migration route of this bird was consistent in the two years, and the timing of the major phenological events were within the same week (Fig. B.1 & B.2 & B.3).

This study is the second to report migration tracks of crab plovers. Earlier, one crab plover was deployed with a tracker at its breeding area in the United Arab Emirates. It migrated to Aldabra on the Seychelle islands (also see Chapter 5) (Javed *et al.* 2011).

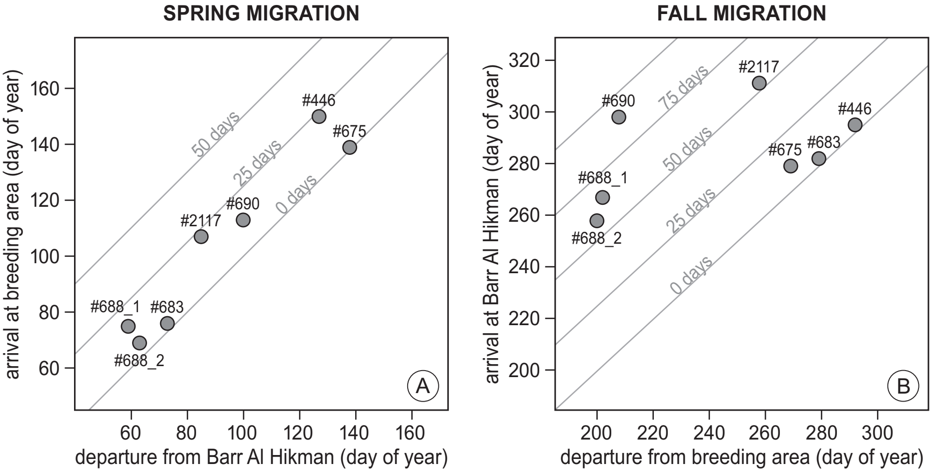
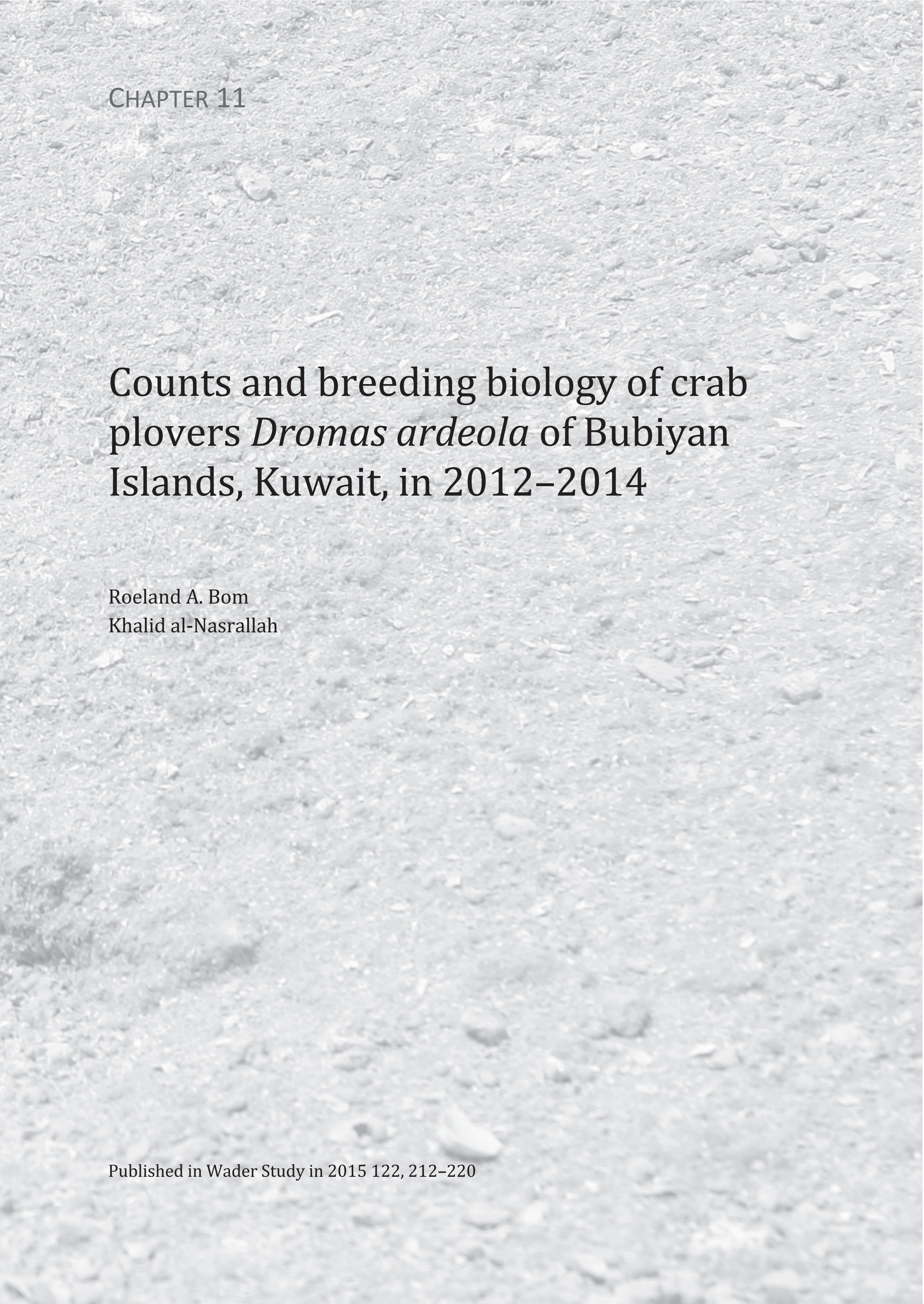


Figure B.3. (A) Spring migration. The day of arrival at the breeding areas is plotted against the day of departure from Barr Al Hikman. (B) Fall migration. The day of arrival at Barr Al Hikman is plotted against the departure day at the breeding areas. Numbers in the circles refer to the tracker IDs.



CHAPTER 11

Counts and breeding biology of crab plovers *Dromas ardeola* of Bubiyan Islands, Kuwait, in 2012–2014

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Abstract

The crab plover *Dromas ardeola* is an uncommonly studied wader, renowned for breeding in colonies inside self-excavated burrows on islands around the Arabian Peninsula. This study presents counts and observations on the breeding biology in several colonies on the Bubiyan Islands in Kuwait during 2012–2014. Up to 1,750 burrows of crab plovers were found in a single year. We estimate that at least 3–5% of the world population uses the Bubiyan Islands for reproduction, making it a very important area for this species. Burrow densities were much higher than those reported in Iran, United Arab Emirates and Eritrea, but nesting habitat availability did not seem to limit the number of nests because colonies never extended over entire islands. The breeding season extended from April to July, and this timing was similar to nearby areas in Iran. The food that the Bubiyan crab plovers brought to the colonies for their young consisted of crabs (75% of all observed prey items) and mudskippers (25%). A review of the currently known breeding areas shows that the breeding areas of crab plovers are confined to at least 56 colonies at 19 sites. All colonies except two can be found in the Arabian Gulf and Red Sea, with the Arabian Gulf hosting about two thirds of all breeding crab plovers. The colonies on the Bubiyan Islands are among the five largest known colonies of crab plovers around the world.

Introduction

Crab plovers *Dromas ardeola* are enigmatic birds, living on the shores of the Indian Ocean. They nest in colonies on small islands around the Arabian Peninsula inside self-excavated burrows (Cramp *et al.* 2004). Crab plovers normally lay a single large white egg that is only partly incubated by the parents, since temperatures inside burrows are thought to be near-optimal for incubation (De Marchi *et al.* 2008; De Marchi *et al.* 2015a). After hatching, both parents provide their offspring with food (Almalki *et al.* 2015). Provisioning continues after the post-breeding migration (De Sanctis *et al.* 2005).

Information on numbers and ecology of breeding crab plovers is limited. The non-breeding population of crab plovers is currently estimated at 60,000–80,000 birds (Wetlands International 2002). In 1996, the number of breeding birds was estimated at only 14,000–15,000 (Aspinall & Hockey 1996), but several colonies have been discovered since then and therefore this estimate needs to be updated. Characteristics of the breeding biology such as timing of breeding, between-year variation in colony size, burrow construction, diet composition during provisioning, social behavior and factors determining reproductive success have been studied at a few colonies, but remain largely anecdotal.

Crab plovers occur year round in the State of Kuwait (Gregory 2005), but there is confusion about the current breeding status of the species. Cowan (1990) suggested that crab plovers probably breed in Kuwait, perhaps on the Bubiyan Islands. Al-Nasrallah and Gregory (2003) confirmed 100 pairs to breed on the Bubiyan Islands. Delany *et al.* (2009) also noted that the species probably breed in Kuwait, but reaches highest densities in autumn and winter. The Arabian Breeding Bird Atlas states that about 1,600 active breeding burrows were estimated on the Bubiyan Islands in 2004 (Aspinall 2010). In September 2015, part of the Bubiyan Islands (Mubarak Al-Kabeer reserve) was designated as a Ramsar site (https://rsis.ramsar.org/ris/2239), partly because it hosts the largest breeding colonies of crab plovers in the world, although actual numbers were not given.

Here, we describe the number of breeding crab plovers in several recently re-discovered colonies on the Bubiyan Islands based on surveys in 2012, 2013 and 2014. Furthermore, we describe aspects of their breeding ecology including timing of breeding, diet composition when provisioning, burrow construction and burrow length. We conclude by updating the list of known colonies and their estimated number of burrows and confirm that the Bubiyan Islands indeed hosts one of the largest breeding colonies of crab plovers in the world, although not the largest as was stated by the Ramsar convention.

Methods

Study area

The Bubiyan complex in NE Kuwait consists of a number of islands, of which Bubiyan Main Island (863 km^2) and Warba Island (37 km^2) are the largest (Fig. 11.1). The area consists of flat sandbanks, which are sparsely vegetated with *Halocnemum strobilaceum*, and a muddy intertidal area intersected by many small and some larger gullies. The intertidal area is home to two species of mudskippers (*Periophthalmus waltoni* and *Boleophthalmus dussumieri*), a number of crab species and large number of species of mollusk and polychaetes species (Al-Yamani *et al.* 2012). The islets in the north-west of the Bubiyan Islands are known to host several breeding colonies of spoonbills *Platalea leucorodia*, slender-billed gulls *Chroicocephalus genei*, gull-billed terns *Gelochelidon nilotica*, caspian terns *Hydroprogne caspia*, swift terns *Thalasseus bergi*, lesser-crested terns *Thalasseus bengalensis*, and crab plovers (Ramadan *et al.* 2004). The area is rarely visited by humans because the many shallow gullies make it difficult to navigate, and because a permission from the Kuwait coastguard is required to access the area. The climate in the area is hot and dry in summer, with average temperatures of 46°C and virtually no precipitation. Winters in Kuwait are cold and wet, with average temperatures of 8°C and average precipitation up to 50 mm per month (data from *http://www.worldweatheronline.com*).

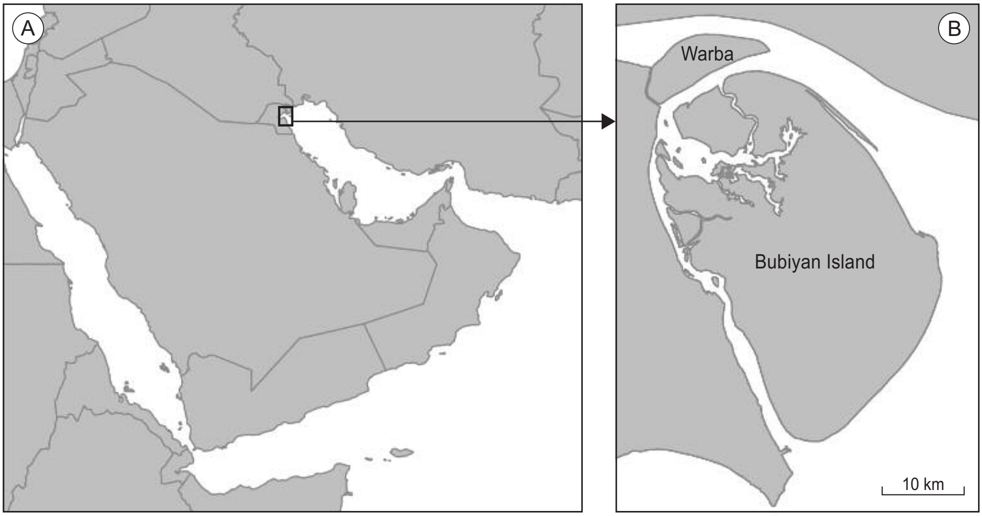

Figure 11.1. The Arabian peninsula with the Bubiyan Islands in the enlargement.

Fieldwork

In 2012, 2013 and 2014, KN searched the area by boat about 7–8 times annually during March–August. In this way, all small islands in the area were checked for breeding colonies. Two visits to the area were attempted per month, but often, especially later in the season, boating was not possible due to prolonged strong winds. In 2013, one of the larger islands was searched by foot twice. In other years, the larger islands were not searched for colonies. Once a crab plover colony was encountered, it was mapped in a handheld GPS. The number of burrows was estimated from a distance; walking in the colony would cause the burrows to collapse. Timing of breeding events was estimated to the month, partly because data collection during visits was descriptive and not systematic, and partly because visits to the area were dictated by favorable winds for boating which resulted in long intervals between visits.

The stage in the breeding cycle was estimated based on the behavior of the adults (e.g. burrow digging, mating, and provisioning prey to hatched chicks). Whenever possible, photographs were taken to identify prey that adults carried to the colony. Occasionally, prey remains were collected adjacent to the colonies. The length of four burrows at the edge of the colonies was measured with a ruler. The interiors of three burrows were inspected using a camera on a stick. During some visits, dead chicks near the burrow entrance were observed and on one occasion measured to estimate the age, using methods presented by Tayefeh *et al.* (2013b).

Results and Discussion

Number and size of colonies

Three colonies were discovered in 2012, estimated to include 100, 100 and 400 active burrows, respectively (600 in total; Fig. 11.2). In subsequent years, more colonies were found due to better knowledge of the area. Five active colonies were found in 2013, estimated at 150, 200, 400, 500 and 500 active burrows (1,750 in total); the latter two colonies were found on one large island. In 2014, four active colonies were found, estimated at 170, 200, 300 and 700 active burrows (1,370 in total), but the large islands were not checked. The colonies described here were all in the same area, and most of them on the same islands, as those reported earlier (by Al-Nasrallah & Gregory 2003, Ramadan *et al.* 2004, Gregory 2005, Aspinall 2010). These earlier reports gave estimations ranging from 100 to 1,600 active burrows. We confirm that the 1,600 active burrows reported by Aspinall (2010) currently are a more realistic number then the 100 burrows presented by Al-Nasrallah & Gregory (2003). The actual number is probably even higher, as some areas still remain unvisited.

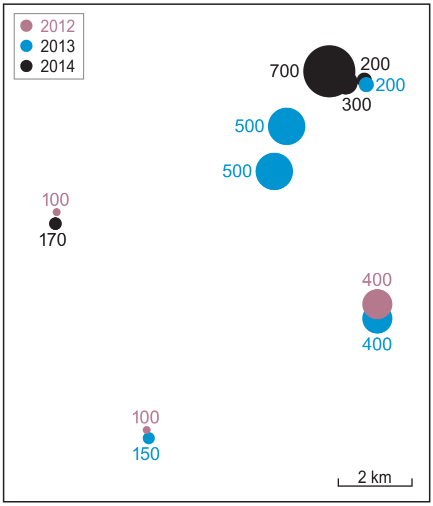

Figure 11.2. Locations of the colonies and their estimated number of burrows in 2012–2014. On request of the local authorities the points are not drawn on a map and the exact locations are not given in order to avoid disturbance.

Tayefeh *et al.* (2013b) found that 25% of burrows were empty in a colony in the Islamic Republic of Iran. In a sub-colony established later in the season, 50% of burrows were empty (Tayefeh *et al.* 2013b). If we assume that 75%of burrows are occupied by one pair each, we calculate that at least 2,625 birds use our study area for reproduction. As the world population of crab plovers is estimated at 60,000–80,000 birds, at least 3–5% of the world population breeds on the Bubiyan Islands, making it an important breeding area for the species as a whole.

Estimated timing of breeding events

Crab plovers are observed in the Bubiyan area all year round (Gregory 2005), but large number of birds started to arrive around mid-March in each year. During the first month after arrival, birds were seen in distinguishable pairs (Fig. 11.3), together forming larger groups. Actual mating was observed once, on 20 April 2014. Burrow excavating started in April (this study), which usually takes a few days (Tayefeh *et al.* 2013b). Presumably, the first eggs were laid after burrow excavation ceased in the beginning of May. Incubation takes around 33 days in crab plovers (Tayefeh *et al.* 2013b). Indeed, eggs hatched in early June, judging by the first day the parents were seen with food in the colonies (on 14 June in 2012, 6 July in 2013, and 4 June in 2014). The relatively late date in 2013 is due to the area not being visited the second half of June that year; judging by the size of chicks, eggs must have hatched in early June in 2013 as well. In June and July juveniles were occasionally spotted outside the burrows. Provisioning in the colonies continued until the end of July. Around August, birds moved out of the colonies and were observed scattered in the area. The number of birds in the area decreased in September and October.

Figure 11.3. A pair of crab plovers at the start of the breeding season. The smaller bird on the left is the female.

In August 2013 one bird moulting its two inner primaries was photographed (Fig. 11.4A) and several other moulting adults were observed. Moulting of outer primaries has been observed moulting in the winter areas (Bom *et al.*, unpublished). Hence, wing feather moult in crab plovers is probably suspended during migration (as was suggested by Cramp *et al.* 2004). Two crab plovers ringed in Barr al Hikman, Sultanate of Oman were resighted in the Bubiyan area (Box B), suggesting that Oman is an important wintering area for the Bubiyan birds. Most crab plovers leave Kuwait in the winter; the maximum winter count in Kuwait was 300 birds (Gregory 2005). We suggest that crab plovers migrate out of Kuwait to more south-eastern areas to avoid the relatively cold winters.

We detected little variation in the timing of breeding among years. The length of the breeding season was also similar to that described for a nearby area in Iran (Tayefeh *et al.* 2013b). The timing differed from colonies further away in the Red Sea in the Kingdom of Saudi Arabia and the State of Eritrea, where crab plovers nest much later in the season (De Marchi *et al.* 2015b). These timing differences are thought to reflect adaptation to local peaks in food availability (De Marchi *et al.* 2015b).

Figure 11.4. (A) Crab plover carrying a crab to the colony. Note the wing moult in the two innermost primaries. (B) Provisioning time: crab plovers with a mudskipper (left) and a crab (right).

Burrows

Crab plovers excavated new burrows every year. They dug burrows with their bills, while sand was moved out with their feet. Small stones were carried out of the burrow in the bill. Similar to other areas, burrows were never occupied a second season (Chiozzi *et al.* 2011), presumably because they become unstable after winter rains. Four of eleven colonies were established adjacent to their locations one or two years earlier. Most colonies were on small (<0.1 ha) islands (e.g. Fig. 11.5), but two colonies, both with around 500 burrows, were found in the middle of a large, barely vegetated island of 10 ha in 2013.

Colonies had high burrow densities, averaging 1.7, 2.3 and 3.0 burrows/m^2 in 2014. These densities are much higher than those measured in Eritrea (Chiozzi *et al.* 2011), Iran (Tayefeh *et* *al.* 2013a) and the United Arabian Emirates (Javed *et al.* 2012) where densities were estimated at 0.33 (range: 0.09–0.95), 0.20 (range: 0.14–0.26), and 0.21 burrows/m^2, respectively. Why burrow densities on the Bubiyan Islands are so high remains a question. Habitat does not seem to be limited, as colonies never filled an entire island. This confirms that crab plovers are true colony breeders (Chiozzi *et al.* 2011). Burrows were much closer to the waterline (Fig. 11.5, but note that this photograph was taken with spring tide high water) than in other areas, judging by photographs and literature (Chiozzi *et al.* 2011). It is likely that with spring floods, these burrows get flooded. It is unclear why some birds choose to nest so close to the shore, as nesting habitat appears not to be limited.

Four burrows at the edge of a colony, measured in June 2014, were on average 140 cm long (SD ± 14 cm). This is similar to Iran, where burrowing length ranged 126–181 cm (Tayefeh *et al.* 2013b), but very different from Eritrea where burrows were on average 310 cm long at the end of the breeding season (De Marchi *et al.* 2008). In both Iran and Eritrea, Crab Plovers were seen to deepen their burrows throughout the breeding season, but this was never observed in the Bubiyan colonies. The deepening of burrows may be a reaction to regular disturbance or an adaptation to increasing temperatures. Inspection of several burrows with a camera on a stick showed that burrows had multiple side tunnels with dead ends.

Figure 11.5. Typical crab plover colony on the Bubiyan Islands, with high burrow densities. See the crab plovers in the back of the colony for the scale. The burrows are remarkably close to the waterline. Note the high burrow density. The picture was taken during spring flood high tide.

Hatchling diet composition

After eggs hatched, adult crab plovers with prey were always present in the colony, during both high and low tides. Birds were observed flying in with prey from all directions, possibly from long distances. We suspect that all food brought to the colonies was for provisioning, although prey delivery was only seen once, at the entrance of the burrow. Prey items identifiable in photographs (e.g. Fig. 11.4) included both crabs (n = 39) and mudskippers (n = 12; Table 11.1). Crabs were identified as Macrophthalmus sp. (n = 11), *Macrophthalmus dentipes* (n = 4), ghost crab Ocypode sp. (n = 6) and swimming crab Portunidae (n = 1). Crabs were on average 0.64 times the length of the bill. Mudskippers were larger, on average 1.8 times the length of the bill. For reference, the average crab plover bill length is 62.3 mm for females and 67.6 mm for males (De Marchi *et al.* 2012). Prey remains in the colonies collected in June 2014 were identified as crab *Macropthalmus dentipes* (n = 5) and Dussumier's Mudskipper *Boleophthalmus dussumieri* (n = 7).

Table 11.1. Prey items identified on pictures.

Family	**Species or families**	**n**	**Average size** (relative to bill)	**Range size** (relative to bill)
Crab	*Macrophthalmus dentipes*	4	0.69	0.5–0.75
Crab	*Macrophthalmus* sp.	11	0.64	0.5–0.75
Crab	Ocypode	6	0.75	0.5–1
Crab	Portunidae	1	0.50	-
Crab	Unknown	17	0.60	0.25–1
Mudskipper	Gobiidae	12	1.81	1–2.5

Several studies report that crabs are a major food source for Crab Plovers, during both the breeding season (Almalki *et al.* 2015, De Marchi *et al.* 2015b) and winter (Swennen *et al.* 1987; Hockey *et al.* 1996; Soni 2007; Chapter 8). Occasionally, fishes, prawns, worms, mollusks (Soni 2007, Almalki *et al.* 2015) and mudskippers (Cramp *et al.* 2004; Behrouzi-Rad & Behrouzi-Rad 2010) have been observed in the diet of Crab Plovers. In our study area, mudskippers made up as much as 25% of the chick diet. The importance of mudskippers was unexpected because we found no previous studies reporting that mudskippers were a sig-nificant food source for either adult or juvenile Crab Plovers. We suspect that mudskippers are an energy-rich and easily digestible prey. To compare their nutritional value relative to other prey, more detailed studies are needed on their energy content and digestion time, but also on searching efficiency and handling time required to capture and ingest mudskippers.

Other observations

Each year, large numbers of dead chicks were found near the entrances of burrows. For instance, on 26 June 2013 two colonies on a large island were completely deserted, presumably after all chicks died (Fig. 11.6). Bill length measurements by RB (June 2014; n = 6, mean: 46.3 mm, SD ± 5.1) in one colony indicated that most chicks died in the first week after hatching, based on formulas derived by Tayefeh *et al.* (2013b). The reasons for this mass mortality are unclear, but may have involved food shortage, diseases and/or heat stress. Heat stress may have occurred if high tides flooded the lower ends of burrows, forcing chicks to move out of their burrows.

Crab plovers appear to be social animals when in the colony. Aggressive interactions between pairs or loud noises were seldom observed during the breeding season. At the start of breeding seasons, many (presumable) pair members were close to each other for long periods of time. It is unknown whether crab plovers pairs form a bond for life. On one occasion, a two-week old chick, apparently far away from its nest, was observed being followed/herded back to its nest by a group of adult crab plovers. A similar observation was described in a colony in the Red Sea by Almalki *et al.* (2015), who suggested that there may be a cooperative care system in crab plovers.

Conservation

With 3–5% of the world population of crab plovers utilizing the Bubiyan Islands for reproduction, this area is of major importance for the conservation of this species. Crab plovers are currently not listed as threatened (IUCN 2016), but their breeding area is restricted to just a few colonies (see below), of which most or all are within an area that is rapidly exploited and subject to substantial coastline alterations and pollution (Sheppard *et al.* 2010; Sale *et al.* 2011). This makes the species vulnerable, because the destruction of one breeding colony affects a substantial part of the breeding habitat of the entire population. Other threats to breeding crab plovers include disturbance and destruction of nests by humans, egg col-lection

Figure 11.6. A recently abandoned crab plover colony with many dead chicks near the burrow entrances.

by fishermen (Tayefeh *et al.* 2013b; Almalki *et al.* 2014) and introduction of rats and cats (De Marchi *et al.* 2006, Javed *et al.* 2012).

As for the Bubiyan Islands, threats are still hypothetical. Cats and rats were never observed on the breeding islands. We have no indication that the part of the Bubiyan Islands where crab plovers were found breeding is frequently visited by tourists, egg-collecting fishermen or soldiers. Some car tracks can be seen on the larger island, but they are probably very old. The colonies are all within the Mubarak Al-Kabeer nature reserve, which was recently declared a Ramsar site and for which there are no current developmental plans. A possible threat to the colonies, for example in the form of (oil) pollution, might come from the southern part of the Bubiyan Islands, where massive port developments are going on, and are expected to continue in the near future (see for instance http://www.gulfconstructionworldwide.com/news/12095_Project-Watch.html). This southern part of the Bubiyan Islands was occupied by humans for a longer time. The habitat of these islands seems ideal for breeding crab plovers, and the species might have previously bred on these islands, although no historical records confirm this. Regardless, we conclude that crab plovers are still breeding on the Bubiyan Islands in large numbers. With a good conservation plan, much of the area and its peculiar inhabitants can be saved for the future (Al-Zaidan *et al.* 2003; Sale *et al.* 2011).

Solving the missing colony problem?

Since the last review on the distribution and size of the breeding colonies of crab plovers (Aspinall & Hockey 1996) several new colonies have been discovered or better described. All currently known breeding colonies are listed in Table 11.2 and depicted in Fig. 11.7. Table 11.2 includes data of the last complete survey of each area, and presents per site the number of burrows, the number of colonies, the burrow density (if known) and the year in which the survey was conducted. Most of the reviewed studies are conducted relatively recently although the surveys in Eritrea, and especially Oman, Yemen and Somalia may be somewhat outdated. No references could be found for suspected colonies in the Republic of Sudan and Arab Republic of Egypt.

Crab plovers were found breeding at just 19 sites consisting of at least 56 colonies, 30 of which were found in one area in Eritrea (De Marchi *et al.* 2006). Of 19 breeding sites, eight were found in the Arabian Gulf, one in the Arabian Sea, one in the Gulf of Oman and the other nine in the Red Sea. In total, 32,120 burrows were recorded. Most burrows were found in the Arabian Gulf: ~17,200 in total, compared to ~12,200 in the Red Sea, 2,600 in the Gulf of Oman and 60 in the Arabian Sea. The largest colony, Dara Island in Iran, included 10,246 burrows during the last survey in 2011. Note that the number of burrows on Dara Island the year prior was even higher: 12,762 burrows (Tayefeh *et al.* 2013a), illustrating that the number of burrows can change substantially between years. Ideally, for more reliable estimates in the future, all colonies should be surveyed in the same year. Nevertheless, we can conclude that the Bubiyan Islands do not host the largest breeding colony of crab plovers, as is suggested by the Ramsar convention (https://rsis.ramsar.org/ris/2239), but the site ranks within the top five most important breeding areas for crab plovers around the world.

It is not clear how many crab plover are associated with the number of burrows counted throughout the range. If all 32,120 burrows were occupied by one pair each, then the reviewed breeding sites would hold ~64,200 birds. It is more likely that not all burrows were occupied, and the actual number of breeding birds is lower. Indeed, Tayefeh *et al.* 2013b found an occupancy rate of 75% because non-breeding pairs may excavate a burrow that will remain empty, or individuals occupying a burrow may fail to find a partner. We therefore estimate that the actual number of breeding birds is approximately 48,200–64,200 individuals. Currently, the winter population of crab plovers is estimated at 60,000–80,000 birds (De Marchi *et al.* 2006, Delany *et al.* 2009). Not all of those birds are breeding because birds are seen year-round at non-breeding areas (e.g. Eriksen & Victor 2013); assuming these are mostly young birds, this suggests that crab plovers start breeding after their second winter or later. In a winter area in Oman the percentage of 1st winter birds was estimated at 6% over four subsequent years and the annual survival of crab plovers was estimated at 90% (Chapter 6). Using these demographic parameters and assuming crab plovers start breeding in their second year, the expected number of (non-)breeding birds can be calculated. Assuming the population consists of 60,000 birds, the number of 1st winter birds is 60,000 * 0.06 = 3,600 birds, and the number of 2nd winter birds is 3,600 * 0.90 = 3,240 birds; therefore the total population consists of

Table 11.2. Currently known crab plover breeding areas, the estimated number of burrows per site, the number of colonies and the estimated burrow density, if available. The presented data shows the last complete survey of each area. KSA = Kingdom of Saudi Arabia; UAE = United Arab Emirates.

Country	Area	Lat	Lon	# burrows	# colonies	Year	Reference
Eritrea	Assab bay	12.9	42.83	3,250	4	2001–2007	(Semere *et al.* 2008)
Eritrea	Dahlak island, Howakil and Amphile Bay	15.5	40	5,500	30	2002–2004	De Marchi *et al.* 2006 & Semere *et al.* 2008
Iran	Dara	30.1	49.1	10,246	2	2011	Tayefeh *et al.* 2013a
Iran	Nakhilu	27.82	51.47	1,594	1	2011	Tayefeh *et al.* 2013a
Iran	Omol–Karam	27.83	51.56	402	1	2011	Tayefeh *et al.* 2013a
Iran	Ghabr–e Nakhoda	30.31	48.91	1,306	1	2011	Tayefeh *et al.* 2013a
Iran	Govater Bay	25.18	61.55	500	1	2005	Behrouzi–Rad & Behrouzi–Rad 2010
Iran	Bandar khmir	26.88	55.67	2,600	1	2005	Behrouzi–Rad & Behrouzi–Rad 2010
Kuwait	Bubiyan Island	29.9	48.09	1,750	3	2014	this study
Oman	Masirah	20.5	58.75	60	1	2013	J. Eriksen pers. comm.
KSA	Al Sheick Marbat	25.87	36.6	79	1	2011–2013	Almalki *et al.* 2014
KSA	Umm Ar Rak	19.27	40.98	624	1	2011–2013	Almalki *et al.* 2014
KSA	Mandhar	16.95	41.8	138	1	2011–2013	Almalki *et al.* 2014
KSA	Humr	16.78	42	552	3	2011–2013	Almalki *et al.* 2014
Somalia	Saacada Din Island	11.26	43.28	1,000	1	-	(Ash & Miskell 1998)
Sudan	Brasit island	20.82	37.27	330–500	1	-	(Shobrak *et al.* 2003)
UAE	Abyad–2	24.18	53.77	1,353	1	2010	Javed *et al.* 2012
UAE	Umm Amin	24.22	53.42	86	1	2010	Javed *et al.* 2012
Yemen	Kamaran Island	15.33	42.67	680*	1	2003	(Jennings 2003)

*Estimated number of burrows based on the number of pairs seen near the colonies

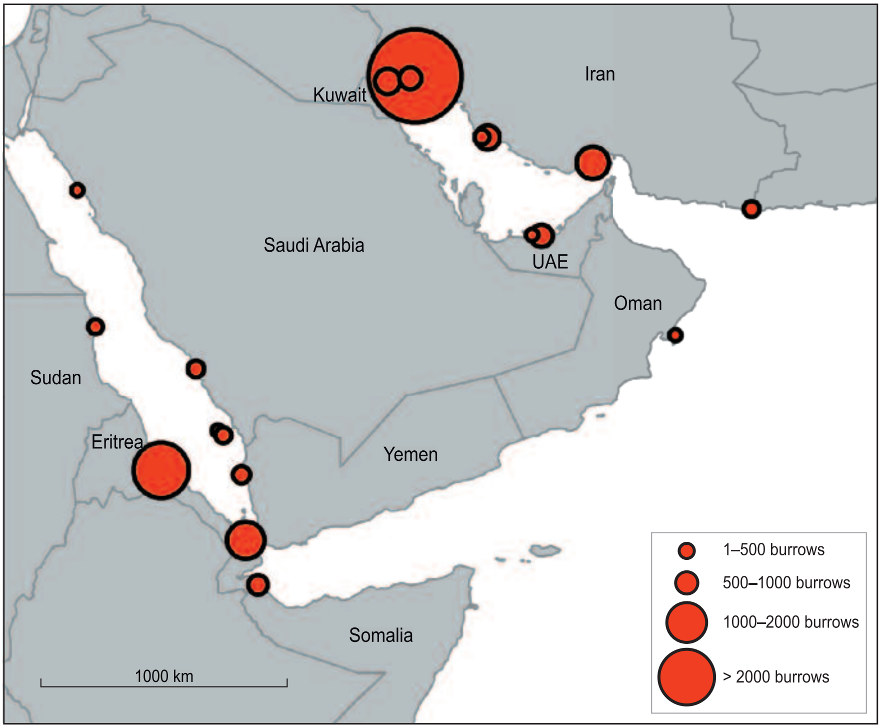

Figure 11.7. Distribution of the currently known breeding colonies of crab plovers. The size of the dots refers to the size of the number of active burrows. See Table 11.2 for details. UAE = United Arabian Emirates.

3,600 + 3,240 = 6,840 non-breeding birds and 53,160 breeding birds. If the population were 80,000 birds, then it would consist of 9,120 non-breeding and 70,880 breeding birds. Based on these rough calculations, we expect that the number of breeding birds is somewhere between 52,200 and 69,500 birds. This number is much higher than the 14,000–15,000 estimated by Aspinall & Hockey (1996) and close to the number of breeding birds we estimated from currently known breeding colonies. Thus, we can conclude that a large part of the 'missing colonies' problem raised by Aspinall & Hockey (1996) is solved.

Acknowledgements

We kindly thank the Kuwaiti authorities for allowing us to access the area. We thank Nasser al-Nasrallah for boating. Pekka Fagel is thanked for establishing contact between RB and KN, and kindly arranged all kind of logistics when RB visited the breeding colonies and for further contacting KN during the development of the manuscript. We thank Thomas Oudman, Jan van Gils, Theunis Piersma, Mike Jennings, Giuseppe De Marchi and an anonymous reviewer for comments on earlier drafts.

Box C

Provisioning

Crab plovers are the only shorebird known to continue provisioning their offspring after their first migration and throughout the winter (De Sanctis *et al.* 2005). Provisioning by adults includes both accompanying as well as feeding young birds, and is observed throughout the entire wintering area of crab plovers (Rands 1996). Observations on provisioning crab plovers has been made in Kenia by De Sanctis *et al.* (2005), but many details remain unknown. While catching and observing crab plovers at Barr Al Hikman, we regularly observed young crab plovers, and occasionally caught one. Here I present some findings that are based on these catches and observations concerning the provisioned young and the adults that were provisioning.

Biometry data show that first-winter crab plovers were consistently smaller than adult crab plovers (see Chapter 5 for details on how biometry data was obtained). Especially the bill of first-winter crab plovers was significant smaller (Fig. C.1). Theoretically, this observation can be explained in two ways: (1) the bill of young birds is still growing or (2) birds with small

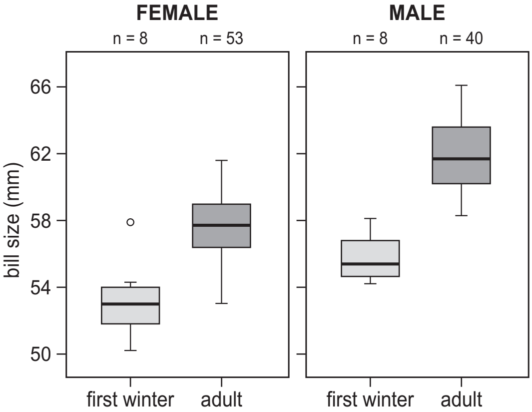

Figure C.1. Bill size of male and female crab plovers, distinguishing first-winter and adults birds. Sex was determined by molecular analysis of blood samples (Fridolfsson & Ellegren 1999). Note that these measurements differ substantially from De Marchi *et al.* (2012), who reported larger bills on crab plovers breeding at Eritrea (i.e. females in Eritrea had similar-sized bills as males in Barr Al Hikman). Although presumable bills were measured in the same way, we cannot exclude that methodological issues are responsible for the observed differences. Either way, we could not use the discriminant function provided by De Marchi *et al.* (2012) to determine sex of the Barr Al Hikman crab plovers on the basis of biometry. Instead, using the same method as De Marchi *et al.* (2012), we found that sex in the crab plovers of Barr Al Hikman can be predicted with biometric measurements by the formula:

$D = 0.1420991(\textit{head bill length}) + 0.3336184(\textit{bill length}) - 35.42618$

Measurements in mm. Negative values of D denote females and positive values males. Using this function on average 87% of the crab plovers are sexed correctly.

bills suffer from higher mortality, and therefore become rarer in older age classes (van Gils *et al.* 2016). Because we found hardly any overlap in bill size between adult and first-winter crab plovers, we suggest that their bills continue to grow during the first year.

First-winter birds were always accompanied by one adult, which we assumed was the parent. This is different from the situation at the breeding areas, where apparently both parents provision (Almalki *et al.* 2015). In the course of the study period (2008–2015) we observed 12 colour-ringed birds to provision a young. One birds was observed to provision a young in three different years (2009, 2013 and 2014). In six provisioning birds, sex was determined on the basis of blood samples and these birds were identified as male. Based on biometry, another three provisioning birds could also be identified as a certain males (De Marchi *et al.* 2012, and see below). Of three other birds sex could not be determined because no blood or biometry was taken. Interestingly, provisioning males were significantly larger than average male crab plovers (Fig. C.2). We speculate that birds with juveniles may be older and more successful birds, and that their larger bill may be explained by their age; they might continue to growth even after the first year. Unfortunately, we never recaptured birds to substantiate this hypothesis.

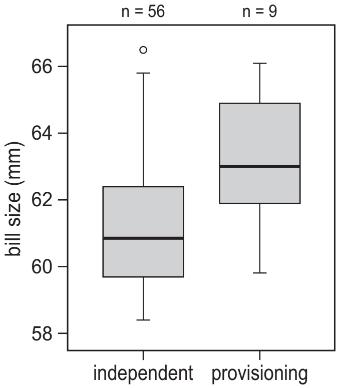

Figure C.2. Bill size of males that were observed foraging alone or provisioning a first winter bird.

During five expeditions in November-December (2011–2015) we observed that all first-winter birds were accompanied by an adult that provisioned regularly. During 10.5 hours of video observations (similar as those presented in Chapter 8) on five first-winter birds we never observed that young birds caught a prey item themselves. During two expeditions in March (2012 and 2015) we did not make structural observations, but the first winter birds that we observed were all being provisioned by a parent. Thus, we do not know the exact timing when young birds become independent but because we never observed second-winter birds, which look like adult birds (Chapter 5), to be provisioned, it is expected that adults repel their offspring around a year after hatching.

Although all second-winter birds that we observed foraged independently, we made one observation that offspring can still be found close to their parent after they become 'independent'. That is, a bird that was ringed as a first-winter bird in 2009 and which in that year regularly was observed being provisioned by another colour-ringed bird (its supposed father), was again observed in 2014 foraging within 100 m from its supposed father.

We managed to put colour rings on two more 'first-winter adult couples". In one of them we did not observed the first-winter on the year after release. In the other, the young and adult were observed one year after catch, but not in close proximity. The observation that crab plovers can forage in close proximity with their offspring up to 5 years suggests that that crab plovers are social birds. This is in line with previous observations at the breeding areas, were it was suggested that there may be a cooperating family care system operating among crab plovers (Chapter 11, (Almalki *et al.* 2015).

Why crab plovers provision remains unknown. Young birds may be unable to catch their own prey, perhaps because they have a relatively small bill. Provisioning can also have a learning function (Thornton & McAuliffe 2006). In case of the crab plover this seems plausible as swimming crabs, their preferred prey, have large and powerful claws, which may require specific handling skills (Chapter 8). In our video observations (similar as those described in Chapter 8) we observed 17 times that an adult transferred a prey items to a young. Twelve of these prey items were identified as swimming crabs, five remained unidentified. Eight of the transferred crabs were large (> 30 mm) and adult crab plovers detached the claws and legs and removed the carapax before offering it to the young. The young could simply swallow this prey. Thus, if provisioning has a learning function, than crab plovers learn from their parent by observations. Note that the causality also may be reversed, i.e. that young crab plovers do not have to grow large bills because they are being provisioned, or that swimming crabs became powerful under a strong selection pressure by crab plovers, that became efficient swimming crab handlers because they learned from their parents.

During our studies, we never managed to catch large numbers of first-winter birds together with their parent(s). If this issue is somehow solved, the provisioning system of crab plovers provides ample opportunities to study the implications of provisioning on behaviour.

CHAPTER 12

General Discussion

Roeland A. Bom

Barr Al Hikman. A coastal area in the Sultanate of Oman with intertidal mudflats that are teeming with life. Thousands of birds, fish, crabs, molluscs and a great variety of other invertebrates make their living in an area that seems untouched by humans, and that remains mostly unstudied. If you are to understand the richness of such an ecosystem, its functioning, its inhabitants, its present interactions, its past and its future, where do you start?

The answer, of course, is natural history. Natural history is the science that observes and describes the natural world, in which the study of organisms and their linkages to the environment take the centre stage (Tewksbury *et al.* 2014). It is a part of the biological sciences that is de-emphasized nowadays, but which remains the basis for all further studies in biology and beyond (Bijlsma *et al.* 2014; Tewksbury *et al.* 2014; Dijkstra 2016). Natural history is also at the basis of this thesis.

In this final chapter I will begin with highlighting some of the main findings of the presented chapters. This includes natural historical observations: the spatiotemporal abundances of molluscs, crabs and shorebirds. I will also highlight some of the interactions that we observed between species, and in the same time will explain some of these interactions. In doing so, I will emphasize that several of the studied species show morphological traits that are relatively 'outspoken', beyond the average, when compared to species in other ecologically similar regions in the world. Then, in an attempt to place the work in a wider context, I will contemplate on how these morphological traits became so outspoken in the course of evolution. I will argue why this is of great interest, not only from a general scientific perspective, but also from a conservation perspective.

The thesis in a nutshell: molluscs, crabs, shorebirds, and well-developed armature

The intertidal mudflats of Barr Al Hikman consist of a diverse community of molluscs (Chapter 2), crabs (Chapter 3) and shorebirds (Chapter 4). Whereas the densities and diversity of molluscs and crabs are comparable with those found on other intertidal areas in the Indo-West Pacific, Barr Al Hikman has a remarkable large and diverse community of shorebirds (Chapter 5). The number of birds per species were stable or increased (Chapter 5). This latter finding contrasts to many other areas in the world, which suggests that the relevant conditions for birds in the area did not change as much as in other areas. In-depth analysis of the demographics (survival and reproduction) of crab plovers showed that the observed stable population can only be explained if the area receives immigrants on a yearly basis. This illustrates that Barr Al Hikman is an open ecosystem (Chapter 6).

Most shorebirds in the area were found to feed on benthic invertebrates (Chapter 2). And, although most benthic biomass resided in molluscs, there were hardly any shorebirds foraging on molluscs. Detailed measurements on molluscs showed that they were mostly unavailable to shorebirds, either because of their hard-to-crush shells, or because they lived too deeply in the sediment. A comparison with molluscan communities at other intertidal mudflats showed that molluscs at Barr Al Hikman are distinctly better defended than those reported from anywhere else (Chapter 2).

Most shorebirds were observed feeding on crabs (Chapter 2). Almost all crab-eating shorebirds consumed burrow-hiding crabs (Chapter 2 and unpublished data). Only crab plovers also consumed swimming crabs (Chapter 8). In fact, in-depth analyses of the diet of crab plovers showed that they strongly preferred swimming crabs over burrow-hiding crabs, also in years when burrow-hiding crabs were abundant. The preferred swimming crabs include a species with especially strong claws that can crush the hard-to-break molluscs (Chapter 2). We showed that the observed preference for swimming crabs emerges from efficient handling of swimming crabs by the crab plover and the fact that burrow-hiding crabs hide for long time-periods. Undoubtedly, crab plovers owe the unique talent of handling swimming crabs to their equally unique heavy bill (Chapter 8).

The evolution of powerful armature

Why do crab plovers have such heavy bills, swimming crabs such powerful claws and molluscs such hard-to-break shells? I will address these questions from an evolutionary perspective (cf. Tinbergen 1963), as I believe that this is a promising approach to gain insight in the functioning of the Barr Al Hikman ecosystems and the interactions between its species. But note that these questions could have been addressed in other ways too. See Tinbergen (1963), Bateson & Laland (2013) Hogan & Bolhuis (2009) and Piersma (2018) for contemplation on this topic.

In general it is thought that predation and anti-predatory traits are adaptive characteristics which have evolved in interaction with their environment. In the environment, the “relation of organism to organism is the most important of all relations” (Darwin 1859). Thus, if we want to understand how species evolved their attack and defence mechanisms, a first step is to define the interactions between and within species. This also relates to the question why certain species show more powerful armature than others, because powerful competitors are thought to have evolved under conditions of intense competition and predation (Vermeij 1987). Yet, other aspects of the environment may also contribute to the evolution of powerful armature (Darwin 1859). Here I will first discuss the interactions (selective pressures) under which the heavy bill of the crab plover, the powerful claws of the swimming crab and the hard-to-break molluscs could have evolved. Next, I will more general discuss the role of the environment.

Well-developed armature: species interactions

Species can evolve their attack and defence mechanisms in interaction with their enemies and their prey. Geerat Vermeij (1987, 2004) has argued that species will evolve more powerful armature in response to enemies (predators, competitors, kleptoparasites and parasites) than in response to prey, because enemies often impose stronger selection over their victims than victims over their enemies. In the case of a predator-prey interaction this is because if a predator fails in an attack it loses a meal (and some time and energy), whereas failure for the prey means death, a principle commonly referred to as the ‘life-dinner’ principle (Dawkins & Krebs, 1979).

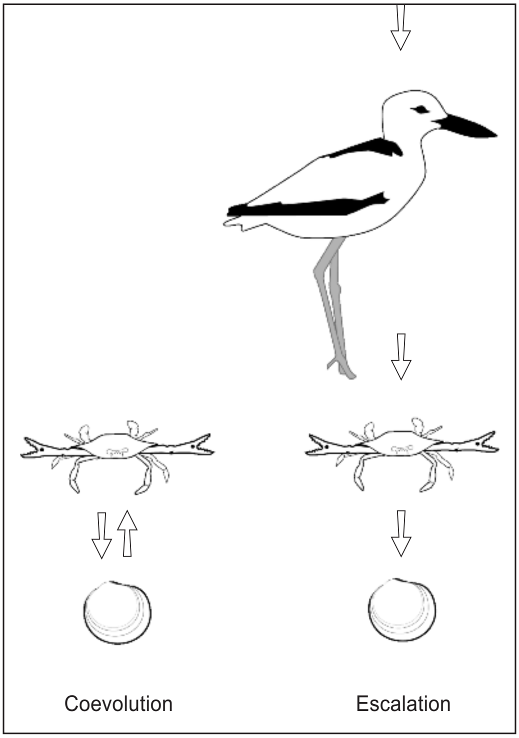

Figure 12.1. Direction of selective pressures in coevolution and escalation. The term 'evolutionary arms races' is sometimes used to collectively refer to both of these processes (Dawkins & Krebs 1979), adapted from Dietl and Kelley (2002).

The process in which species evolved their traits in response to enemies was coined 'escalation' by Vermeij (1987). The process in which species evolve their armature in response to each other is often referred to as 'coevolution' (Thompson 2005). Thus, in escalation shells get thicker in response to stronger crab claws which get stronger in response to its own enemies, whereas in coevolution claws of crabs get stronger, so shells get thicker, so claws get stronger still (Fig. 12.1) (Dawkins & Krebs 1979). The conventional wisdom is that defensive traits mainly evolve in a process of coevolution, yet Vermeij (1987, 2004) emphasizes that in almost all species, escalation is a more appropriate mechanism to explain traits related to armature. This is because predator-prey interaction never take place in isolation, and almost all predators have their own enemies (Vermeij 2004).

In order to evaluate competing hypotheses about the evolution of predator–prey systems, the long-term direction of selective pressure should be known. Despite some successes in single predator-prey interactions (e.g. Kingsolver & Diamond 2011; Bijleveld *et al.* 2015a), it remains difficult to quantify the long-term direction of selective pressures when the interactions involve more than two species (Kingsolver & Diamond 2011). Especially, there is little empirical evidence on predator traits that coevolve in response to the traits of the prey (Brodie

& Brodie 1999; Dietl 2003). If the direction of selective pressure is unknown, a qualification of the interaction between species will still be informative. In this respect, it is also important to know whether predators sometimes fail to kill their prey after an encounter. Anti-predation traits that evolved to resist attacks (such as shells) only have the chance to evolve if some prey survive and reproduce after being detected and/or assaulted by a predator; if predators have a 100% success rate, there will be no selection taking place on defence mechanisms (Vermeij 1982; Wade & Kalisz 1990). Likewise, improvements of the attack mechanisms in predators may be related to predation failure, but, due to the 'life-dinner' principle, the evolutionary response will be less strong because one event of unsuccessful predation mostly does not mean the death of a predator (Vermeij 1982).

Based on the results presented in this thesis we have several indications that the traits that are involved in the crab plover-crab-mollusc interactions have evolved under a process of escalation. Most importantly, we provided evidence in Chapter 2 that the molluscs in Barr Al Hikman are subject to predation by swimming crabs and conceivably fish. Moreover, crabs are sometimes unsuccessful in their predation attempt, as inferred from the repair scars that we found in all species of gastropods (Chapter 2). This indicates that swimming crabs are important selective agents for the evolution of anti-predation traits in the molluscs of Barr Al Hikman.

Swimming crabs themselves conceivable also evolved their claws in response to enemies, i.e. in a process of escalation, as swimming crabs have many enemies. An obvious enemy of swimming crabs is the crab plover. This bird could well be selective agents for crab claws, as sometimes crab plovers forego attacking a swimming crab seemingly because of the powerful claws (Fig. 12.2). In addition, swimming crabs have several more enemies such as a suite of fish species (Golani & Galil 1991). Moreover, swimming crabs are a potential selective agent for their own defence traits, as swimming crabs are known to be ferocious cannibals (Cannicci *et al.* 1996; Safaie 2016). In line with this we regularly observed swimming crabs attacking each other with their claws. In such interactions, crabs may exert strong selection pressure over one another (West *et al.* 1991). In fact, this selection pressure could be higher than that by crab plovers as crab plovers migrate to other areas for breeding and are not present at Barr Al Hikman for a large part of the year (Box B, Chapter 11).

Figure 12.2. Swimming crabs sometimes successfully defend themselves against attacks of crab plovers. While analysing 101 hours of video footage of foraging crab plovers (Chapter 2), we observed 5,031 prey capture attempts of which 1,262 were successful and of which 379 prey items could be identified as swimming crabs (two species) (Chapter 8). Presumably, most attempts failed because crabs or other prey items escaped by means of swimming or running. At one occasion we observed that a crab plover gave up attacking a swimming crab, seemingly because it was afraid for the claws of the crab. Pictures show video stills of that occasion.

Enemies may impose strong selection pressure on the claws of swimming crabs, yet processes of coevolution cannot be excluded, and potentially act simultaneous with escalation. The plastic development of defence and attack traits may enhance the coevolution process. Experiments with captive crabs showed that crabs raised on shelled prey developed larger and stronger claws than crabs raised on unshelled prey (Smith & Palmer 1994). Other experiments showed that molluscs respond to water-borne stimuli released by predatory crabs by growing thicker, more difficult to break shells (Appleton & Palmer 1988). Thus, crabs and shell can coevolve their armature in short-term phenotypic responses, which could yield long-term changes if the net changes are directional (Agrawal 2001; West-Eberhard 2003)

Based on the observations presented in this thesis it is difficult to distinguish between escalation or coevolution where it concerns the bill of the crab plover. Although crab plovers are often referred to as apex predators, they do have enemies which may be selective agents. This would be an argument in favour of escalation. In our video recordings (Chapter 8) we observed that five of the 379 caught swimming crab were stolen, either by conspecifics or by gulls. These were is all cases large (and thus energy-rich) crabs. Although these interactions are unlikely to be lethal, kleptoparasitism can be a major driving force in the evolution of the morphology and behaviour of the interacting species (Iyengar 2008). For instance, a bill that can process crabs faster may be advantageous to a crab plover if this can keep its conspecifics at a distance, or if this means faster handling of the crabs.

An argument in favour of a coevolution process is that it is also conceivable that swimming crab are dangerous prey and thereby exert selection pressure on defensive traits of crab plovers (Vermeij 1982; Brodie & Brodie 1999). Some observations indeed suggest that the defence strategies of swimming crabs can be dangerous for crab plovers. First of all, crab plovers can ‘fight’ with swimming crabs up to several minutes (Chapter 8). Crab use their claws in such fights, which can scare-off crab plovers (Fig. 12.2). Furthermore, we often observed that crab plovers close their eyes while probing in the mudflats, which we speculated as being an anticipation on the big powerful claws of swimming crabs. But there are also observations that imply that crab plovers are not so afraid for the defences of swimming crabs. For example, crab plovers preferred swimming crabs even when alternative prey were also available. In years when swimming crabs were not available, crab plovers seemed to be able to collect enough food on the alternative prey (Chapter 8), suggesting that they do not attack swimming crabs out of necessity, but out of preference. In line with this, our experiments with captive crab plovers showed that crab plovers switched to swimming crabs when their stomach was full, while the easier-to-handle, but more-difficult-to-digest sentinel crabs were still *ad libitum* available (Chapter 8).

To determine whether crabs can exert selective pressure on crab plovers, future research could focus on investigating if (the bill of) crab plovers show a phenotypically plastic response to (the claws of) swimming crabs. Although the bills of birds generally do not show phenotypic plasticity (Grant & Grant 2011; Piersma & van Gils 2011), some examples do exist in shorebirds (Pol *et al.* 2009; van Gils *et al.* 2016). The growth of the bill in crab plovers continues throughout the first year after hatching, and maybe even longer (Box C), which does allow a large time window in which crab plovers can phenotypically respond to swimming crabs. This line of research perhaps may be facilitated by an unintended ‘experiment’. Swimming crabs, a commercially important crab (Chapter 3), are currently overfished in the area (Mehanna *et al.* 2013). If this continues, the species can become less abundant in the area and this may affect bill growth in crab plovers.

It is important to realize that the above statements are speculative. In reality, the selection processes could be more complex, and selection processes could have changed over the course of history. A large body of literature shows how the type and strength of interactions between and within species can change in the course of generations, for instance because diets change with ontogenetic development, which in turn depends on competition with conspecifics (de Roos & Persson 2013). These changes can be rapid, as currently, many evolutionary biologists are considering a more active role for behaviour in evolution than has traditionally been acknowledged (Laland *et al.* 2014), with plastic behavioural responses triggering evolutionary change in morphological characteristics (Piersma & van Gils 2011; Bateson & Laland 2013). Nevertheless, at least it is safe to assume that the evolutionary interactions between crab plovers, crabs and molluscs are by no means isolated.

Complex interactions are a prerequisite for the evolution of powerful armature, but this alone cannot explain why species have evolved powerful armature. In the next section I will elaborate on the role of the environment more generally.

Well-developed armature: The role of the environment

Darwin (1859) was the first to clearly articulate that that species show striking differences between environments in the amount of armature. He noted that species are relatively docile when they live in small areas such as the Galapagos Islands, whereas animals in populations that cover large areas show more powerful armature. This pattern has been confirmed many times, both in terrestrial and marine environments (Darlington 1959; Vermeij 2004). The proposed underlying mechanism is rather straightforward: in large areas, populations are larger so there is a higher chance that favourable armature will arise, for instance through genetic mutation (Darlington 1959). Furthermore it is suggested that the number of interactions is generally larger in large areas, which further favours the selection of armature (Darwin 1859; Darlington 1959; Briggs 1966; Vermeij 2004). In addition, evolutionary theory suggests that in a small population, a mutant with only a very small advantage will behave as a neutral mutant because the effects of random fluctuations in population size then overshadows the effects of selection (Kimura 1983 cited in Vermeij 1987). Besides the size of an environment, also temperature is thought to be of fundamental importance for the evolution of powerful armature. Warm conditions are favourable to the evolution of high performance, as metabolic rates increase when temperature rises (at least op to 40 degrees) (Darlington 1959; Gillooly *et al.* 2001; Vermeij 2004). Moreover, in marine areas several functions (i.e. filter-feeding and swimming) become energetically less expensive as temperature rises and the viscosity of the water drops. Higher ambient temperatures also enable higher precipitation of calcium carbonate in skeletons (Vermeij 2002; Vermeij 2003). Attack and defence mechanisms are energetically costly, and are observed to evolve particularly in productive environments where resources are available and accessible.

It is thought that these conditions together have contributed to the well-developed attack and defence mechanisms of the organisms of the shallow coastal areas and the intertidal rocky shores in the Indo-West Pacific (Vermeij 1978, 2004; Briggs 2006, and see introduction). It is conceivable that these same conditions have led to the well-developed armature that we currently see at the intertidal mudflats of Barr Al Hikman. Indeed, the area is warm and may be especially nutrient rich as it is situated in the Somali upwelling (Sheppard *et al.* 1992). Moreover, Barr Al Hikman can be considered a large area that is part of the Indo-West Pacific biogeographical region as faunas of intertidal mudflat areas are generally connected with the faunas of shallow marine waters and the intertidal rocky shores. Indeed, many of the fishes and swimming crabs that we observed at Barr Al Hikman have home ranges that extend into the sublittoral (Chapter 3), and their distributions often extend to large parts of the Indian Ocean (Lai *et al.* 2010). Also the larval stages of the benthic invertebrates can disperse over large distances (Williams & Reid 2004). The only point that perhaps contrasts with the idea that powerful attack mechanisms prosper in large populations is the crab plover. The current population of crab plovers is small compared to populations of other shorebirds, and confined to small breeding areas (Chapter 11).

The idea that Barr Al Hikman is part of a much larger Indo-West Pacific biographical area, and therefore has a shared evolutionary history with the rocky shores and the shallow waters in this area, suggests that faunas at other intertidal mudflat areas in the Indo-West Pacific should also show well-developed armature. There is not much data to substantiate this, but the earlier chapters of is thesis offer several suggestions that they do. First of all, crab plovers occur throughout the Indo-West Pacific and are reported to encounter swimming crabs with 'vast and powerful claws' at several non-breeding sites (Swennen *et al.* 1987). Furthermore, the only shorebird that has a similar-shaped bill as the crab plover is the beach thick-knee (Rands 1996) (Fig. 12.3). Beach thick-knees are not closely related to crab plovers (Pereira & Baker 2010), and they are also endemic to the Indo-West Pacific, where they primarily eat crabs

Figure 12.3. The bill of the crab plover (A) and the bill of the beach thick-knee (B) are strikingly similar. Both species are endemic to the Indo-West Pacific and primarily eat crabs. But they are not closely related.

(Rands 1996). We speculate in Chapter 8 that the bill of the crab plover and the beach thick-knee could have evolved in a world where other fauna also show well-developed armature. A final argument is the near absence of red knots not only in Barr Al Hikman, but in almost all parts of the Indo-West Pacific (Chapter 2). Red knots are molluscivorous shorebirds that are abundant on almost all other intertidal mudflat areas of the globe. In Chapter 2 we showed that at Barr Al Hikman there is hardly any molluscan biomass available to molluscivorous shorebirds. We argued that this is because molluscs are not available to red knots there because of their hard-to-crush shells, and/or because they live too deeply buried in the sediment (Chapter 2). Hence, the absence of red knots from the Indo-West Pacific may well be a direct consequence of the above described escalation process, if that is indeed the evolutionary cause of the well-developed armature in molluscs (earlier proposed by T. Piersma, but only published in a hidden way by Piersma 2006).

Global change, consequences of evolutionary arms races

Understanding the evolutionary history of species and the arms races under which they evolved their armature can help to illuminate the current and future distribution of species (Vermeij & Dietl 2006). This has become increasingly important because we humans have been moving species all across the globe. In addition, many barriers have been neutralized that previously prevented species from dispersal. In this respect, the Indo-West Pacific is an interesting area: it became connected with the Mediterranean after the opening of the Suez Canal in 1869. This specific human project resulted in what is now known as the Lessepsian migration: more than 200 species of Red Sea organisms have made it into the Mediterranean. On the contrary, less than a dozen species have taken the reverse course into the Red Sea or other parts of the Indo-West Pacific (Briggs 2003). It is thought that this migration is largely unilateral because the marine species in the Indo-West Pacific have better developed armature (Vermeij 2004). Indeed all the mollusc species listed in Chapter 2 and crab species in Chapter 3 are native to the Indo-West Pacific (http://www.marinespecies.org/introduced/). I propose that Barr al Hikman has remained free of invasive species; not because of a lack of human influences, but due to its evolutionary history.

Having emphasized the importance of defensive traits for molluscs in Barr al Hikman, it might be surprising that there actually are some mollusc species at Barr Al Hikman that show hardly any defensive traits at all. For instance, bivalves from the Tellinidae family are easy to break by predators and live in the top of the sediments (Chapter 2). Several authors were puzzled by similar observations and referred to them as ‘hanging relicts’ (Briggs 1966). Perhaps, such species have survived by adopting a life-history strategy in which they direct most of their energy towards reproduction (Vermeij 1976). But if this is true, then they should still differ from other thin-shelled and shallow burying mollusc species to explain why they are able to survive, and mollusc species from the Mediterranean apparently are not. There are still many questions out there!

Global change, will there be an end to evolutionary arms races?

Over the past centuries, many of the worlds' coastal ecosystems have been changed by humankind due to land reclamation, eutrophication, climate change and overfishing (Lotze *et al.* 2006). In fact we have now lost over 50% of the coastal natural habitats (Davidson 2014). Originally, habitats in Europe and North America have been affected most strongly, but the current rate of habitat loss is highest in Asia (Davidson 2014). Barr Al Hikman is now one of the most pristine areas in the Indo-West Pacific, and also in the rest of the world.

This thesis gives several arguments that can guide decision makers to protect Barr Al Hikman as an ecosystem. First an economic one: the area functions as a nursery ground for crabs (Chapter 3). Secondly, an important shared responsibility of the government of Oman and other countries along the flyway are the migrant shorebirds: Barr Al Hikman is a key area for shorebirds in the West-Asian East-African flyway (Chapter 5). Thirdly, the area has been recognized as an important feeding ground for sea turtles (Ross 1985) and a nursery ground for shrimps (Mohan & Siddeek 1996), and most likely also for fish (Bom *et al.* 2018).

I hope that these arguments, and the mere pristine beauty of the area, will contribute to a better protection and managing of the Barr Al Hikman ecosystem. In addition, what I hope to have shown in this final chapter, is that the species of Barr Al Hikman cannot be seen as isolated identities. They evolved their characteristics, the way they look and behave, in an endless number of interactions with other species in the large and productive Indo-West Pacific, an environment in which intertidal mudflats, shallow coastal areas and rocky shores have the same evolutionary history because they are interconnected habitats. All these areas needs protection to make sure that they remain interconnected. Only then, the complex interaction that have led to the described evolutionary arm races can continue.

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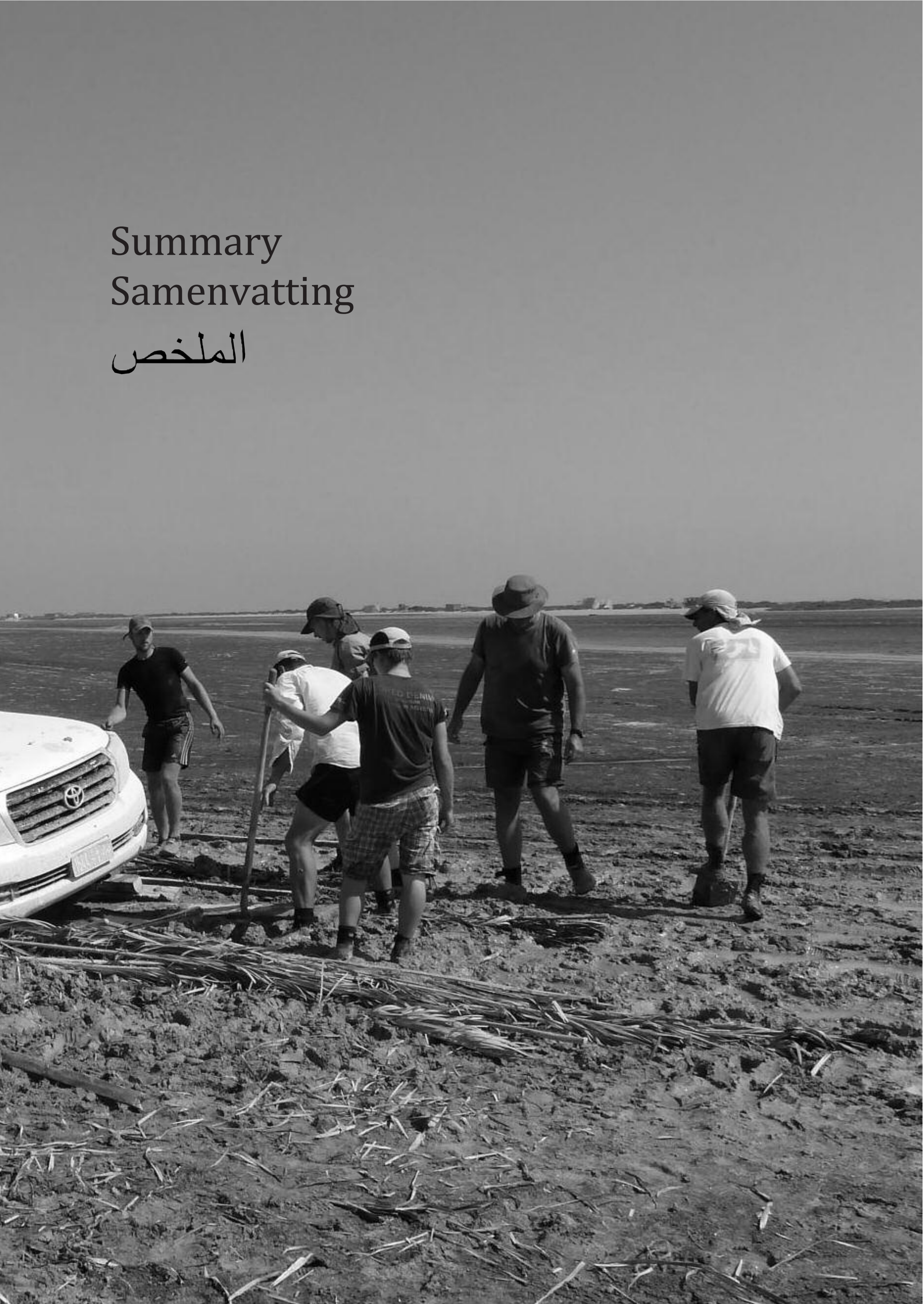
TOURS

Summary
Samenvatting
الملخص



Barr Al Hikman is an intertidal area along the east coast of the Sultanate of Oman. The area is teeming with life and has remained relatively untouched and unstudied by humans. Ecological studies are needed to better understand and appreciate coastal areas such as Barr Al Hikman. Such studies provide insight into the area itself and, if placed in perspective, can also deepen our general understanding of marine areas. Thereby it also provide tools for the effective conservation of these areas.

In this thesis, I had a closer look at the molluscs, crabs, crab plovers *Dromas ardeola* and other shorebirds of Barr Al Hikman. I studied the interaction between species and other part of their environment, and studied the evolutionary processes that have shaped them. Much of the presented work relies on natural history: the science that observes and describes the natural world. I relied on traditional tools such as binoculars and notebooks, but I also used state-of-the-art bird-tracking techniques. With additional experiments and optimal foraging models I delved into the processes underlying some of the observations. Finally, much of the insight in this work was gained by relating my findings to work in marine habitats elsewhere in the world.

Barr Al Hikman, molluscs, crabs and shorebirds

Barr Al Hikman consists of 190 km^2 of intertidal mudflats, an area of soft-sedimented sea bottom which is exposed at low tide about twice each day. The tidal area harbours a large diversity of animals, of which birds are the most conspicuous group. Surveys of high-tide roosts in three winters between 2008 and 2016 showed that about half a million birds winter in the area, representing 42 species (**Chapter 5**). The majority of these birds were shorebirds, of which the majority comprised birds that foraged on crabs and other crustaceans and polychaetes (**Chapter 2**). Molluscivorous specialists were almost absent from the area.

At first glance, the lack of molluscivorous specialists was surprising, as an extensive sampling programme in 2008 showed that most of the biomass and numerical densities of the macrozoobenthic community of Barr Al Hikman consisted of molluscs (gastropods and bivalves). Yet, detailed measurements showed that molluscs were mostly unavailable to molluscivorous shorebirds, either because of their hard-to-crush shells, or because they were buried in the sediment at depths unavailable to the shorebird species in this region. We interpreted these traits as anti-predation traits. Direct observations and repair scars on gastropods showed that molluscs are currently prone to predation by blue swimming crabs *Portunus segnis*, which suggests that the observed anti-predation traits have evolved in response to the risk of predation by swimming crabs (**Chapter 2**).

These observations teached us how important crabs are in the Barr Al Hikman ecosystem. In the **Chapters 3** and **4** we took a closer look at the crabs of Barr Al Hikman. To study the spatiotemporal distribution in relation to relevant habitat as well as some of the life histories, we sampled crabs across the mudflats in four winters. Sentinel crabs of the genus *Macrophthalmus* were found to be most abundant. The studied sentinel crabs were found to complete most or their entire life cycle in the intertidal zone, where they live in self-excavated burrows. These burrows ranged from simple, single-tunnelled burrows to cathedral-like complex constructions. Most of the sentinel crabs were found in seagrass at intermediate distance from the coast. Swimming crabs were the second most abundant group of crabs. Unlike sentinel crabs, swimming crabs are mobile; they do not burrow. Swimming crabs were mostly found in seagrass beds, which they presumably use for shelter and as food. Our data suggests that the larger blue swimming crabs leave the area and spawn in deeper waters.

In Barr Al Hikman most of the shorebirds that forage on crabs were found to specialize on the sentinel crabs that lack large and strong claws (contrary to swimming crabs) and are therefore easy to handle. Yet, sentinel crabs hide in their burrows when they see a predator approaching (again unlike swimming crabs) and shorebirds can spend quite some time waiting above burrows for an occupant to re-emerge. There is only one bird species that forages both on burrowing crabs and swimming crabs: the crab plover. Crab plovers are large black-and-white shorebirds with heavy, dagger-like bills. In **Chapter 8** we show that crab plovers strongly preferred swimming crabs over sentinel crabs. Crab plovers included sentinel crabs in their diet only when the densities of swimming crab were below a threshold of 9 crabs per m^2. In years when densities of swimming crabs where above 9 crabs per m^2, crab plovers were found to exclusively forage on swimming crabs, even if sentinel crabs were abundant. We concluded that the crab plovers' preference for swimming crabs emerges from a combined effect of the efficient handling of swimming crabs and of the efficient hiding of sentinel crabs.

We validated this conclusion in an experiment with three captive crab plovers that we kept in a large cage in our field camp for about two weeks. These birds were offered sentinel crabs *ad libitum* (readily available) and large blue swimming crabs (**Chapter 7**). Crab plover can ingest the latter species only after opening the carapax, which involves long handling times, but makes the crab easier to digest. With an empty stomach the captive birds preferred sentinel crabs, which is exactly what is to be expected from an energy maximizing point of view when both crabs are readily available. Birds with a full stomach switched their preference from sentinel crabs to large swimming crabs. It is likely that this switching of prey is due to the relatively high digestive quality of large swimming crabs. These results show that prey choice can be context-dependent, but how this translates to free-ranging crab plovers is not clear. Free-ranging birds hardly consumed larger swimming crabs, presumably because the densities of large swimming crabs were low. Because free-ranging crab plovers mainly consumed small swimming crabs, which have an equal or lower digestive quality than sentinel crabs, stomach fullness cannot explain the observed preference for small swimming crabs in free-ranging crab plovers (**Chapter 8**).

To further study the foraging behaviour of crab plovers we tracked 20 individuals with state-of-the-art GPS and accelerometer tracking technology. Accelerometers are movement sensors, of which the signal after calibration can be used to infer behaviour. First we developed a method to classify crab plover behaviour based on acceleration data (**Chapter 9**). In **Chapter 10** we used this method to study the whereabouts of the crab plovers in relation to the tidal cycle. We found that the behaviour and movements of crab plovers is tightly related to the tidal cycle, as birds almost always foraged close to the water line, day and night. We suggest that this spatially restricted behaviour can be explained by swimming crabs being most active and abundant around the moving waterline.

Perspective

Several species at Barr Al Hikman show morphological traits that are more extreme than in other intertidal areas across the world. First of all, the molluscs at Barr Al Hikman are distinctly better defended than those reported from anywhere else (**Chapter 2**). Furthermore, the massive bill of the crab plover, which gives them the unique capacity to handle swimming crabs, is seen in only one other shorebird species (**Chapter 8**, see below).

These results are in line with studies on rocky shores and shallow waters in other regions. For example, species of the Indo-West Pacific biogeographical area have distinctly stronger armature than species in any other (climatically similar) areas. In general, species are thought to evolve their armature in the interaction with other species in so-called evolutionary arms races. Observations and theory show that well-developed armature are more likely to evolve in large, warm and productive environments. The Indo-West Pacific is a typical example of such an area. We find that many of the species, ranging from molluscs to crabs and shorebirds, have home ranges that extend far beyond the 'borders' of Barr Al Hikman. Barr Al Hikman is therefore a characteristic part of the larger Indo-West Pacific environment, their inhabitants having a shared evolutionary history with the faunas of rocky shores and shallow waters in this biogeographical region (**Chapter 12**).

Whether other intertidal mudflats in the Indo-West Pacific region are also characterized by species with well-developed armature remains to be tested, but two observations suggest that this is the case. Firstly, the only shorebird that has a similar-shaped bill as the crab plover is the beach thick-knee *Esacus magnirostris*, a shorebird not closely related to crab plovers, but, like crab plovers, consuming armoured crabs and endemic to the Indo-West Pacific (**Chapter 12**). Furthermore, red knots *Calidris canutus* are molluscivorous shorebirds that are abundant on almost all intertidal mudflats around the globe except for most parts of the Indo-West Pacific. We speculate that the near absence of red knots may be a direct consequence of the above described well-developed armature in molluscs (**Chapter 2**). Thus, evolutionary arms races can have far-ranging consequences both for the morphology and the distribution of species.

The importance and conservation of Barr Al Hikman

The work presented in this thesis shows that Barr Al Hikman is a very rich and biodiverse ecosystem. It gives several arguments that can guide decision makers to protect Barr Al Hikman as an ecosystem. First, the area functions as a nursery ground for economically important swimming crabs (**Chapter 3**). Second, Barr Al Hikman is a key area for shorebirds in the West-Asian East-African flyway, since the area harbours more than 1% of the (sub)population for eighteen different species (**Chapter 5**). The survey data further showed that over the years the numbers of most bird species in the area were stable or increased (**Chapter 5**). This latter finding contrasts to many other areas in the world, which suggests that the relevant conditions for birds in the area did not change as much as in other areas.

It is important to note that Barr Al Hikman lies in a part of the world that is now rapidly changing by human development and expansion. Crab plovers may be specifically vulnerable for environmental change in the Indo-West Pacific as they are endemic to this region. They breed at specific habitats that they currently finds at only 20 sites, all of them around the Arabian Peninsula (**Chapter 11**). The crab plovers wintering at Barr Al Hikman breed in south-west Iran and Kuwait (**Box B**). Demographic estimates, on top of the survey data, suggest that this population of crab plovers is currently stable but vulnerable (**Chapter 6**). Now is the time to protect the breeding and wintering habitats of this extraordinary species.

Besides the practical arguments for conservation, this thesis provides tools for how we should approach and consider the conservation of ecosystems like Barr Al Hikman (**Chapter 12**). That is, the species of Barr Al Hikman cannot be seen as isolated identities. They evolved their characteristics in an endless number of interactions with other species in the large and productive Indo-West Pacific. For the conservation of ecosystem and the species of Barr Al Hikman, not only Barr Al Hikman should be protected, but also similar coastal habitats in the Indo-West Pacific. Only then, the complex interaction that have led to the described evolutionary arm races can continue.

Barr Al Hikman is een waddengebied in het oosten van het Sultanaat van Oman dat bruist van het leven en waar natuurlijke processen weinig gestoord zijn door menselijke activiteiten. Ecologische studies zijn nodig voor een beter begrip en waardering van waddengebieden zoals Barr Al Hikman. Ze geven niet alleen inzicht in de processen die spelen in een lokaal ecosysteem, ze kunnen ook, als ze in perspectief worden gezet met andere gelijksoortige ecosystemen, kennis opleveren over de algemene werking van kustsystemen en daardoor ook handvatten geven voor bescherming.

In dit proefschrift heb ik gekeken naar de weekdieren (slakken en schelpen), krabben, krabplevieren *Dromas ardeola* en andere wadvogels van Barr Al Hikman. Ik heb bestudeerd hoe ze elkaar en andere aspecten van hun omgeving wederzijds beïnvloeden, en ik heb gekeken hoe die gevormd zijn door evolutionaire processen. Veel van het werk is gebaseerd op natuurhistorisch onderzoek. Daarbij heb ik gebruik gemaakt van traditionele methoden, inclusief telescoop en opschrijfboekjes. Maar ook gebruikte ik meer moderne technieken waarbij we vogels met zenders uitrustten. Met aanvullende experimenten en modellen die zich baseren op optimaliteits-theorie heb ik geprobeerd de mechanismes achter sommige observaties beter te begrijpen. Daarnaast heb ik veel inzichten verkregen door mijn observaties te vergelijken met waddensystemen elders in de wereld.

Barr Al Hikman, weekdieren, krabben en wadvogels

Het intergetijdegebied van Barr Al Hikman bestaat uit 190 km^2 droogvallend wad (ter vergelijking: het Nederlandse waddengebied bestaat uit ongeveer 1200 km^2 aan droogvallende wadplaten). Het herbergt een enorme diversiteit aan leven, waarvan wadvogels het meest in het oog springen. Tijdens hoogwatertellingen in 2008, 2013 en 2015 telden we ongeveer een half miljoen vogels, bestaande uit 42 soorten (**Hoofdstuk 5**). Het overgrote deel van deze vogels waren wadvogels en het overgrote deel van de wadvogels bestond uit vogels die zich specialiseren op krabben, garnaalachtigen en wormen (**Hoofdstuk 2**). Wadvogels die zich specialiseren op weekdieren zagen we nauwelijks in het gebied.

Op het eerste gezicht was de afwezigheid van vogels die zich specialiseren op weekdieren opvallend, omdat een bemonsteringsprogramma uit 2008 liet zien dat het overgrote deel van de benthische organismen bestond uit weekdieren. Maar gedetailleerde metingen aan de weekdieren lieten zien dat er weinig eten te halen valt voor weekdier-etende vogels: we vonden dat bijna alle weekdieren leefden in schelpen die steltlopers niet kunnen kraken. Daarnaast leefden veel schelpdieren erg diep in het sediment, buiten het bereik van vogelsnavels. Directe observaties en littekens op slakken lieten zien dat weekdieren onderhavig waren aan predatie van krabben, waarschijnlijk voornamelijk de blauwe zwemkrab *Portunis segnis*. Dit suggereert dat de harde schelp en het ingraven van schelpdieren zijn geëvolueerd als antwoord op het gevaar van predatie door zwemkrabben.

Krabben zijn dus een belangrijke component in het Barr Al Hikman ecosysteem. In **Hoofdstuk 3** en **Hoofdstuk 4** hebben we de krabben van Barr Al Hikman nader bekeken. Om de ruimtelijke en temporele verspreiding van de krabben beter te begrijpen hebben we gedurende vier winters op verschillende biotopen van het intergetijde-systeem krabben bemonsterd.

‘Oogsteelkrabben’ van het genus *Macrophthalmus* waren de meest voorkomende krabben. Deze krabben verblijven hun hele leven in de intergetijde zone waar ze voornamelijk leven in zelf gegraven holletjes. Afgietsels van krabbenholletjes lieten zien dat sommige soorten erg simpele holletjes graven, terwijl andere enorm complexe gangenstelsels maken. De meeste oogsteelkrabben werden gevonden op plaatsen waar zich ook zeegras bevond, op enige afstand van de kust. Zwemkrabben van de Portunidae familie waren de tweede groep krabben die we veel tegenkwamen in onze monsters. Anders dan oogsteelkrabben waren de zwemkrabben die we vonden mobiel; ze graven geen holletjes. Zwemkrabben vonden we vooral in zeegras, dat ze waarschijnlijk gebruiken als voedsel en als bescherming. We zagen geen grote blauwe zwemkrabben in het intergetijde gebied. Blijkbaar verlaten die het gebied om hun eieren in dieper water te leggen.

De meeste wadvogels in Barr Al Hikman foerageerden op oogsteelkrabben. Die hebben, anders dan zwemkrabben, geen sterke klauwen, en zijn daardoor makkelijk te hanteren. Maar oogsteelkrabben schuilen in hun holletje als ze gevaar zien, en wadvogels die op oogsteelkrabben foerageren moeten regelmatig boven die holletjes wachten totdat een krab weer aan het oppervlak komt. De krabplevier, een grote, zwart-witte vogel met een zware, dolkachtige snavel, is de enige vogel die zowel op oogsteelkrabben als op de beter bewapende zwemkrabben foerageert. Sterker nog, in **Hoofdstuk 8** laten we zien dat krabplevieren in sterke mate zwemkrabben verkozen boven oogsteelkrabben. Alleen in jaren dat er weinig zwemkrabben waren, aten krabplevieren ook oogsteelkrabben. In jaren dat er veel zwemkrabben waren, aten krabplevieren bijna uitsluitend zwemkrabben, ook als er veel oogsteelkrabben waren. Blijkbaar hebben krabplevieren een voorkeur voor zwemkrabben, waarschijnlijk zowel omdat krabplevieren goed zijn in het vangen en verwerken van zwemkrabben, alsmede omdat de manier van schuilen van de oogsteelkrabben een effectieve anti-predatie tactiek is.

Deze laatste conclusie konden we deels valideren in een experiment met krabplevieren die we drie weken in gevangenschap hielden in een grote kooi in ons veldstation. Deze vogels konden kiezen uit *ad libitum* (direct beschikbare) oogsteelkrabben en grote zwemkrabben (**Hoofdstuk 7**). Deze laatste groep kunnen krabplevieren alleen doorslikken als ze eerst het schild van de krabben verwijderen, wat ze veel tijd kost, maar wat de zwemkrabben wel makkelijker verteerbaar maakt. Krabplevieren met een lege maag hadden een voorkeur voor oogsteelkrabben, waarschijnlijk omdat die de meeste energie opleveren zolang er maar ruimte is in de maag voor al die harde delen. Maar met een volle maag bleek hun voorkeur te verschuiven van oogsteelkrabben naar grote zwemkrabben. We weten deze verandering aan de mogelijkheid dat krabplevieren met een volle maag beperkt worden door de snelheid waarmee hun maag het voedsel kan verteren, en grote zwemkrabben zijn makkelijker te verteren. Maar hoe dit resultaat zich vertaald naar de veldsituatie is niet precies duidelijk. De vogels in het veld aten nauwelijks grote zwemkrabben. Misschien was dat omdat de dichtheden van grote zwemkrabben te laag waren. De ‘vrije’ vogels aten voornamelijk kleine zwemkrabben, en deze voorkeur kan niet worden verklaard vanuit het idee van beperking door verteringssnelheid, omdat we vonden dat kleine zwemkrabben net zo goed te verteren zijn als oogsteelkrabben (**Hoofdstuk 8**).

We bestudeerden het foerageergedrag van de krabplevieren met behulp van 20 miniatuur zenders. Deze zenders hadden zowel een GPS als een versnellingsmeter (accelerometer). In

Hoofdstuk 9 presenteren we een methode om met behulp van de versnellingsmeter gedrag te classificeren. In **Hoofdstuk 10** gebruikten we deze methode om de omzwervingen van de krabplevieren nader te bestuderen. We vonden dat alle bewegingen van krabplevieren sterk gerelateerd zijn aan het getij. Ze foerageerden bijna altijd dichtbij de waterlijn, zowel overdag als ’s nachts. Waarschijnlijk bleven de krabplevieren dichtbij de waterlijn omdat in dit gebied de zwemkrabben en mogelijk andere prooien het meest actief en abundant waren.

Perspectief

Een aantal soorten in Barr Al Hikman hadden extremere morfologische eigenschappen dan in andere waddensystemen. Zo konden we geen ander waddengebied vinden waar de weekdieren zo’n dik pantser hebben als in Barr Al Hikman (**Hoofdstuk 2**). Daarnaast is er maar één andere wadvogel die zo’n stevige dolksnavel heeft als de krabplevier (**Hoofdstuk 8** en zie onder).

Deze resultaten zijn in lijn met eerdere studies aan rotskusten en ondiepe kustzeeën. Die lieten zien dat organismen, voornamelijk weekdieren, krabben en vissen, in de Indo-West Pacifische biogeografische regio opvallend meer bewapening hebben dan soorten in andere (klimatologisch identieke) gebieden. In het algemeen wordt aangenomen dat soorten hun bewapening evolueren in zogenaamde evolutionaire wapenwedlopen. Observaties en theorie laten zien dat goed ontwikkelde bewapening vooral wordt gevonden in grote, warme en productieve milieus. De Indo-West Pacific is typisch zo’n gebied. Omdat we vonden dat veel soorten in Barr Al Hikman, inclusief weekdieren, krabben en wadvogels, een leefgebied hebben dat veel groter is dan Barr Al Hikman, beschouwen we Barr Al Hikman als een onderdeel van de Indo-West Pacifische regio. Dat impliceert dat de soorten die we vinden in waddengebieden zoals Barr Al Hikman een gedeelde evolutionaire geschiedenis hebben met de soorten van rotskusten en ondiepe wateren in deze biogeografische regio (**Hoofdstuk 12**).

Of andere waddengebieden in de Indo-West Pacifische regio ook worden gekenmerkt door soorten met goed ontwikkelde bewapening moet nog worden uitgezocht, maar er zijn twee observaties die suggereren dat dit inderdaad het geval is. Allereerst is er maar één andere soort die een gelijkvormige snavel heeft als de krabplevier, en dat is de rifgriel *Esacus magnirostris*. De rifgriel is een wadvogel die niet verwant is aan de krabplevier, maar die, net als krabplevieren, endemisch is voor de Indo-West Pacific en zwaarbewapende krabben op het menu heeft staan (**Hoofdstuk 12**). Daarnaast is een andere wadvogel, de kanoet *Calidris canutus*, juist bijna volledig afwezig in de Indo-West Pacifische regio terwijl die soort talrijk is in bijna alle andere waddengebieden. We speculeren in **Hoofdstuk 2** dat dat is omdat de schelpen in de Indo-West Pacifische regio niet of nauwelijks beschikbaar zijn voor deze soort, omdat ze te zwaar bewapend zijn. Ons werk laat dus zien dat evolutionaire wapenwedlopen grote gevolgen kunnen hebben voor zowel de morfologie als de verspreiding van soorten.

Belang en bescherming van Barr Al Hikman

Dit proefschrift laat zien dat Barr Al Hikman een gebied is met grote biodiversiteit. Het biedt ook een aantal argumenten die van belang zijn voor beleidsmakers. Zo functioneert het gebied als een belangrijke kraamkamer voor economisch belangrijke zwemkrabben (**Hoofdstuk 3**). Daarnaast is Barr Al Hikman een sleutelgebied voor wadvogels in de West-Aziatische Oost-Afrikaanse 'flyway', omdat het gebied voor 18 soorten meer dan 1% van de populatie herbergt (**Hoofdstuk 5**). De tellingen lieten ook zien dat de aantallen van veel wadvogelsoorten in het gebied stabiel waren of toenamen. Deze laatste bevinding verschilt van andere waddengebieden. Dit suggereert dat de voor vogels relevante condities in Barr Al Hikman niet zoveel zijn verslechterd als in andere gebieden.

Dat komt misschien omdat er in Barr Al Hikman langer dan in andere gebieden weinig verandering door menselijk handelen is geweest. Echter, Barr Al Hikman ligt op het Arabisch Schiereiland, waar veel gebieden nu veranderen door menselijk toedoen. Krabplevieren kunnen extra kwetsbaar zijn voor veranderingen omdat de soort broedt in specifiek habitat. Dit habitat vinden krabplevieren in ongeveer 20 plaatsen die allemaal op of bij het Arabische schiereiland liggen (**Hoofdstuk 11**). De krabplevieren die in Barr Al Hikman overwinteren broeden voor zover bekend uitsluitend in het zuidwesten van Iran en in Kuwait (**Box B**). Met tellingen en overleving- en reproductie schattingen konden we laten zien dat de populatie van krabplevieren in Barr Al Hikman momenteel stabiel is, maar wel kwetsbaar (**Hoofdstuk 6**). Het is nú tijd om de broed- en wintergebieden van de krabplevier te beschermen.

Naast praktische argumenten voor bescherming biedt dit proefschrift ook ideeën over hoe we moeten nadenken over de bescherming van gebieden als Barr Al Hikman (**Hoofdstuk 12**). Namelijk, Barr Al Hikman is geen geïsoleerd ecosysteem. De eigenschappen van de organismen die er leven zijn geëvolueerd in eindeloze interacties met andere organismen in het grote en productieve biogeografische gebied van de Indo-West Pacific. Als we het unieke ecosysteem van Barr Al Hikman willen behouden moeten kustgebieden in de hele Indo-West Pacific worden beschermd. Alleen dan blijft het complexe systeem bestaan waarbinnen de in dit proefschrift beschreven evolutionaire wapenwedlopen zich afspelen.

بر الحكمان منطقة شاسعة من الأراضي المدية تقع في الساحل الجنوبي الشرقي من سلطنة عمان .المنطقة تعج بالحياة وتخلو من البشر كما تفتقر للدراسة. أهدف في هذه الأطروحة إلى الحصول على فهم عميق للكائنات الحية التي يمكن العثور عليها هنا. ودرست بشكل خاص التفاعل بين الأنواع وبيئتها والعمليات التطويرية التي شكلت الكائنات الحية فيها في المنطقة. الأنواع التي اعتمدت عليها كنموذج هي الرخوياتوالسلطعونات وطائر الحنكور(*Dromas ardeola*) وطيور أخرى. أكثر العمل المعروض يعتمد على التاريخ الطبيعي العلم الذي يلاحظ ويصف العالم الطبيعي لهذا الغرض اعتمدت على تقنيات التقليدية كالمنظار ودفتر الملاحظات لكنني أيضا استخدمت تقنيات تتبع الطيور الحديثة. كذلك تم استخدام نماذج تغذية لفهم وشرح الملاحظات بشكل أفضل. وأخيراً، تم الحصول على الكثير مما يتم عرضه من أفكار عبرربط استنتاجاتنا بأعمال غيرها في بيئات بحرى بأماكن أخرى.

برالحكمان، الرخويات، السلطعونات والطيور الشاطئية

يتكون بر الحكمان من 190 كيلو متر مربع من الأراضي المدية الطينية التي تتعرض الى الجَزر مرتين في اليوم تقريباً. تشكل المنطقة المدية مرفأ لأعداد كبيرة وتنوع كبير من الكائنات الفطرية التي تكون الطيور الشاطئية بلا شك المجموعة الابرز بينها. الدراسات الاستقصاءية للمجاثم المدية في ثلاث شتاءات بين 2008 و 2016 أظهرت أن قرابة نصف مليون من الطيور الشاطئية تقضي الشتاء في المنطقة. تتشكل غالبية هذه الطيور من طيور شاطئية، وهي طيور تتخصص في التغذية على الكائنات البحرية الصغيرة مثل الرخويات والشوكيات والقشريات. غالبية الطيور الشاطئية في برالحكمان هي طيور تتغذى على السلطعونات وانواع أخرى من القشريات والشوكيات (**الفصل الثاني**).

للوهلة الأولى يبدو عدم وجود المختصين في الرخويات مفاجنا لأن برنامج عينات مكثف أُجري في 2008 أظهر أن أكثر الكثافة الحيوية والكثافه العددية لمجتمع الكائنات البحرية الصغيرة في برالحكمان تتكون من الرخويات والصدفياتبينما شكلت القشريات (معظمها سلطعونات) والشوكيات نحو 10% من إجمالي الكثافه الحيوية فحسب. مع ذلك فإن القياسات المفصلة التي أجريت على الرخويات أظهرت أن اتقشرات على الرخويات التي تسببها الطيور التي تتغذى على الرخويات كانت في الأغلب غير متوفرة اما بسبب أصدافها التي يصعب كسرها او نتيجة لكونها تعيش مدفونة عميقا في الرواسب. تشير الملاحظات المباشرة وندوبات التشافي على الرخويات إلى أن الرخويات هي حاليا عرضة للافتراس من قبل السلطعونات الزرقاء مما قد يدفع إلى التفكير الى أن الخواص المضادة للإفتراس قد تطورت كرد مناهض لهذه السلطعونات (**الفصل الثاني**).

وهكذا فإن السلطعونات تمثل مجموعة مهمة من الكائنات في النظام الحيوي ببرالحكمان ذلك أنها توفر مصدراً للغذاء لآلاف الطيور الشاطئية وتفرض في نفس الان ضغطاً على الرخويات في سلسلة الاختيار الطبيعي. في **الفصلين الثالث والرابع** ولدراسة توزيعها الزماني والمكاني وعلاقتها بالبيئة المحيطة إضافة إلى تاريخ حياتها اخذنا عينات من السلطعونات من الاراضي الطينية في اربعة شتاءات. ووجدنا أن السلطعونات الحارسة من المجموعة *Macrophthalmus* هي الأكثر وفرة. ووجد أن السلطعونات التي تم دراستها تعيش في جحور تحفرها بنفسها، تختلف بينها من بناء بسيط ذات نفق واحد الى بناء كاتدرائي معقد. أثناء فترة الجَزر تتغذى السلطعونات الحارسة بالقرب من جحورها بحيث تتمكن من العودة إليها حين تشعر بالخطر. معظم السلطعونات الحارسة التي تم العثور عليها كانت في الأعشاب البحرية على مسافة متوسطة من الساحل.

كانت السلطعونات السابحة في المرتبة الثانية من حيث كثرة العدد بين فصائل السلطعونات. وعلى خلاف السلطعونات الحارسة، فإن السلطعونات السابحة متحركة وتم العثور عليها في أغلب الأحيان في شعب الاعشاب البحرية التي يعتقد أنها تستخدمها للمأوى والأكل، بينما تقضي السلطعونات الحارسة حياتها في المنطقة المدية، مما يمثل اختلافاً عن السلطعونات السابحة الزرقاء الأكبر منها حجماً حيث وجد أنها تترك المنطقة وتفرخ بالمنطقة المقاربة للشاطئ.

معظم الطيور الشاطئية التي تتغذى على السلطعونات في برالحكمان تتخصص في افتراس الأنواع التي لها جحور والتي تفتقد إلى المخالب الكبيرة والقوية التي تمتلكها السلطعونات السابحة مما يجعلها في المتناول. لكن الأنواع التي تختبئ في الجحور قد تظل مختبئة في جحورها حين ترى اقتراب مفترس لذا قد تقضي الطيور الشاطئية أوقاتاً طويلة على جحر منتظرة خروج قاطنه. وهناك طائر يتغذى على السلطعونات ذات الجحور والسلطعونات السابحة المسلحة؛ هذا الطائر هو طائر الحنكور، وهو طائر شاطئيّ كبير الحجم أسود وأبيض اللون له منقار طويل يشبه النصل. وسنظهر في (**الفصل الثامن**) أن طائر الحنكور يفضل السلطعونات السابحة، واعتمدت التركيبة الغذائية لهذا الطائر الطليق بشكل حصري على كثافة السلطعونات السابحة وتتوقف عن البحث عن السلطعونات الحارسة حين تصل كثافة السلطعونات السابحة إلى 9 سلطعونات في المتر المربع، وحتى وإن كانت السلطعونات الجحرية متوفرة هي الأخرى. ونستخلص من ذلك أن تفضيل طائر الحنكور للسلطعونات السابحة يبرز من التأثير المزدوج لقدرة الطائر على تناول السلطعونات السابحة بفعالية واختباء السلطعونات الحارسة.

تحققنا من هذه النتيجة عبر تجربة من خلال ثلاثة من طيور الحنكور التي قبضنا عليها واحتفظنا بها لمدة اسبوعين في قفص كبير في مخيمنا الحقلي. عرض على هذه الطيور ما تم توفيره من سلطعونات حارسة وأخرى سابحة أكبر منها (**الفصل السابع**). في بداية تجربتنا فضلت الطيور المأسورة السلطعوناتَ الحارسة، وهو تماماً ما يُتوقع منها حين يتوفر النوعان كون هذا النوع من السلطعونات يوفر طاقة قصوى. لاحظنا كذلك أن الطيور التي امتلأت بطونها حولت تفضيلها من السلطعونات الحارسة إلى السلطعونات السابحة والتي قد تم فتحها قبل استهلاكها. يعزى هذا التحول إلى خاصية سهولة هضم السلطعونات السابحة الأكبر حجماً. يظهر ذلك أن اختيار الفرائس قد يعتمد على السياق لكن كيفية ترجمة ذلك بعلاقته مع طائر الحنكور الطليق ليس أمراً واضحاً تماماً ذلك لأنها بالكاد استهلكت السلطعونات السابحة الأكبر حجماً ربما لأن كثافة تواجد هذا النوع من السلطعونات كانت قليلة. لكون طيور الحنكور الطليقة استهلكت بشكل أساس السلطعونات الحارسة- التي لها جودة هضمية مساوية للسلطعونات الحارسة أو متدنية عنها- فإن امتلاء البطن لا يمكن أن يشرح تفضيل طيور الحنكور الطليقة الملاحظ للسلطعونات السابحة الأصغر حجماً (**الفصل الثامن**).

لدراسة أكبر لسلوكيات الغذاء لدى طيور الحنكور قمنا بتتبع 20 طائراً بأنظمة متقدمة للتتبع عبر الأقمار الصناعية وتقنيات تتبع تسارعية. تقنيات التتبع التسارعية هي استشعارات حركة يمكن استخدام اشاراتها بعد المعايرة لاستنتاج السلوك. لذلك قمنا أولاً بتطوير طريقة لتصنيف سلوكيات طيور الحنكور اعتماداً على بيانات تسارعية (**الفصل التاسع**). في **الفصل العاشر** استخدمنا هذه الطريقة لدراسة مكان تواجد طيور الحنكور نسبة إلى دوران المد والجزر إذ أن الطيور كانت دائماً تقريباً تتغذى قرب خط الماء لأن هذه هي المنطقة التي تنشط فيها السلطعونات السابحة وتتواجد فيها بكثرة.

إنطباع

بمقارنة مع دراسات أخرى تعلمنا أن الكثير من الأنواع ببرالحكمان تظهر صفات مورفولوجية واضحة نوعاً ما. في المقام الأول، الرخويات في برالحكمان تتمتع بحماية أفضل من تلك المذكورة في أي مكان آخر (**الفصل الثاني**). إضافة إلى ذلك فإن المنقار الكبير لطائر الحنكور- الذي يمنحه تلك الموهبة الفريدة لتناول السلطعونات السابحة- يمكن رؤيته في نوع واحد آخر فحسب من الطيور الشاطئية (**الفصل الثامن**، أنظر أدناه).

هذه النتائج متسقة مع دراسات أجريت على شواطئ صخرية ومياه ضحلة أظهرت أن الأنواع الفطرية في المنطقة الحيوية الواقعة في غرب الإنديز على المحيط الهادئ لديها أسلحة أفضل عن تلك الموجودة في مناطق أخرى. بشكل عام، من المعتقد أن الأنواع الفطرية تتطور أسلحتها عبر تفاعلها بالأنواع الأخرى فيما يعرف بسباق التسلح. تظهر الملاحظات والنظريات أن الأسلحة المتطورة تتوافر لديها بشكل أخص فرصة التطور في بيئات واسعة ودافئة ومنتجة. والمحيط الهادئ غرب الأنديز هو نموذج لمثل هذه البيئات. من المهم ولأن الأنواع لديها فرصة أفضل لتطوير أسلحتها في المناطق الواسعة، فإن ذلك قد يشير إلى أن الأراضي المدية الطينية مثل برالحكمان تشكل جزءً من بيئة المحيط الهادئ غرب الإنديز الواسعة، فالكائنات الحية في المناطق المدية الطينية يشترك تاريخ تطورها مع الكائنات الحية في الشواطئ الصخرية والمياه الضحلة (**الفصل الثاني عشر**). وقد وجدنا أن العديد من الأنواع- تتراوح من الرخويات إلى السلطعونات والطيور الشاطئية- لديها نطاق معيشي يتجاوز نطاق برالحكمان.

فيما إذا كانت الأنواع في المحيط الهادئ غرب الإنديز لديها أسلحة متطورة بشكل مشابه فهو أمر يتطلب الاختبار لكن هنالك ملاحظتان تشيران إلى ذلك؛ أولاهما أن الطائر الشاطئيّ الوحيد الذي يمتلك منقاراً يشبه هيئة منقار طائر الحنكور هو طائر الكروان الشاطئي (*Esacus magnirostris*) وهو طائر لا علاقة قرابة تجمعه بطائر الحنكور ولا يوجد إلا في المحيط الهادئ غرب الإنديز، لكنه - كطائر الحنكور- يستهلك سلطعونات مسلحة (**الفصل الثاني عشر**). إضافة إلى ذلك فإن طائر الطيطوى الحمراء (*Calidris canutus*) من الطيور الشاطئية الآكلة للرخويات يوجد بكثرة في معظم السهول الطينية في العالم بإستثناء معظم مناطق المحيط الهادئ غرب الإنديز. نعتقد بأن الغياب شبه الكامل للطيطوى الحمراء من تلك المنطقة هو نتيجة مباشرة للأسلحة المتطورة للرخويات والتي تم وصفها أعلاه (**الفصل الثاني**). وهكذ فإن سباقات التسلح قد يكون لها نتائج على نطاق واسع سواء من ناحية التطور المورفولوجي أو التوزع الجغرافي للأنواع.

أهمية برالحكمان

العمل المعروض في هذه الأطروحة يبرز أن برالحكمان منطقة مذهلة في ثراءها وتنوعها الحيوي. توفر هذه الأطروحة عدة أسباب يمكنها ان ترشد صناع القرار إلى حماية برالحكمان كنظام حيوي. في المقام الأول، تعمل المنطقة كأرض حاضنة للسلطعونات السابحة المهمة اقتصادياً (**الفصل الثالث**). ثانياً، برالحكمان منطقة أساسية في الجسر الجوي للطيور الشاطئية بين غرب آسيا وشرق إفريقيا إذ تشكل المنطقة مرفأً لأكثر من 18 نوعاً تمثل 1% من التعداد العالمي (**الفصل الخامس**). كذلك أظهرت بيانات الدراسة الاستقصائية أن أعداد الطيور كانت مستقرة عبر الأعوام أو ارتفعت (**الفصل الخامس**)، وذلك يختلف عن الكثير من المناطق في العالم مما قد يشير إلى أن الظروف المتعلقة بحياة الطيور في المنطقة لم تتغير بقدر تغيرها في مناطق أخرى. لكننا نشير أيضاً إلى أن برالحكمان يقع في منطقة بالعالم تشهد تغيراً سريعاً مصدره "التطور" الذي يقوم به البشر. قد يكون طائر الحنكور مهدد بالانقراض نتيجة للتغيرات البيئية في المحيط الهادئ غرب الإنديز إذ أنه متوطن في تلك المنطقة ويتكاثر في بيئة معينة لا يجدها حالياً إلا في 20 موقعاً فحسب في شبه الجزيرة العربية (**الفصل الحادي عشر**). تشير بياناتنا إلى أن طيور الحنكور التي تقضي الشتاء في برالحكمان مرتبطة بمنطقة تكاثر في جنوب غرب إيران والكويت (**الصندوق ب**). تشير بيانات الدراسة الاستقصائية والتوقعات الديموغرافية إلى أن أعداد طائر الحنكور مستقرة في الوقت الحالي، لكنها تسلط الضوء على هشاشة تأثر النوع (**الفصل السادس**). لذلك، ومن ناحية الحفاظ على النوع، فالوقت مناسب لحماية مناطق التكاثر والتشتية لهذا النوع المذهل.

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