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Front cover picture: An albino Guanay Cormorant *Phalacrocorax bougainvillii* stands out among its normal conspecifics at Isla Pescadores, Peru (see Delord *et al.*, p. 123). Photo courtesy Karine Delord.



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DIETARY VARIATION IN CHICK-FEEDING AND SELF-PROVISIONING CAPE PETREL *DAPTION CAPENSE* AND SNOW PETREL *PAGODROMA NIVEA* AT SIGNY ISLAND, SOUTH ORKNEY ISLANDS, ANTARCTICA

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SUMMARY

FIJN, R.C., VAN FRANEKER, J.A. & TRATHAN, P.N. 2012. Dietary variation in chick-feeding and self-provisioning Cape Petrel *Daption capense* and Snow Petrel *Pagodroma nivea* at Signy Island, South Orkney Islands, Antarctica. *Marine Ornithology* 40: 81–87.

Food web knowledge is a prerequisite for adequate resource management in the Antarctic ecosystem. Accurate dietary specifications for the major consumers within the Antarctic ecosystem are needed. Procellariid species are the most numerous avian species in Antarctica and account for 20% to 40% of the overall consumption by seabirds in the area. Diet composition of two important procellariids, Cape and Snow Petrels, was studied at Signy Island during the breeding season 2005–2006. Food samples were obtained by stomach flushing of both chick-feeding birds and self-provisioning birds. Original prey mass was reconstructed from identifiable remains in the stomach samples. Significantly different diet compositions were found between chick-feeding and self-provisioning Cape Petrels based on reconstructed weight (chick-feeders 39:61:0:0, fish:crustacean:squid:other; self-provisioning birds 28:65:7:1, F:C:S:O). By contrast, no significant differences were found between chick-feeding Snow Petrels (66:34:0:0, F:C:S:O) and self-provisioning birds (68:32:0:0, F:C:S:O). Dominant prey items were Antarctic Krill *Euphausia superba* and the myctophid fish *Electrona antarctica*. Compared with findings undertaken at other locations, Cape Petrels at Signy Island had higher dietary fractions of crustaceans. Similarly, this study shows higher fractions of krill and lower fractions of fish in Snow Petrels at Signy Island than at other locations. A reasonable explanation for the high crustacean fraction in both seabird species might be the local high abundance of Antarctic Krill. This emphasises that local differences in diets need to be taken into account in modelling studies. Also, fish is an abundant prey item in both species, showing that, even in a strongly krill-dominated region, fish may remain an important part of the diet of Antarctic petrel species. The differences in diet between chick-feeding and self-provisioning Cape Petrels also show the importance of studying both groups in overall dietary research.

Key words: diet, water-off-load, Snow Petrel, Cape Petrel, chick-feeding, self-provisioning, Antarctica

INTRODUCTION

Procellariids are the most numerous Antarctic seabirds and are thought to account for between 20% and 40% of the overall prey consumed by seabirds in the region (Van Franeker *et al.* 1997). Antarctic Krill *Euphausia superba* has long been considered the main link between the lower trophic levels and all Antarctic consumers, including warm-blooded vertebrates (Everson 1977) such as petrels. However, the distribution of krill in the Southern Ocean is not homogeneous (Atkinson *et al.* 2004, 2008), and many procellariids occur in areas where Antarctic Krill is less abundant (Ridoux & Offredo 1989). Past studies show that fish and squid are also important food sources for petrels (e.g. Ainley 1992, Creet *et al.* 1994, Coria *et al.* 1995, Hodum & Hobson 2000, Van Franeker *et al.* 2001). The idea that petrels eat more fish than previously believed does not undermine the position of krill as the “cornerstone” or “keystone” species of the Antarctic ecosystem, as many fish consume krill.

A quantitative approach is critical if we are to understand nutrient cycling and food web interactions. Many previous studies of Antarctic procellariid diets were qualitative rather than quantitative

(Bierman & Voous 1950) or used such different sampling methods (e.g. Ainley *et al.* 1992, Liddle 1994, Soave *et al.* 1996, Hodum & Hobson 2000, Soave *et al.* 2000, Van Franeker *et al.* 2001, Cherel *et al.* 2002) that comparisons between studies are difficult.

The diets of Cape Petrel (e.g. Arnould & Whitehead 1991, Coria *et al.* 1997, Casaux *et al.* 1998, Van Franeker *et al.* 2001) and Snow Petrel (e.g. Ferretti *et al.* 2001, Van Franeker *et al.* 2001) have been studied extensively but only once, and in little detail, at Signy Island, South Orkney islands (Beck 1969). Krill is abundant around the Antarctic Peninsula and many studies have been carried out there, perhaps biasing perceptions of the importance of krill in petrel diets and skewing representations of Antarctic food webs. In general, diets of Cape Petrels are thought to be dominated by krill, whereas Snow Petrels are thought to prefer fish.

Studies of the interactions between predators and their prey in Antarctic marine ecosystems have provided important information about the diet and food consumption of seabirds and about their potential interactions with commercial fisheries, particularly that for Antarctic Krill. Indeed, increasing exploitation of marine resources in the Southern Ocean has focused scientific research on the

management of marine ecosystems (Croxall, 1994). One important input for management is knowledge about what is required by natural predators in the system. However, to date, most dietary research has been carried out on chick-feeding seabirds, although chick-feeding accounts for only 5% of the total annual food intake of fulmarine petrels (Van Franeker *et al.* 2001). Separating the diets of chick-feeding and self-provisioning birds is important because the diet of chick-feeding and self-provisioning Antarctic petrel species are thought to be different (e.g. Van Franeker *et al.* 2001, Quilfeldt 2002). Whether we assume that self-provisioning and chick-feeding diets are similar has major consequences for modelling Antarctic food webs and hence for management of natural resources. Our aim was therefore to determine whether the abundance of krill in the Peninsula area, including the South Orkney islands, would be reflected in petrel diets and whether there are dietary differences between self-provisioning (non-breeding) and chick-feeding seabirds, by revisiting the diet of Cape and Snow Petrels at Signy Island.

STUDY AREA AND METHODS

The feeding ecology of adult Cape and Snow Petrels was studied at Signy Island, South Orkney Islands (60°42'S, 45°35'W) from 14 December 2005 to 21 February 2006. Two colonies were used to study both self-provisioning and chick-feeding birds at Factory Cove and Pinder Gully on the east coast of Signy Island. Other colonies visited only for self-provisioning bird sampling were at Gourlay Peninsula, Observation Corner and North Point.

Non-breeding birds were used to study self-provisioning diets of both species. To study chick-feeding diets, birds raising chicks were sampled when they returned to the colony to feed the chick. Birds were captured with a noose pole on days when there was no precipitation or strong winds. As a precaution to minimize disturbance and food-deprivation to the chick, sampling was carried out on only one parent per nest site per season and only after the chick-guarding period ended. Morphometric measurements were taken to determine the sex of all captured birds following methods described in Van Franeker & Ter Braak (1993). We obtained complete diet samples by the stomach flushing or Water-Off-Loading (WOL) technique (Wilson 1984). To confirm that all stomach contents were collected, a second flush was applied, which yielded clear water in all cases. In the field, samples were drained over a 0.5 mm sieve and stored in a polyethylene container. Some birds regurgitated before the WOL sampling was done. These regurgitates were collected, stored and analysed separately. After handling, birds were released close to the nest site on a spot that permitted the bird to decide whether to return immediately to the nest site.

In the laboratory, within two days after collection, diet samples were rinsed under running tap water and drained over a 0.5 mm sieve. Drained contents were weighed to record total drained weight (DRW). All recognizable items were sorted into the main prey groups (fish, crustacean, squid or "other") using a binocular microscope. The fish part was divided into fish meat, fish bones (vertebral columns and other hard material were measured), fish eyes (fresh and old, diameter was recorded) and fish otoliths (identified to the lowest taxonomic level and otolith length recorded). The crustacean part was divided into different species of crustaceans and, if possible, eyeball diameter and carapace lengths were recorded. Squid were rarely encountered in the samples but if

encountered, beaks and arm lengths were measured. In the "other" category, most items were non-food.

The total weight of the stomach contents was reconstructed (reconstructed weight, REW) based on several parts of the prey items found. Fish otoliths, fish eyes, euphausiid carapaces and euphausiid eyes were used to estimate the original size and weight of prey items. REW was determined only in diet samples with a total DRW over 1 g to avoid uncertainties about meal size and composition. Samples with a DRW of 1 g or less were often old and had probably undergone substantial digestion, increasing the chance of missing specific remains of prey items. All fish taxonomic otolith identification was carried out following Hecht (1987), Williams and McEldowney (1990) and Reid (1996). Otolith length and/or height were measured using a Zeiss Discovery Stereomicroscope and Axiovision (version 4.8.2.0). The total length and mass of each individual identified was estimated from otolith length (OL) using the equations in Williams and McEldowney (1990) and Reid (1996). No correction was made for erosion of otoliths, as no correction factor could be determined due to the absence of fresh, uneroded otoliths in the samples. We recognise that disregarding otolith erosion leads to a conservative measure of the proportion of fish in the reconstructed diets. If no otoliths were found in the samples, the number of eye lenses was used to estimate the number of fish in the sample. In this case, the average otolith length of all samples (1.81 mm for the most common fish prey *Electrona antarctica*) was used to provide an estimate of consumed fish. Crustacean identification was carried out following Morris *et al.* (1988), Hill (1990), Reid & Measures (1998) and Shreeve (2005). Reconstructed mass of krill in a diet sample was calculated from the number of eye pairs classified as either adult (eye diameter > 1.5 mm) or juvenile (eye diameter < 1.5 mm). A sub-sample of intact Antarctic Krill *Euphausia superba* was taken from each of the two groups to estimate average carapace lengths for both demographic categories and thus to calculate the average mass of one individual of the group. The total length and mass of the individuals identified were estimated from carapace length (CL) using the equations in Reid & Measures (1998). Most other crustaceans encountered were intact, so mass could be determined with some certainty. Squid remains were occasionally encountered, but complete individuals or identifiable remains, including complete squid beaks, were not retrieved. To reconstruct original prey mass, the size of body parts, such as arms, was recorded and total length was estimated, following which the equation for original mass following Clarke (1986) of the most common squid species known to occur around the South Orkney Islands (*Histioteuthis spec.*) was used to generically estimate original mass.

Diet composition was compared within species between self-provisioning and chick-feeding birds. Differences in diet composition between the different prey groups were tested using a non-parametric Mann-Whitney U test (Quinn and Keough 2002) using SPSS version 15.0.

RESULTS

A total of 90 Cape Petrel samples were collected from 31 chick-feeding and 59 self-provisioning birds. In the latter category, only seven samples had more than 1 g of food (DRW), so these were used in the REW analysis. For Snow Petrels, a total of 20 chick-feeding and four self-provisioning birds were sampled (of which three had > 1 g DRW).

Prey items found included fish, crustaceans and squid (Tables 1 and 2). In chick-feeding Cape Petrels, five species of fish were found: *Electrona antarctica*, *E. carlsbergi*, *Lepidonotothen larseni*, *Gymnoscopelus nicholsi* and *G. braueri*, in contrast to only two species in self-provisioning birds (*E. antarctica* and *E. carlsbergi*). In chick-feeding Snow Petrels, *E. antarctica*, *L. larseni* and *G. braueri* were found as prey items, whereas in self-provisioning Snow Petrels only remains of *E. antarctica* were found (Table 1).

At least six species of crustaceans were found in the diets of the two petrel species, with *Euphausia superba* being the most abundant (Table 2) as well as *Themisto gaudichaudii* (common, but sometimes suspected to originate from fish prey; i.e. secondary consumption), several species of Gammarid amphipods (common, especially in self-provisioning Cape Petrels), *Pasiphaea scotiae* (infrequent, only in Snow Petrel) and *Calanoides acutus* (infrequent). Squid remains were found; however, identification to species level was not possible.

Four Cape Petrels had manmade non-biological material in the stomach, including fragments of plastic. Other non-food items found in bird stomachs were grapefruit particles, stones, moss, terrestrial arthropods and parasitic worms. No other prey items of nutritional value were found in this study.

Drained and reconstructed food mass and proportional composition of the reconstructed samples are shown in Table 3. Frequency of occurrence of different prey types is shown for all samples, including those of less than 1 g DRW. For chick-feeding Cape Petrels, the mean mass of drained stomach samples was 33.6 g (SD = 14.7 g, range: 2.7–55.4 g, n = 31) compared with 10.1 g (SD = 12.7 g, range: 1.1–37.0 g, n = 7) for self-provisioning individuals. In chick-feeding Snow Petrels, the mean mass of drained stomach samples was 23.9 g (SD = 11.5 g, range: 11.7–48.3 g, n = 20) and in self-provisioning birds 29.1 g (SD = 8.2 g, range: 1.4–17.9 g, n = 3). In further analyses, only the reconstructed weight based on identifiable prey remains was used to determine diet composition for both species (Table 3).

TABLE 1
Main fish prey items found in Cape and Snow Petrels at Signy Island in 2005–2006

| Petrel species, prey sample | Mean otolith length (mm) ± SD (range) | Mean reconstructed weight (g) ± SD (range) |
|--|---------------------------------------|--|
| Chick-feeding Cape Petrel (n = 31) | | |
| <i>Electrona antarctica</i> (n = 88) | 1.81 ± 0.36 (0.93–2.88) | 7.15 ± 4.16 (0.84–26.59) |
| <i>Electrona carlsbergi</i> (n = 2) | 3.07 (2.76–3.38) | 6.60 (4.75–8.44) |
| <i>Lepidonotothen larseni</i> (n = 6) | 1.66 ± 0.23 (1.50–2.00) | 0.29 ± 0.10 (0.22–0.43) |
| <i>Gymnoscopelus nicholsi</i> (n = 4) | 1.52 ± 1.46 (2.51–5.64) | 19.81 ± 15.39 (1.36–33.24) |
| <i>Gymnoscopelus braueri</i> (n = 2) | 3.03 (2.77–3.28) | 30.97 (22.81–39.13) |
| Self-provisioning Cape Petrel (n = 7) | | |
| <i>Electrona antarctica</i> (n = 8) | 1.66 ± 0.35 (1.19–2.08) | 5.51 ± 3.20 (1.79–9.80) |
| <i>Electrona carlsbergi</i> (n = 1) | 2.79 | 4.89 |
| Chick-feeding Snow Petrel (n = 20) | | |
| <i>Electrona antarctica</i> (n = 129) | 1.73 ± 0.33 (0.60–2.37) | 6.27 ± 3.22 (0.22–14.73) |
| <i>Lepidonotothen larseni</i> (n = 11) | 1.72 ± 0.44 (1.07–2.55) | 0.31 ± 0.19 (0.03–0.67) |
| <i>Gymnoscopelus braueri</i> (n = 1) | 2.56 | 17.67 |
| Self-provisioning Snow Petrel (n = 3) | | |
| <i>Electrona antarctica</i> (n = 16) | 1.66 ± 0.22 (1.24–1.98) | 5.16 ± 1.96 (2.03–8.46) |

TABLE 2
Euphausia superba found in Cape and Snow Petrels at Signy Island in 2005–2006

| Petrel species, <i>E. superba</i> sample | Mean carapace length (mm) ± SD (range) | Mean total length (mm) ± SD (range) | Mean reconstructed weight (g) ± SD (range) |
|--|--|-------------------------------------|--|
| Cape Petrel | | | |
| <i>Euphausia superba</i> juvenile (n = 32) | 10.9 ± 1.46 (8–14) | 36.2 ± 3.1 (29.9–42.7) | 0.36 (0.19–0.62) |
| <i>Euphausia superba</i> adult (n = 248) | 16.7 ± 1.89 (12–20) | 47.0 ± 4.0 (38.4–55.4) | 0.85 (0.44–1.45) |
| Snow Petrel | | | |
| <i>Euphausia superba</i> juvenile (n = 13) | 11.2 ± 1.24 (9–13) | 26.4 ± 12.2 (13.0–40.5) | 0.38 (0.24–0.52) |
| <i>Euphausia superba</i> adult (n = 24) | 15.8 ± 1.44 (13–19) | 46.4 ± 3.1 (40.5–53.3) | 0.82 (0.52–1.26) |

Significantly higher proportions of fish were found in chick-feeding Cape Petrels than in self-provisioning birds ($U = 38.00$, $P < 0.01$, $r = -0.43$) as well as lower proportions of crustaceans ($U = 27.00$, $P < 0.01$, $r = -0.50$). Both squid ($U = 84.50$, n.s., $r = -0.28$) and other ($U = 93.00$, n.s., $r = -0.34$) fractions were not significantly different; however, these latter components were both minor dietary elements. Chick-feeding Cape Petrels had a diet composition, based on REW, of 39:61:00:00 (fish:crustacean:squid:other) with a mean REW of 71.7 g (SD = 31.7 g; range: 4.1–135.7 g; $n = 31$). Self-provisioning Cape Petrels had a diet composition, based on REW, of 28:65:07:01 (F:C:S:O) with a mean REW of 20.8 g (SD = 26.3 g; range: 1.7–78.2 g; $n = 7$).

No significant differences were found between chick-feeding and self-provisioning Snow Petrels in fish ($U = 19.00$, n.s., $r = -0.21$), crustacean ($U = 18.00$, n.s., $r = -0.23$), squid or other (both: $U = 28.50$, n.s., $r = -0.39$) fractions. Chick-feeding Snow Petrels had a diet composition, based on REW, of 68:32:0:0 (F:C:S:O) with a mean REW of 61.9 g (SD = 32.6 g; range: 9.6–136.2 g; $n = 20$). Self-provisioning Snow Petrels had a diet composition, based on REW, of 66:34:0:0 (F:C:S:O) with a mean REW of 83.1 g (SD = 8.0 g; range: 19.8–35.8 g; $n = 3$).

Fish and crustaceans represented the most common prey items in terms in frequency of occurrence (Table 3). The major difference between Cape and Snow Petrels in frequency of occurrence of the different fractions was the low representation of fish in self-provisioning Cape Petrels (8%), compared with 87% in chick-feeding birds. Among Snow Petrels, 100% contained fish. No squid was found in chick-feeding Snow Petrels, unlike self-provisioning birds (Table 3).

DISCUSSION

The diet composition of Cape Petrels at Signy Island was dominated by crustaceans and fish, based on percentage REW. Several previous studies have been undertaken on Cape Petrel diets from other study sites in the South Orkney islands; these reported diet compositions based on DRW proportions of 15:64:0:21 (F:C:S:O) at Signy Island (Beck 1969, recalculated in Croxall & Prince 1980), 65:35:0:0 (Coria *et al.* 1997) and 2:97:0:1 (Soave *et al.* 1996). Although based

only on drained food mass, these studies confirm that, within the South Orkney islands, both fish and krill are predominantly taken, but diet composition is highly variable between sites and years. One study using the reconstructed weight of WOL samples collected from Cape Petrels from colonies in Wilkes Land, Antarctica, found diet compositions of 46:18:36:0 (self-provisioning) and 62:34:4:0 (chick-feeding) (Van Franeker *et al.* 2001). An analysis of self-provisioning birds collected at sea found a diet composition of 69:3:19:9, based on REW (Ainley *et al.* 1992). The main difference between these two studies and our study is the lower percentage of fish prey found at Signy Island for both self-provisioning and chick-feeding birds. In addition, the proportion of squid found in the diet of self-provisioning Cape Petrel was much lower in our study.

The diet of Snow Petrels at Signy Island was also dominated by fish and crustaceans, based on REW. Within the South Orkney islands, Ferretti *et al.* (2001) found a diet composition of 90:9:0:0 for Snow Petrels (Ferretti *et al.* 2001). A high fish fraction and minor crustacean fraction has generally been reported for Snow Petrels (e.g. Ridoux & Offredo 1989, Ferretti *et al.* 2001) except for one at-sea study that reported a composition of 52:32:15:2 (Griffith 1983). As with Cape Petrels, all of these studies were based on DRW instead of REW. Studies using the REW method for Snow Petrel diets showed a composition of 59:2:38:0 (self-provisioning) and 92:3:4:0 (chick-feeding) (WOL samples collected at colonies, Van Franeker *et al.* 2001) and 92:6:2:0 (Ainley *et al.* 1992, birds collected at sea). Crustaceans were less important in previous studies of Snow Petrels diets, but our study clearly showed that crustaceans can form a substantial dietary component at some locations or in some years.

At several locations throughout the Antarctic, fish have been found to be the major component of the diet of fulmarine petrels (Arnould & Whitehead 1991; Ainley *et al.* 1992; Creet *et al.* 1994; Coria *et al.* 1997; Van Franeker *et al.* 2001), although the species taken varies. The notothenid *Pleuragramma antarcticum* was found mostly in diets in the Antarctic Peninsula region (Creet *et al.* 1994) and Wilkes Land (Van Franeker *et al.* 2001), while the myctophid *Electrona antarctica* was found mostly in the Weddell Sea (Ainley *et al.* 1992) and around the South Orkney islands (Coria *et al.* 1997; Casaux *et al.* 1998). In our study, *E. antarctica* was also found to be the most commonly

TABLE 3
Diet composition of complete stomach samples from Cape and Snow Petrels at Signy Island in 2005–2006

| Species, sample | n for samples > 1 g | n for all samples | Average DRW, samples > 1 g (g) | Average REW, samples > 1 g (g) | REW composition fish: crustaceans: squid: other, samples > 1 g (%) | Frequency of occurrence fish: crustaceans: squid: other, all samples (%) |
|--------------------|---------------------|-------------------|--------------------------------|--------------------------------|--|--|
| Cape Petrel | | | | | | |
| All | 38 | 90 | 29.3 | 62.3 | 38:61:0:0 | 36:83:6:1 |
| Self-provisioning | 7 | 59 | 10.1 | 20.8 | 28:65:7:1 | 8:75:5:2 |
| Chick-feeding | 31 | 31 | 33.6 | 71.7 | 39:61:0:0 | 87:100:6:0 |
| Snow Petrel | | | | | | |
| All | 23 | 24 | 22.0 | 57.5 | 68:32:0:0 | 100:96:4:4 |
| Self-provisioning | 3 | 4 | 29.1 | 83.1 | 68:32:0:0 | 100:100:25:0 |
| Chick-feeding | 20 | 20 | 23.9 | 61.9 | 66:34:0:0 | 100:95:0:0 |

caught fish for both Cape and Snow Petrels. The nutritional value of myctophids is high compared with other prey items (Van der Putte *et al.* 2006), and thus it must form an attractive prey for seabirds. Although myctophids occur mainly over deeper water and are not commonly found over shelves, around the South Orkneys islands this species constitutes a major energy source for surface feeding predators. *E. antarctica* is also one of the most commonly taken fish items around the South Orkney islands by Antarctic Fur Seals *Arctocephalus gazella* (Daneri & Coria 1994). Around the South Shetland islands, Blue-eyed Cormorants *Phalacrocorax atriceps brandsfieldensis* (Coria *et al.* 1995) commonly take myctophids as their main prey item, although some previous studies found negligible proportions of myctophids in the closely related South Georgia Shag *Phalacrocorax georgianus* (Casaux & Ramon 2002). *E. antarctica* is supposed to make a diel migration of 300–650 m during the day and occurs close to the surface at night (Torres & Somero 1988). However, its prevalence in surface-feeding seabird diets indicates that it must sometimes remain close to the surface during daylight (including dusk and dawn).

Crustaceans, in particular Antarctic Krill, are known to be important components of Antarctic seabird diets. Beck (1969) and Arnould & Whitehead (1991) suggest that all fulmarine petrels probably feed on krill and that this forms their staple diet. Other studies suggested that krill is more important in the subantarctic regions (Croxall & Prince 1980; Ridoux 1984), while some propose that diets are diverse and that krill is just one of the crustaceans taken (Ainley *et al.* 1992). Our study shows that for both Cape and Snow Petrels feeding around Signy Island, Antarctic Krill is indeed a major dietary item for both self-provisioning and chick-feeding birds, although for Snow Petrels fish is the most important component. The high proportion of larger adult krill (and thus higher energy content) found in this study compared with the lower proportion of juvenile krill might explain the higher fraction of crustaceans in the diets of petrels at Signy Island in contrast to other studies (Ainley *et al.* 1992; Van Franeker *et al.* 2001). Targeting crustaceans in areas where immature krill dominates the population is less attractive due to the lower energy content per prey item, compared to areas where adult (larger and higher energy content per prey item) krill is present. Similarly to this study, Soave *et al.* (1996) and Coria *et al.* (1997) reported larger mean krill lengths than in other study areas (Van Franeker *et al.* 2001) suggesting a higher proportion of adult krill around the South Orkney islands. Other crustaceans found in this study were *Themisto gaudichaudii*, Gammarid amphipods, *Calanoides acutus* and the decapod *Pasiphaea scotiae*. These are all species also found in previous studies of fulmarine petrel diets.

The squid fraction in this study was very small in both Snow Petrels and Cape Petrels. Squid are supposedly an important food source for fulmarine petrels (Lipinski and Jackson 1989). Van Franeker *et al.* (2001) showed higher squid fractions in the self-provisioning diets of both Snow and Cape Petrels and concluded that squid is an important dietary item throughout the year. Both Soave *et al.* (1996), Coria *et al.* (1997) and our study show a low overall occurrence of squid in petrel diets around the South Orkney islands, but this might be related to levels of local abundance and distribution, or to seasonal shifts in prey. The occurrence of squid in the diet of fulmarine petrels may be more common in offshore wintering areas (Ainley *et al.* 1992).

Four diet samples from Cape Petrels were found to include manmade non-biological material in the stomach, including plastics. This is a

common phenomenon in seabirds, but the incidence of plastics in true Antarctic seabirds such as the Snow Petrel is generally lower than for more northerly migrating species such as Cape Petrels (Van Franeker & Bell 1988). Finding plastic items in our study right at the beginning of the breeding season might indicate “plastic-import” from the wintering areas rather than from a local source. In our study no other prey items of nutritional value were found. Elsewhere, other prey items found in petrel diets have included carrion (Ridoux & Offredo 1989), gelatinous prey items such as jellyfish and salps (Ainley *et al.* 1992) and pteropods (Van Franeker *et al.* 2001). The scavenging nature of fulmarine petrel foraging behaviour is a factor that may influence the quantitative approach of diet studies. In our study, one Snow Petrel was found to have eaten a fish eyeball of 13 mm diameter, representing a prey item very much larger than could normally be taken; generally fish eyeballs with diameters of approximately 3 mm are found. This may indicate the scavenging of a large fish.

Several studies have shown differences between chick-feeding and self-provisioning diets in fulmarine petrels (e.g. Creet *et al.* 1994; Lorentsen *et al.* 1998; Van Franeker *et al.* 2001). Causes of such compositional shifts might be local abundance of prey items, higher energy content of certain prey items or specific nutritional requirements for chicks (Van Franeker *et al.* 2001). For example, in albatross chicks, faster growth rates have been shown to be associated with fish and krill diets rather than with squid diets (Prince and Ricketts 1981); this might cause chick-rearing adults to prefer certain prey items in favour of others. Climate variability and change can have major impacts on Southern Ocean ecosystems (Trathan *et al.* 2007), affecting prey abundance and availability to predators (Murphy *et al.* 2007). This means that accurate dietary information can be derived only from studies covering a wide range of temporal and spatial variability. Our study, although based on a modest sample size, when compared with earlier publications, shows the relevance of such widespread sampling.

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A SIMPLIFIED METHOD OF DETERMINING THE SEX OF *PYGOSCELIS* PENGUINS USING BILL MEASUREMENTS

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SUMMARY

POLITO, M.J., CLUCAS, G.V., HART, T. & TRIVELPIECE, W.Z. 2012. A simplified method of determining the sex of *Pygoscelis* penguins using bill measurements. *Marine Ornithology* 40: 89–94.

We examined sexual dimorphism in bill size in adult Adélie Penguins *Pygoscelis adeliae*, adult Chinstrap Penguins *P. antarctica* and adult and juvenile Gentoo Penguins *P. papua* at King George Island, Antarctica, using a DNA-based molecular sexing technique. Bill length and depth were the most consistent dimorphic character examined, with measurements 5.4%–11.5% larger in males than in females, on average. Within breeding pairs sampled, male Chinstrap and Gentoo Penguins had consistently longer and deeper bills than their mates, although bill measurement overlapped between sexes at the population level. We used bill measurements to calculate species- and age-specific discriminant functions that correctly classified 83.2%–96.7% of the individuals in our study following cross-validation. The discriminant functions derived from this analysis provide a practical method of sex determination for all three *Pygoscelis* penguin species in the South Shetland Islands where they breed sympatrically. Posterior probability analysis can also be used to identify individuals that are likely to be incorrectly classified using discriminant function analysis, allowing DNA-based tests for gender to be reserved for targeted use. Furthermore, we report raw morphometric data to facilitate future analysis and discriminant function improvement.

Key words: Discriminant function analysis, sexing, Adélie Penguin, Chinstrap Penguin, Gentoo Penguin, *Pygoscelis*

INTRODUCTION

While some avian taxa have conspicuous sexual variation in plumage, penguins have monomorphic plumage and are difficult to sex by direct observation. Methods of sexing penguins have focused on dissection, cloacal examination, behavior cues, morphometric analysis and, more recently, molecular techniques (Ainley & Emison 1972, Scolaro *et al.* 1987, Williams 1990, Costantini *et al.* 2008). Penguins exhibit a slight sexual size dimorphism, with males tending to be larger in body, bill and flipper size (Davis & Renner 2003). This has led several researchers to calculate species-specific discriminant functions to classify the sex of penguins based on single or multiple morphological characters (Williams & Croxall 1991, Zavalaga & Paredes 1997, Renner *et al.* 1998, Setiawan *et al.* 2004). While DNA-based molecular techniques are considered to be more reliable than morphometric analysis (Hart *et al.* 2009), discriminant functions can provide a quick, minimally invasive and cost-effective method of sex classification (Dechaume-Moncharmont *et al.* 2011).

Previous studies have calculated discriminant functions for the three *Pygoscelis* penguin species: the Adélie (*P. adeliae*), Chinstrap (*P. antarctica*) and Gentoo Penguin (*P. papua*) (Scolaro *et al.* 1987, Kerry *et al.* 1992, Amat *et al.* 1993, Renner *et al.* 1998). However, none of these studies has validated methods of sex classification using DNA-based molecular sexing. These studies also differ in their methods of statistical validation and in the number and type of morphological characters used to assign sex, both within and

across species. In addition, there is evidence that morphometric traits can vary between geographically distinct *Pygoscelis* penguin populations, and thus population-specific discriminant functions are often required (Kerry *et al.* 1992, Renner *et al.* 1998).

The objective of this study was, first, to identify male and female adult Adélie Penguins, adult Chinstrap Penguins and adult and juvenile Gentoo Penguins at Admiralty Bay, King George Island, Antarctica using a DNA-based molecular sexing technique. Second, we aimed to assess the extent of sexual dimorphism in each group and provide discriminant functions based on morphological characters that can be used to identify males and females in future studies. In addition, we wished to provide a method to calculate the classification accuracy of discriminant functions at the individual level. We restricted the morphological character examined in our study to bill measurements as these are the most common measurements reported in the literature; are easily repeatable, with well-defined anatomical landmarks; and also tend to exhibit the greatest degree of sexual dimorphism (Davis & Renner 2003).

STUDY AREA AND METHODS

Captures and measurements

We conducted fieldwork within the Antarctic Specially Protected Area (ASPA) no. 128 along the western shores of Admiralty Bay, King George Island, South Shetland Islands, Antarctica (62°10'S,

58°27'W). All three species of *Pygoscelis* penguins can be found breeding sympatrically at this location (Trivelpiece *et al.* 1987). While this area has been the site of a long-term study of the breeding biology and population dynamics of a population of *Pygoscelis* penguins since the late 1970s, discriminant function-based morphological sexing has never been applied to these populations. During the late incubation and early chick-rearing period (December) of 2010, we captured each member of 11, 15 and 10 actively breeding pairs of adult Adélie, Chinstrap and Gentoo Penguins, respectively. In addition, we supplemented these pairs with nine breeding adult Adélie Penguins, four breeding adult Gentoo Penguins and 18 non-breeding juvenile Gentoo Penguins (approximately 1 year old and identified by white head patches that did not reach the eye, incomplete white eye-rings and the lack of a brood patch) (Trivelpiece *et al.* 1985). Using calipers, we measured bill (culmen) length (BL), bill depth (BD, taken through the center of the nostrils) and bill width (BW, taken across the center of the nostrils) to an accuracy of 0.1 mm. All measurements were conducted by the same person (MJP). In addition, we collected one or two breast feathers and, in some cases, a single tail feather from each individual to facilitate molecular sexing.

Molecular sexing

DNA was extracted from two breast feather calamus per bird using QIAGEN DNEasy Blood & Tissue 96 Well Kits (QIAGEN Ltd., West Sussex, UK). Each calamus was finely sliced using a sterile razor blade. When only one calamus was available, tissue from the inside of a tail feather was also used. The manufacturer's protocol was followed with the following modification: during the incubation step, 30 μ L proteinase K was added to each sample with 180 μ L buffer ATL and incubated at 56°C for 48 h. The extracted DNA was stored in 400 μ L buffer AE at -20°C.

DNA sexing was carried out using a multiplex consisting of three primers: P0, P2 and P8 (Han *et al.* 2009). PCR amplifications were carried out in 8.5 μ L reactions containing 4 μ L 2X Multiplex PCR Master Mix (QIAGEN), 2.5 μ L template DNA and 2 μ L of the multiplex (2 μ L of each primer at 100 μ mol/L made up to 1000 μ L with sterile water). The thermal cycling conditions were: 95°C for 5 min; 35 cycles of 95°C for 30 s, 53.5°C for 90 s, 72°C for 30 s, followed by a final extension phase at 72°C for 10 min.

The amplified product was electrophoresed through a 2% agarose gel for 1 h at 125 V. Products were detected using ethidium bromide staining and ultraviolet transillumination. Males, the homogametic sex (ZZ), had a single band on the gel due to a single amplified fragment approximately 400 bp long. This corresponds to a region of the CHD-Z gene that is amplified by the P2 and P8 primer pair. Females, the heterogametic sex (ZW), had two bands on the gel at approximately 400 bp and 500 bp. These correspond to amplified regions of the CHD-Z and CHD-W genes, respectively. The partial CHD-W fragment is amplified by the P0 and P2 primer pair.

Using these molecular techniques, we successfully sexed 97 of the 103 individuals tested. The six individuals that could not be sexed were all breeding adults with eggs or chicks whose mates (four males and two females) had been successfully sexed using DNA. While same-sex mating behaviors have been observed in penguins (Davis *et al.* 1998), truly same-sex breeding pairs, which last long enough to result in successful reproduction, are likely extremely rare (Young *et al.* 2008, Pincemy *et al.* 2010). Therefore, we

assumed that the eight individuals that could not be sexed using DNA were the opposite sex of their mates.

Statistical analysis

We compared morphological measurements between males and females using *t*-tests and calculated an index of sexual dimorphism (DI, %) using the mean morphological measurement of males (M) and females (F) as $DI = 100 \times (M - F)/F$ (Greenwood 2003). Next, we conducted separate stepwise discriminant analyses to select the morphological variables (BL, BD, BW) that had significant influence on classification of males and females for each group. We used the *F*-test of Wilks' λ value as a criterion to enter the variable contributing the most, or to remove the variable contributing the least, discriminatory power to the model. The equality of group covariance matrices was tested with Box's *M*-test (Manly 2005). Pearson's correlation matrices found that all values were less than 0.66, indicating there was no multicollinearity between bill characters from our four sample groups (Zar 1984; Arnould *et al.* 2004). Selected variables were used to calculate discriminant functions, and individuals were classified as male or female on the basis of their discriminant score (D). We calculated the percentage of correct classification before and after a cross-validation or "leave-one-out test" (Dechaume-Moncharmont *et al.* 2011).

Similar to Zavalaga *et al.* (2009), we also calculated the posterior probability (PP) of membership of each bird as the probability that an individual with a particular value of D is, or is not, likely to be a male, following Bayes' rule. Values of PP and D were then fitted to a logistic curve to create group-specific functions that can be used to calculate the level of classification accuracy (PP) of an individual for any given D score. Statistical calculations were performed using SAS (version 9.1). All tests were two-tailed, and significance was defined at the $P < 0.05$ level.

RESULTS

Sexual dimorphism

While there was overlap in some morphological measurements, male penguins tended to have larger bills than female penguins in each group examined (Table 1; raw bill measurement data are in Appendix 1 available online). In adults, bill measurement were 8.1%–9.9% larger in Adélie Penguin males, 8.8–11.5% larger Chinstrap Penguin males and 5.4%–10.3% larger in Gentoo Penguin males, relative to females. BL and BD, but not BW, were larger in juvenile males than in female juvenile Gentoo Penguins (Table 1). We also found that, within our sample of breeding pairs of Gentoo and Chinstrap Penguins, males consistently had a larger BL and BD than their female mate. Within-pair comparisons in Adélie Penguins were less diagnostic, with males having the larger BL and BD in 63.6% and 90.9% of all pairs, respectively.

Discriminant function analysis

Stepwise discriminant analysis selected BL and BD as the two variables that best classified adult male and female penguin in all three species (Table 2). There was low overlap between males and females when examining these two bill measurements (Fig. 1). The classification accuracy of the linear discriminant function for adult Adélie Penguins was 90.3% and 83.8% after cross-validation (Wilks' $\lambda = 0.38$, $P < 0.0001$; Box's *M* = 2.32, $P = 0.5082$). Adult Adélie Penguins with $D \geq 0.000060$ were classified as females

when the posterior probability was set at 0.5 (Table 2). Chinstrap Penguin classification accuracy did not change after cross-validation (96.7%; Wilk's $\lambda = 0.25$, $P < 0.0001$; Box's $M = 5.8$, $P = 0.1197$). Adult Gentoo Penguin classification accuracy was 91.7% and 83.2% after cross-validation (Wilk's $\lambda = 0.44$, $P = 0.0002$; Box's $M = 2.25$, $P = 0.5221$). Adult Chinstrap and Gentoo Penguins with $D \geq 0.000053$

and ≥ 0.000231 , respectively, were classified as females at a posterior probability of 0.5 (Table 2). Stepwise discriminant analysis selected BL, BD and BW as the three variables that best classified male and female juvenile Gentoo Penguin (Fig. 1; Wilk's $\lambda = 0.32$, $P = 0.0009$; Box's $M = 11.18$, $P = 0.0830$). The classification accuracy of the linear discriminant function for juvenile Gentoo Penguins was

TABLE 1
Bill size measurements and sexual dimorphism in *Pygoscelis* penguins at Admiralty Bay, King George Island, Antarctica

| Group, measurement | Mean \pm SD (range) | | DI (%) ^a | t-test |
|-------------------------------|----------------------------|----------------------------|---------------------|---------------------------|
| | Male | Female | | |
| Adélie Penguin - adult (n) | 16 | 15 | | |
| Bill length (mm) | 40.8 \pm 2.1 (37.6-43.7) | 37.7 \pm 2.5 (33.2-40.6) | 8.2 | $t = 3.66$, $P = 0.0010$ |
| Bill depth (mm) | 19.9 \pm 0.7 (18.9-21.1) | 18.1 \pm 0.9 (16.8-19.6) | 9.9 | $t = 6.59$, $P < 0.0001$ |
| Bill width (mm) | 13.4 \pm 0.9 (12.0-15.0) | 12.4 \pm 1.0 (9.7-14.2) | 8.1 | $t = 2.88$, $P = 0.0074$ |
| Chinstrap Penguin - adult (n) | 15 | 15 | | |
| Bill length (mm) | 50.4 \pm 1.6 (47.5-53.5) | 45.2 \pm 3.0 (37.3-49.5) | 11.5 | $t = 5.97$, $P < 0.0001$ |
| Bill depth (mm) | 19.8 \pm 0.7 (18.6-21.4) | 18.2 \pm 0.5 (17.4-19.2) | 8.8 | $t = 7.02$, $P < 0.0001$ |
| Bill width (mm) | 15.0 \pm 1.2 (13.8-17.6) | 13.7 \pm 1.3 (12.1-17.9) | 9.5 | $t = 2.93$, $P = 0.0066$ |
| Gentoo Penguin - adult (n) | 11 | 13 | | |
| Bill length (mm) | 48.7 \pm 2.6 (44.3-52.0) | 44.9 \pm 2.2 (41.4-49.2) | 8.5 | $t = 4.01$, $P = 0.0006$ |
| Bill depth (mm) | 17.2 \pm 0.9 (16.2-18.9) | 15.6 \pm 0.7 (14.5-16.4) | 10.3 | $t = 4.70$, $P = 0.0001$ |
| Bill width (mm) | 11.8 \pm 0.6 (10.7-12.6) | 11.2 \pm 0.6 (10.4-12.5) | 5.4 | $t = 2.55$, $P = 0.0184$ |
| Gentoo Penguin - juvenile (n) | 6 | 12 | | |
| Bill length (mm) | 46.9 \pm 1.0 (46.1-48.2) | 43.4 \pm 1.9 (39.9-46.5) | 8.1 | $t = 4.2$, $P = 0.0007$ |
| Bill depth (mm) | 15.8 \pm 0.6 (15.2-16.8) | 14.9 \pm 0.5 (14.2-15.8) | 6.0 | $t = 3.67$, $P = 0.0021$ |
| Bill width (mm) | 11.4 \pm 0.3 (11.1-11.9) | 10.9 \pm 0.7 (10.0-12.5) | 4.6 | $t = 1.99$, $P = 0.0642$ |

^a DI (dimorphism index) is the difference in percentage as $100 \times (M - F)/F$, where M is the male measurement and F is female measurement.

TABLE 2
Discriminant and posterior probability of assignment functions for *Pygoscelis* penguins at Admiralty Bay, King George Island, Antarctica

| Group | Discriminant function ^a | Posterior probability (male) ^b | Classification accuracy (cross-validated) ^c |
|---------------------------|--|---|--|
| Adélie Penguin (adult) | $= 64.03041 - 2.85219BD - 0.25089BL$ | $= \frac{1}{1 + \exp(1D - 0.000060)}$ | 90.3% (83.8%) |
| Chinstrap Penguin (adult) | $= 120.25754 - 4.10985BD - 0.87985BL$ | $= \frac{1}{1 + \exp(1D - 0.000053)}$ | 96.7% (96.7%) |
| Gentoo Penguin (adult) | $= 53.19063 - 1.89275BD - 0.47576BL$ | $= \frac{1}{1 + \exp(1D - 0.000231)}$ | 91.7% (83.2%) |
| Gentoo Penguin (juvenile) | $= 129.0415 - 2.86241BD - 1.14292BL - 3.00143BW$ | $= \frac{1}{1 + \exp(1D - 0.060900)}$ | 94.4% (91.7%) |

^a Bill measurements (mm): BD = bill depth, BL = bill length, BW = bill width

^b D = discriminant score

^c Percentage of correct classifications before and after (in parentheses) "leave-one-out" cross-validation.

94.4% and 91.7% after cross-validation. Juvenile Gentoo Penguins with $D \geq 0.060900$ were classified as females when the posterior probability was set at 0.5 (Table 2).

DISCUSSION

Pygoscelis penguins at Admiralty Bay, King George Island, exhibited sexual size dimorphism, with males tending to be significantly

larger in most measurements (Table 1). BL and BD measurements tended to be the most consistently dimorphic characters for all three species. Within breeding pairs, male Chinstrap and Gentoo Penguins had consistently longer and deeper bills than their mates. However, it is important to note that bill measurement overlapped slightly between sexes at the population level. Given this trend, a larger sample of within-pair comparisons may indicate that relative bill size, while a useful sexing tool in Chinstrap and Gentoo

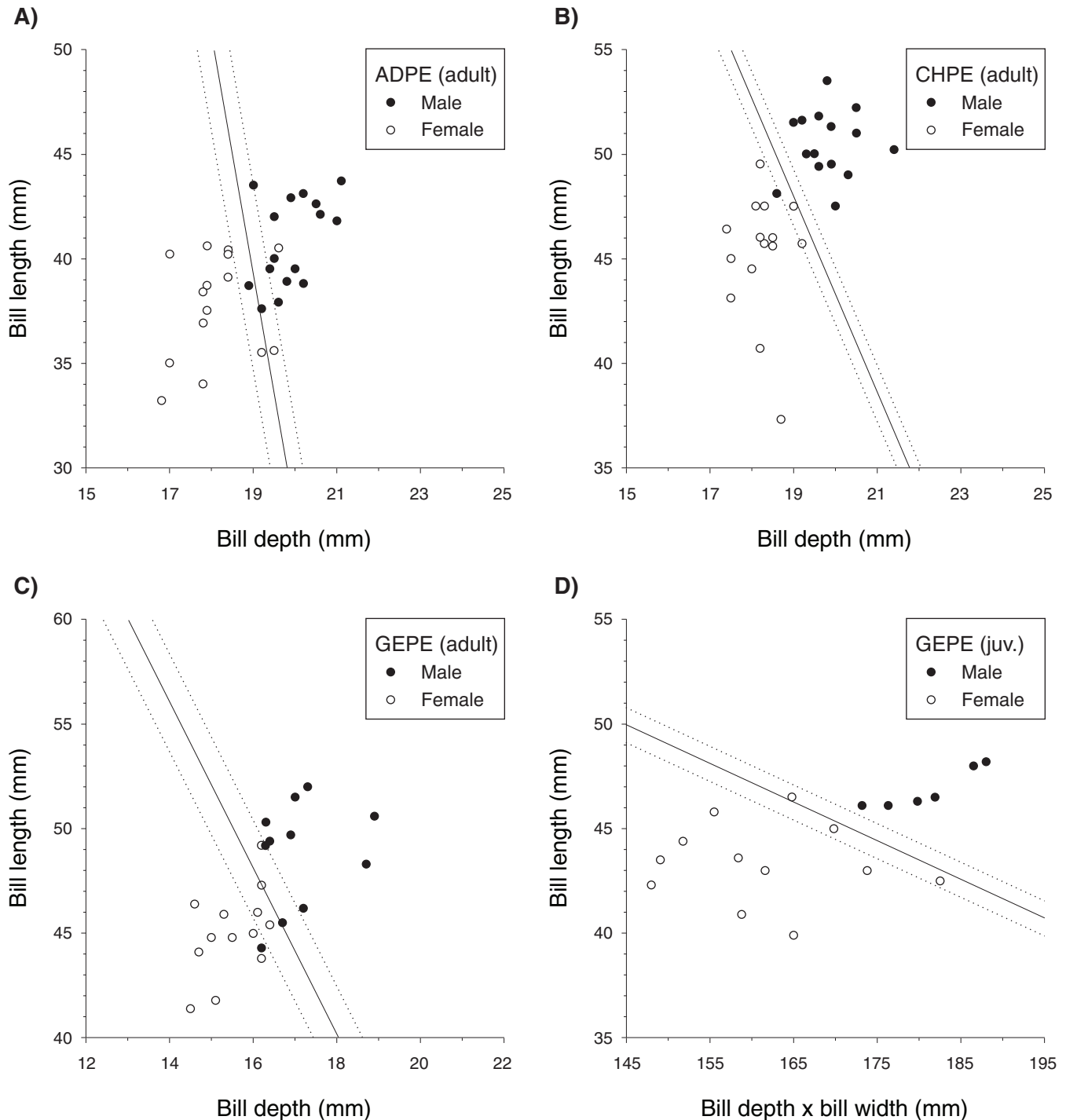


Fig. 1. Bill length and bill depth for breeding adult Adélie (A), Chinstrap (B) and Gentoo (C) penguins, and bill length and bill depth x bill width for juvenile Gentoo Penguins (D) at Admiralty Bay, King George Island, Antarctica. Solid lines represent a 50% posterior probability (PP) of correct sex assignment based on the discriminant functions described in Table 2. All birds above these lines were classified as males. Dotted lines represent 25% and 75% posterior probabilities.

Penguin pairs, is likely less than 100% reliable. The magnitude of bill-size dimorphism we observed in *Pygoscelis* penguins at Admiralty Bay (5.4%–11.5%) was relatively small in comparison with that of other penguin genera such as *Spheniscus* (7.4%–15.3%) and *Eudyptes* (10.2%–17.8%; Agnew & Kerry 1995). Inter-specific variation in sexual dimorphism may be influenced by environmental factors; body size and BL in penguins tend to decrease with both latitude and environmental temperature (Symonds & Tattersall 2010). The higher degree of sexual dimorphism observed in *Spheniscus* and *Eudyptes* penguins may be driven by the greater importance of foraging-related factors, such as resource limitation and competition, in more moderate-temperature habitats and may thus lead to a greater selective pressure on bill size (Agnew & Kerry 1995). Sexual dimorphism in *Eudyptes* penguins can also be related to male mating displays and mate recognition (Warham 1972).

Observed sexual size dimorphism in avian populations may also be influenced by age structure. Mínguez *et al.* (2001) found that first-time breeding Chinstrap Penguins nesting on the edge of the colony had smaller bills than older, more experienced breeders nesting in central positions. At our study site, one-year-old male Gentoo Penguins have bill measurements similar in size to those of breeding adult females. Therefore, age-specific variation may have the potential to influence measures of sexual size dimorphism if avian morphometric characters continue to grow through early adulthood (Coulson *et al.* 1981, Bortolotti 1984, Mínguez *et al.* 1998).

The discriminant functions derived from this study provide classification accuracies roughly similar to those reported in previous studies of *Pygoscelis* penguins (Scolaro *et al.* 1987, Kerry *et al.* 1992, Amat *et al.* 1993, Renner *et al.* 1998). Unfortunately, due to differences in the number and type of morphological characters used to assign sexes, it is difficult to directly compare our results with these previous studies. Only Amat *et al.* (1993) provides a discriminant function using BL and BD measured in the same manner that is therefore directly comparable to ours. Amat *et al.*'s (1993) discriminant function for Chinstrap Penguins at Deception Island would have correctly assigned sex to 93.3% of the individuals in our data set, whereas the discriminant function derived in this study correctly assigned sex to 96.7% of individuals. This suggests that, at least for Chinstrap Penguins, the discriminant function derived in this study may be applicable to other breeding sites in the South Shetland Islands.

Posterior probability analysis allowed us to determine the relative accuracy of sex assignment for individuals sexed with the discriminant functions derived in this study. This approach can allow researchers to identify individuals with intermediate morphometric characters that are most likely to be incorrectly assigned (Hart *et al.* 2009, Zavalaga *et al.* 2009). Assessing the reliability of individual sex classifications can allow the targeted use of the more expensive and labor-intensive DNA-based molecular tests to definitively assign gender when confidence in the discriminant function is low. For example, Kerry *et al.* (1992), suggests that discriminant functions with an overall success rate of > 80% are acceptable for most purposes. This same cut-off value could be applied to the posterior probability values of individuals, although researchers should be cautious to assign cut-off values appropriate to the degree of sexual dimorphism in their study species (Hart *et al.* 2009). Regardless, DNA testing should be preferentially used in field studies when there is likely to be a small effect size between sexes and sex misclassifications would have a disproportionate overall effect (Hart *et al.* 2009).

While the classification accuracies from this study were similar to previous analyses, the discriminant functions resulting from our study have both advantages and disadvantages. For example, the use of DNA-based methods to validate our methods of sex classification represents a more robust methodological approach than found in previous studies. However, we also used generally smaller group sample sizes to calculate the discriminant functions than previous studies (20–31 individuals vs. 35–55 individuals per group). To help address this issue, our raw measurement data have been included as an appendix to facilitate increased sample sizes and the refinement of discriminant function in the future. An advantage of this study is that we provide a method of estimating the posterior probability of sex assignment for individuals sexed via discriminant analysis, which can allow for targeted use of DNA-based sexing methods. In addition, we used consistent morphological characters across adults of all *Pygoscelis* species in our discriminant functions. Furthermore, BL and BD are the most common measurements reported in avian literature, allowing for a greater application across studies (Davis & Renner 2003, Dechaume-Moncharmont *et al.* 2011). Reducing the number and diversity of measurements required to sex individuals is of practical benefit to researchers, especially in the Antarctic Peninsula region where *Pygoscelis* penguins breed sympatrically. Future work using comparable morphological characters is required to determine how well our discriminant and posterior probability functions perform at other breeding locations.

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A ROYAL PENGUIN *EUDYPTES SCHLEGELI* IN THE FALKLAND ISLANDS?

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SUMMARY

DEHNHARD, N., LUDYNIA, K. & ALMEIDA, A. 2012. A Royal Penguin *Eudyptes schlegeli* in the Falkland Islands? *Marine Ornithology* 40: 95–98.

The Royal Penguin *Eudyptes schlegeli* breeds only on Australia's Macquarie Island and its nearby islets, about 1 200 km southwest of New Zealand. Vagrant Royal Penguins have been reported elsewhere in Australia, New Zealand and Antarctica. Reports of Royal Penguins from other subantarctic islands, including Heard, Prince Edward and Marion Islands, South Georgia and the Falkland Islands are controversial, as these penguins could also be aberrant Macaroni Penguins *E. chrysolophus*, and species determination can be difficult because of high variation in facial colour in both species. We discuss here the recent sighting of an apparent immature Royal Penguin on New Island, Falkland Islands. A simultaneously visiting adult male Macaroni Penguin allowed a size comparison between the two individuals. This could be the first documented sighting of a vagrant Royal Penguin in the Neotropical region.

Key words: Royal Penguin, Macaroni Penguin, body size, facial coloration, Falkland Islands/Islas Malvinas

INTRODUCTION

Royal Penguins *Eudyptes schlegeli* breed only on Australia's Macquarie Island and its associated Bishop and Clerk Islands, about 1 200 km southwest of New Zealand (Williams 1995). As in all *Eudyptes* species, Royal Penguins have a strongly synchronised breeding cycle. Both adults are involved in the breeding activities throughout the chick-rearing period, which lasts from the end of September until the beginning of February (Warham 1971a). Thereafter, breeding adults go on an extended foraging trip to gain energy reserves for the moult that takes place in March (Warham 1971a). After moult, breeding Royal Penguins disperse and spend the winter in pelagic waters, staying in relative proximity to Macquarie Island (distribution patterns based on shipboard observations; Reid *et al.* 1999). Royal Penguins start breeding activities at a minimum age of five years (Warham 1971a). Non-breeding birds visit colonies at least once a year to moult. Juveniles and second to third years are smaller than adults and have shorter crest feathers (Warham 1971a, Williams 1995). Besides these age-related size differences, the species exhibits a sexual size dimorphism, with male Royal Penguins being generally about 10% larger than females (Warham 1971a, Williams 1995, Woehler 1995, Hull 1996).

The Royal Penguin has been considered a subspecies or colour morph of the similar Macaroni Penguin *Eudyptes chrysolophus*, which breeds on several subantarctic islands, from South America in the west to Heard Island in the east (Christidis & Boles 1994, Williams 1995). More recently, Macaroni and Royal Penguins have been considered two different species, although confusion in identification remains (Williams 1995, Shirihai 2007). The split has been adopted by the New Zealand Checklist Committee (2010), but not by Christidis & Boles (2008). Royal and Macaroni Penguins are the largest species within the genus *Eudyptes*, and they are the only species in which the

anterior, fibrous-textured, yellowish-golden and black superciliary stripe crest feathers meet on the forehead (Williams 1995).

The main identification characteristic, and the most commonly cited, is the facial colour: the Royal Penguin generally has a pale face, with whitish cheeks and a pale throat, whereas the Macaroni Penguin has a dark grey to black face and throat (Williams 1995, Shirihai 2007). However, this coloration is variable, and Shaughnessy (1975) describes a continuum of white to dark grey cheek colour in breeding Royal Penguins. In this species, the darker facial colour occurs more frequently in females than in males. Dark-faced individuals are more frequent in some breeding colonies, resulting in an uneven distribution of dark-faced females between breeding colonies on Macquarie Island (Shaughnessy 1975).

On the other hand, there are also descriptions of completely white-faced individuals among Macaroni Penguins (see Fig. 2 in Petersen 2002). Notably, these pale-faced penguins make up only 0.02% of the population on Marion Island, and they seem to breed only in particular areas on this island (Petersen 2002). These observations have led some to question whether pale-faced birds among Macaroni Penguins are local variants or hybrids with Royal Penguins (e.g. Williams 1995, Petersen 2002).

Although Royal Penguins have on average 5%–20% larger bills than Macaroni Penguins (Williams 1995, Woehler 1995, Hull 1996), the overlap of variation between the two species makes reliable identification difficult (Williams 1995, Petersen 2002, Shirihai 2007). This is especially true for vagrant penguins away from breeding sites. Vagrant Royal Penguins have been reported from Australia, New Zealand (including the Snares Islands), as well as from Antarctica (Jouanin & Prévost 1953, Berruti 1981, Mitchell 1986, Williams 1995, Shirihai 2007).

For archipelagos further away from Macquarie Island, reports of white-faced *Eudyptes* species are usually treated differently. Williams (1995), on the basis of Berruti (1981), states that pale-faced individuals on Heard, Marion, Crozet and Kerguelen Islands could also be aberrant Macaroni Penguins, but Shirihai (2007) is less conservative and refers to several sightings of Royal Penguins on South Georgia. In contrast, the American Ornithologist's Union (Remsen Junior *et al.* 2011) does not accept the reports of potential Royal Penguins in southern Chile (one sighting) and the Falkland Islands (several sightings, including description by I.J. Strange of breeding attempts). Here, we present the recent sighting of an immature Royal Penguin appearing simultaneously with a black-faced, much smaller, adult male Macaroni Penguin on New Island, Falkland Islands, in January 2011.

OBSERVATIONS

While conducting fieldwork with Southern Rockhopper Penguins *Eudyptes chrysocome chrysocome* between 11 November 2010 and 24 February 2011, we visited the "Settlement Colony" (51°43'S, 61°17'W) of New Island, Falkland Islands, daily. On the morning of



Figure 1. Royal Penguin on New Island, Falkland Islands, 18 January 2011. The head coloration shows the typical white cheeks. Photograph by Nina Dehnhard.



Figure 2. Royal Penguin (top right) next to Southern Rockhopper Penguins on New Island, Falkland Islands, 18 January 2011. Photograph by Nina Dehnhard.

18 January (10h18) ND observed what she believed to be a Royal Penguin resting at the landing site among Rockhopper Penguins. From the distance (about 100 m), looking down from the northern ledge of the Rockhopper colony, the Royal Penguin appeared nearly twice as large as the adjacent Rockhopper Penguins, and the pale face was clearly visible. By around 11h00 the Royal Penguin had left the landing area, and we found it again around 20h00 in a gully that Rockhopper Penguins use to reach the part of the colony known as "The Bowl." This time, we (AA, KL, ND) could approach the penguin to within 2 m. The cheeks, throat and breast of the bird were white; however, there was a thin greyish line of feathers between throat and breast (Fig. 1). The bill was thick, high-ridged and reddish-brown in colour. The facial skin around the bill had a bright pink colour, and some of the immediately adjacent feathers had a yellowish-golden tone. Crest-feathers united in the middle of the forehead and were of golden-yellowish colour, interspersed with some black feathers. Feathers were black from the bill up to the forehead and the neck. Crest-feathers of the penguin were rather short, reaching the back of the head, but not beyond that, as shown in Shirihai (2007) for adult Royal Penguins. In general, feathers looked rather worn, as though approaching moult, and the upper tail coverts were white, as often seen in pre-moult Macaroni and Royal Penguins (e.g. see Warham 1971b). The Royal Penguin appeared to be in a well-nourished state and behaved dominantly against the passing, much smaller, Rockhopper Penguins (Fig. 2). We checked for the presence of a PIT-tag, but the Royal Penguin was not marked. The Royal Penguin was again observed on 19 January in a different gully just east of the



Figure 3. Adult male Macaroni Penguin (front) standing close to Southern Rockhopper Penguins at the landing site, New Island, Falkland Islands, 18 January 2011. Photograph by Nina Dehnhard.

landing area. Thereafter, despite searching in different parts of the colony, we did not see the Royal Penguin again.

Simultaneously with the Royal Penguin, an adult Macaroni Penguin visited the Settlement Colony of New Island. The Macaroni Penguin was first observed by ND on 18 January 2011 around 11h00 in the gully east of the landing area. That evening we observed the Macaroni Penguin coming ashore with a group of Southern Rockhopper Penguins (Fig. 3). In comparison with the Royal Penguin, it appeared slender and much smaller, and feathers appeared less worn. This individual Macaroni Penguin had visited New Island once before, in December 2008, as indicated by the presence of a PIT-tag. On that occasion it had been captured, measured and marked with a PIT-tag by M. Poisbleau and L. Demongin, who kindly gave us their data. The measurements taken at that time (mass 4940 g, bill length 63.4 mm, bill depth 26.2 mm, flipper length 205 mm) clearly identify this individual Macaroni Penguin as a male (compare with measurements in Williams 1995). The Macaroni Penguin stayed several days on New Island, appearing in different parts of the colony, and was last observed on 21 January 2011 in the northern part of the Rockhopper Penguin colony.

DISCUSSION

The identification of a Royal Penguin away from its usual breeding site requires careful evaluation. Previously, sightings of penguins believed to be Royal Penguins, especially in the Neotropical region around the Falkland Islands and South America, have been rejected, and the birds were conservatively considered aberrant Macaroni Penguins. However, for this recent sighting of a white-faced *Eudyptes* Penguin on New Island, we have strong evidence to suggest that it was a Royal Penguin.

The white-faced bird that we observed on New Island had comparatively short crest feathers, indicating that it was not yet a fully grown adult. The state of the feathers of the observed individual suggested that it was just prior to moult. As in other crested penguins, immatures and non-breeding Royal Penguins tend to moult earlier in the season than breeding adults (Warham 1971a). Although we did not catch and measure the bird, we suggest from its overall size and its long and high bill that it was a male (see Woehler 1995 & Hull 1996 for measurement data of Royal Penguins).

Published data on morphometric measurements between Macaroni and Royal Penguins partially overlap, which makes the species identification difficult. The calculation of the bill shape index (derived from bill length, width and depth) results in a better, but still not complete, segregation between the two species (Woehler 1995). For example, the bill measurements from the Macaroni Penguin that visited New Island at the time the Royal Penguin was reported are in the average to upper range of data published in Williams (1995) for male Macaroni Penguins. Compared with published measurement data of Royal Penguins (Williams 1995, Woehler 1995, Hull 1996), the bill measurements of the Macaroni Penguin were smaller than or as small as the lowest values published. The penguin we believe to be a Royal Penguin was larger and had a longer and thicker bill than the Macaroni Penguin (when compared <5 m away), suggesting it was an immature male. We do not have a photograph of the Macaroni and the Royal Penguin next to each other, but the comparison of the two individuals with the Southern Rockhopper Penguins (Figs. 2 and 3) clearly shows the size difference, which is consistent with the literature (Williams 1995, Woehler 1995, Hull 1996).

It seems more likely that the pale-faced bird on New Island was a Royal Penguin than a Macaroni Penguin. On Macquarie Island, Royal Penguins are more commonly pale-faced than dark-faced, and the proportion of pale-faced individuals is higher in males than in females (Shaughnessy 1975). We believe the bird that we observed to be a sub-adult male. In contrast, pale-faced Macaroni Penguins are rather rare (Petersen 2002). Together, the observed size differences and stronger likelihood that a pale-faced individual is a Royal Penguin, argue against the possibility that it was an aberrant Macaroni Penguin.

Assuming our report to be the first documented observation of a vagrant Royal Penguin on the Falkland Islands, it demonstrates another example of a far-travelled vagrant and reinforces the potential for dispersion for this species. Macquarie Island is about 7 600 km from New Island, the shortest route being an eastward crossing of the Pacific Ocean and Cape Horn. However, even smaller penguin species, such as the Snares Penguin (*Eudyptes robustus*), have been shown to travel such long distances (e.g. Demongin *et al.* 2010). Moreover, it seems that sub-adult non-breeding penguins are more often recorded as vagrants in distant places than adults (e.g. Woehler 1992, Miskelly & Bell 2004).

In the light of this recent sighting of a Royal Penguin on New Island, at least some of the previous and historic reports and their classifications as aberrant white-faced Macaroni Penguins could be erroneous. To distinguish between the two species, size comparisons can be helpful. For a clear identification in the future, it would be helpful to amend the dataset collected by Woehler (1995) to get a sufficient sample to determine the variation in size (e.g. bill length, depth and width and flipper length) over the breeding range (including several colonies) for both Royal and Macaroni Penguins. With such a dataset, discriminant functions for accurate species identification could be developed, similar to the discriminant function analyses used for sex-determination in other size-dimorphic species (e.g. see Hull 1996; Poisbleau *et al.* 2010). For future vagrant observations, we therefore recommend capturing and measuring the vagrant bird (especially its bill depth and length) to more positively identify which of these two extremely variable crested penguin species the vagrant represents.

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AN ISLAND-WIDE SURVEY OF ABBOTT'S BOOBY *PAPASULA ABBOTTI* OCCUPANCY ON CHRISTMAS ISLAND, INDIAN OCEAN

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SUMMARY

BOLAND, C.R.J., SMITH, M.J., MAPLE, D., TIERNAN, B., & NAPIER, F. 2012. An island-wide survey of Abbott's Booby *Papasula abbotti* occupancy on Christmas Island, Indian Ocean. *Marine Ornithology* 40: 99–103.

Decades of phosphate mining on Christmas Island in Abbott's Booby *Papasula abbotti* nesting habitat has created a conservation threat to this rare endemic seabird. The status of Abbott's Boobies could be further jeopardised by other processes, such as the impact of Yellow Crazy Ants *Anoplolepis gracilipes* and other invasive species. Here we report on the current distribution of Abbott's Booby on Christmas Island based upon occupancy data collected during an island-wide survey in 2009. We used a combination of sightings and the characteristic vocalisations of the species to establish presence/absence within the area of each survey point. A subset of the survey points was repeat-surveyed, allowing us to estimate detection probabilities. Average detectability using our approach was 0.65 (SE 0.04). We related occupancy by Abbott's Booby to several environmental covariates using site-occupancy species distribution modelling techniques. We did not find any evidence of a significant relationship between occupancy by Abbott's Booby and distance to the nearest road or to high-density Yellow Crazy Ant colonies. However, we did find that occupancy by Abbott's Booby was significantly and positively related to both elevation and distance to the nearest disturbed area. Abbott's Booby nesting habitat is restricted to the central plateau on Christmas Island and has diminished because of major disturbances. There is evidence that the species now inhabits previously unoccupied areas but still does not re-occupy habitat that immediately surrounds areas cleared for phosphate mining several decades ago.

Key words: Abbott's Booby, phosphate mining, Yellow Crazy Ant, Christmas Island, occupancy modelling

INTRODUCTION

Abbott's Booby *Papasula abbotti* is the rarest and largest of the sulids. The species formerly nested on islands in the central and western Indian Ocean, but was lost from these localities because of habitat degradation (Nelson and Powell 1986). Now the only breeding colony is on Christmas Island, an Australian external territory in the eastern Indian Ocean where the most recent Abbott's Booby population estimate was 2 500 pairs in 1991 (Yorkston & Green 1996). Accordingly, the species is listed as endangered under the Australian Government's *Environment Protection and Biodiversity Conservation Act 1999*. The low rate of recruitment of this large, long-lived seabird inhibits its capacity to recover quickly from a population decline. Breeding is biennial, parents raise a single young, and juveniles suffer high mortality. As a result, pairs successfully replace themselves only once every 24 years on average (Nelson & Powell 1986, Reville *et al.* 1990).

On Christmas Island, the population has been threatened by habitat loss due to phosphate mining (Reville *et al.* 1990). From 1968 until 1987, when clearing primary forest for phosphate mining ceased, one-third of the species' remaining nesting habitat was cleared, and the breeding population experienced a concomitant decline (Nelson 1971, Nelson & Powell 1986, Reville *et al.* 1990, Yorkston & Green 1996). Furthermore, Abbott's Boobies build nests on thin lateral branches high in the canopy of rainforest trees. Wind tunnel experiments demonstrated that clearing forest increases turbulence in the canopy (Brett 1989), lowering breeding success and site

fidelity, and increasing adult mortality of Abbott's Booby nesting in surrounding areas (Reville *et al.* 1990). Although forest clearing for phosphate mining stopped in 1987, the resulting clearings remained, probably constraining the rate of recovery of the Abbott's Booby population (Yorkston & Green 1996). This may explain why the population was still found to be in decline in 1989 (Reville *et al.* 1990). In 1996, Yorkston and Green reported that the population on Christmas Island was stable, but still expressed concern for the species should significant habitat disturbance continue.

Unfortunately, significant habitat disturbance has continued in the form of a biological invasion by Yellow Crazy Ants *Anoplolepis gracilipes*. In the late 1990s, vast, high-density Crazy Ant colonies began to be recorded (O'Dowd *et al.* 2003). By 2002, more than 2 500 ha (or about 25% of the island's forest) were invaded by high-density Crazy Ant colonies, now considered to be one of the major environmental threats to Christmas Island (O'Dowd *et al.* 2003). The ants potentially further degrade Abbott's Booby habitat (Department of Environment and Heritage 2004) by extirpating the terrestrial Christmas Island Red Crabs *Gecarcoidea natalis* from the area. Because the Red Crabs are a dominant primary forest floor consumer of leaf, shoot, and seed material, their removal from an area typically results in a denser, more diverse and different forest understorey (O'Dowd *et al.* 2003), which may ultimately degrade Abbott's Booby nesting habitat. Also, they forage for honeydew secreted by introduced scale insects high up in the canopy, swarming over nesting birds, which can cause the birds to abandon their nesting attempt (Davis *et al.* 2008, 2010). However, there are

few data on the threat that Yellow Crazy Ants (or their control) might pose to Abbott's Booby, so claims of an impact relating to Crazy Ants are largely speculative. As the major environmental management authority on the island, Christmas Island National Park attempted to control the spread of high-density colonies by baiting with Presto (active ingredient: fipronil) in 2002 and 2009 (Boland *et al.* 2011).

Since 2001, Christmas Island National Park has been conducting a biennial, island-wide survey for Yellow Crazy Ants and Christmas Island Red Crabs. In 2009, this survey was extended to include an estimate of presence/absence of Abbott's Booby, which allowed the bird's current distribution to be mapped and the relationship between occupancy and several environmental variables to be assessed. As a baseline dataset, this information will allow future monitoring of changes in distribution.

METHODS

Study area

Christmas Island (10°25'S, 105°40'E) is a 135 km² limestone and basalt oceanic island located 360 km south of Java, Indonesia. The island has a central plateau that rises steeply to 361 m above sea level and is fringed by a coastal terrace. The climate is monsoonal with the wet season generally between November and May. Mean annual rainfall is 2 068 mm, mean maximum temperature is 27.3 °C and mean minimum temperature is 22.8 °C (Australian Bureau of Meteorology). About 74% of the island is covered with natural vegetation, mostly structurally simple, broad-leaved rainforest (Claussen 2005). Christmas Island National Park covers 63% of the island (Christmas Island National Park 2002).

Field surveys

Since 2001, Christmas Island National Park has carried out annual ant-baiting programs and biennial island-wide surveys (see Boland *et al.* 2011 for more detail). In 2009, the 889 near evenly spaced survey points (\approx 366 m apart) were sampled once, and a subset of

randomly chosen blocks of sites were surveyed on two ($n = 223$) or three ($n = 14$) occasions (Fig. 1). Sites for repeat surveying were grouped in randomly chosen blocks that encompassed an area around 2.25 km². This approach was required because of the logistical difficulties associated with traversing the island. Once the effort was made to travel to a particular area, it was important to repeat-survey as many sites in that area as possible. The number of sites repeat surveyed in a block on any occasion varied depending on the difficulties associated with moving between sites in a given area, the weather, and the number of surveyors available on a particular day. Each site was surveyed by two or three individuals from a team of 14. At any time, each team always included one of the five most experienced surveyors and all individuals were trained in the survey protocol before commencement of the program.

At each survey point, we counted Abbott's Booby by watching and listening for birds for a minimum of 10 minutes. The species is very vocal and aural assessment of their occupancy was particularly important. High-density Yellow Crazy Ant colonies were identified and mapped after each island-wide survey following the procedures outlined in Boland *et al.* (2011). Surveys were conducted between May and August 2009.

Breeding biology

Abbott's Boobies build their nests near the top of rainforest trees (about 10–40 m above the ground). The breeding cycles last 15–18 months. Successful pairs can nest once every 2 years, but often take rest years between attempts to raise a chick. Most pairs breed only once every 3 years. Mating usually takes place in April. Each pair lays a single egg between April and July, which is incubated for about 56 days. Chicks hatch from June to November; they fledge about 170 days later and become independent after an additional 200 days (Marchant & Higgins 1990).

Statistical approach

We classified survey sites by their linear distance in kilometres to the nearest high-density Yellow Crazy Ant colony, as mapped in

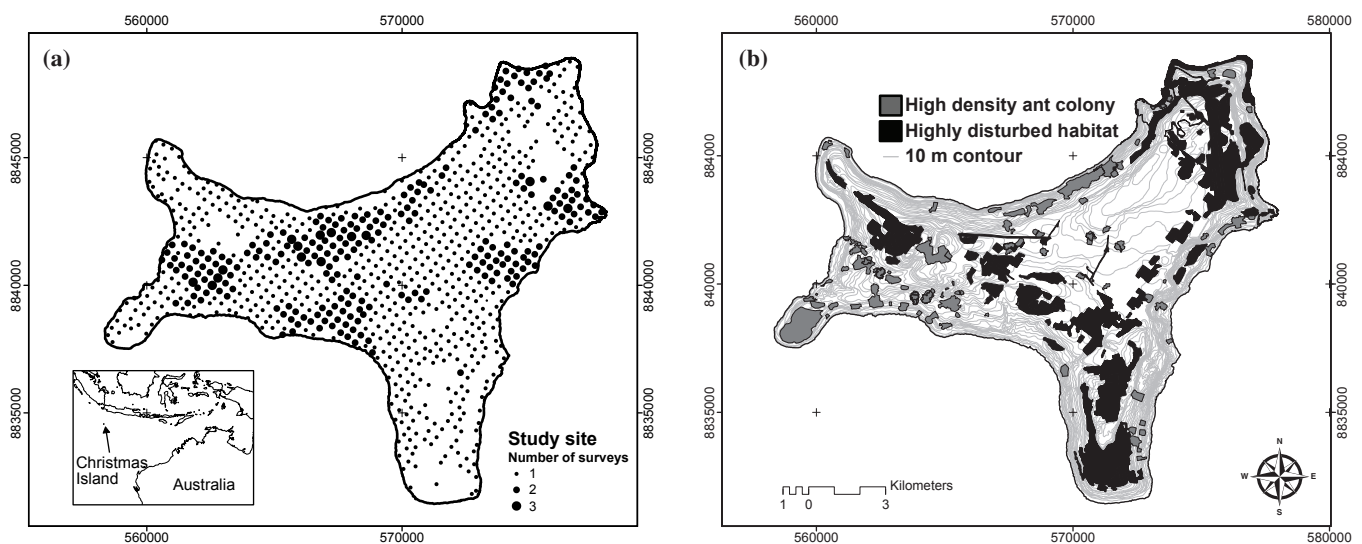


Fig. 1. Christmas Island and the island-wide survey points (a). The size of the point symbol depicts the number of times we surveyed the site. Highly disturbed areas, roads, contours, and high-density Yellow Crazy Ant colonies as of 2009 (b). Projection is in UTM (WGS84, Zone 48 S).

2009 (Fig. 1), and used this value as a covariate in the model. Sites were also classified by their elevation and distance to the nearest road. A habitat disturbance map from the Christmas Island GIS (Commonwealth of Australia 1987–2011) was used to classify sites by their distance in kilometres to the nearest significantly disturbed area. Because most of the disturbed habitat on Christmas Island is in the central part of the island (Fig. 1) and Abbott's Booby does not breed in low elevation coastal habitats, we suspected *a priori* that a quadratic term may better represent occupancy by Abbott's Booby, as occupancy would be more likely with increasing distance from a disturbed area, but less likely with proximity to the coast. If so, we would expect a positive relationship between occupancy and distance from disturbance and a negative quadratic term.

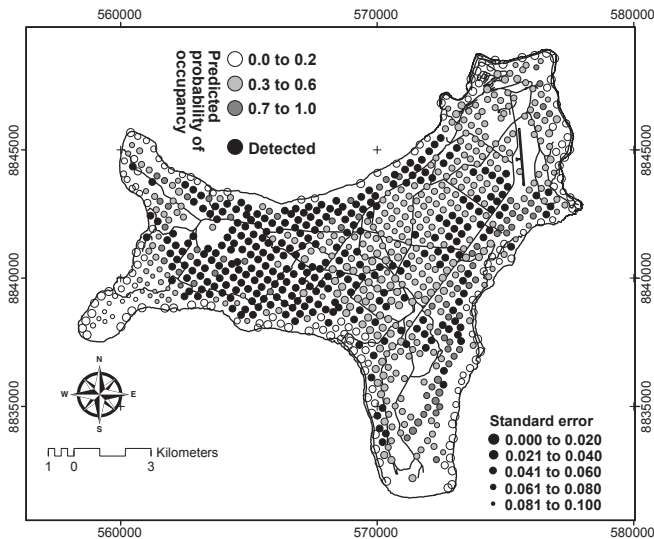


Fig. 2. Sites at which Abbott's Booby was detected (solid black circle), model averaged probability of occupancy (shading of circles) and associated standard error (size of circles) at non-detection sites. Projection is in UTM (WGS84, Zone 48 S).

Because detection of a particular species occupying a site is not guaranteed during a brief visual and aural survey, we used site-occupancy species distribution modelling that explicitly accounted for imperfect detection as part of model-fitting (Royle & Dorazio 2008, Kéry 2010). Each site was categorized as occupied (where on each visit the species can be detected with an unknown probability) or unoccupied (where the probability of detection is zero; Royle & Dorazio 2008, Kéry 2010). Because data were collected from a subset of sites that were repeat surveyed, we could infer the probabilities of detection of Abbott's Booby (cf. Royle & Dorazio 2008, Kéry 2010). By using this approach, we could reduce bias in our inferences about occupancy and better examine relationships between the probability of occupancy by Abbott's Booby and potential indicators of the impacts associated with high-density Yellow Crazy Ant colonies and habitat disturbance.

Accordingly, the probability of occurrence (Ψ_i) of the Abbott's Booby at the *i*th site was modelled as a logistic function of distance to nearest high-density Yellow Crazy Ant colony (YCA_C_i), highly disturbed area (D_i) and road (Rd_i), in addition to site elevation (Ele_i) and a quadratic distance to disturbed area term ($D2_i$), using the logistic regression equation:

$$\log \left(\frac{\Psi_i}{1 - \Psi_i} \right) = \beta + \beta.YCA_C_i + \beta.D_i + \beta.Rd_i + \beta.Ele_i + \beta.D2_i$$

The β parameters represent the intercept and slopes of the relationships between the log-odds of occupancy by Abbott's Booby and the various predictor variables.

The probability of detection was modelled as constant because the detection of Abbott's Booby at each site was predominantly associated with their aural signals and was unlikely to be affected by any of the covariates we could use. Models were run in the "unmarked" package (version 0.8-7) in R software (R Development Core Team 2007). In particular, we used the "occu" function

TABLE 1
Parameter estimates from the models that accounted for 95% of the accumulative AIC weights

| Model | AIC | Δ AIC | AIC weight | Detection | | | Occupancy | | | | |
|-------------------------|---------|--------------|------------|-----------|-----------|-----------|--------------------------|------------------------------------|---|---|--|
| | | | | Intercept | Intercept | Elevation | Distance to nearest road | Distance to nearest disturbed area | Quadratic term (distance to nearest disturbed area) | Distance to nearest high-density Crazy Ant colony | |
| 1 | 1213.05 | 0.00 | 0.58 | 0.61 | 0.40 | 1.27 | | 1.17 | -0.70 | | |
| 2 | 1214.93 | 1.88 | 0.23 | 0.61 | 0.40 | 1.27 | 0.04 | 1.15 | -0.70 | | |
| 3 | 1215.30 | 2.25 | 0.19 | 0.63 | 0.38 | 1.25 | 0.04 | 1.06 | -0.69 | -0.15 | |
| Model-averaged estimate | | | | 0.61 | 0.40 | 1.27 | 0.04 | 1.14 | -0.70 | -0.15 | |
| 2.5 CI ^a | | | | 0.29 | -0.04 | 0.93 | -0.19 | 0.78 | -0.99 | -0.39 | |
| 97.5 CI | | | | 0.93 | 0.83 | 1.61 | 0.27 | 1.51 | -0.41 | 0.09 | |

^aCI = confidence interval

(e.g. `model_1<-occu(~1~Rd, Data)`). All possible covariate combinations were compared with AIC (Burnham and Anderson 2002). Models that accounted for 95% of the cumulative AIC weights were considered to be equally well supported. Model-averaged estimates of the most supported models were calculated within the AICcmodavg R package (e.g. `modavg(cand.set = cand.models, modnames = modnames, parm = "Elevation", parm.type = "psi")` Mazerolle 2012). All covariates were log-transformed and standardised. We checked model fit by examining simulated datasets from each fitted model using the parametric bootstrapping technique of Fiske and Chandler (2010). Specifically, we used a chi-square statistic to compare observed and expected values generated from simulated datasets.

RESULTS

Abbott's Booby was detected at 287 survey sites across the island (32% of sites), mostly on the island's central plateau (Fig. 2). The model-averaged probability of detection for Abbott's Booby using our survey protocol was 0.61 (95% CI 0.29 to 0.93). Three models accounted for over 95% of the AIC accumulative weight and, collectively, these models included all covariates (Table 1). Examination of the goodness-of-fit for the three models indicated adequate model fit.

Despite their inclusion in some of the supported models, the model-averaged 95% confidence intervals for relationship of occupancy to the distance to nearest high-density Yellow Crazy Ant colony and to the distance to nearest road included zero, and consequently, were judged not to be important (Table 1). We did find significant evidence for positive relationships between occupancy and both distance to nearest disturbance and elevation (95% CI did not include zero; Table 1). Additionally, a negative quadratic term was also important (95% CI did not include zero). Collectively, these relationships indicate that Abbott's Booby was more likely to occupy higher elevation sites with increasing distance from disturbance (Fig. 2 and Fig. 3).

DISCUSSION

Before human settlement, Christmas Island had thick vegetation, with an unbroken forest canopy reaching heights of 30–45 m. Abbott's Booby nested principally in the centre and west of the island (Gibson-Hill 1947, Nelson 1971) in the tops of certain species of emergent trees on the central plateau (Nelson and Powell 1986). Our data demonstrate that this preference of Abbott's Booby for nesting on the central plateau has remained. The birds continue to avoid the more exposed fringing coastal terrace and the eastern edge of the island, which is subject to prevailing southeast wind.

Between 1968 and 1987, approximately one-third of the rainforest nesting habitat of the Abbott's booby was felled for phosphate mining (Yorkston & Green 1996). Much of the bird's preferred habitat in the western and central portions of the plateau was cleared (Fig. 1). This land clearing induced a significant edge effect: birds nesting within 300 m of the mined area suffered lower breeding success and increased mortality because of greater wind turbulence (Brett 1989, Reville *et al.* 1990). By comparing rates of recruitment and mortality, Reville *et al.* (1990) concluded that the population was still in decline in 1989, two years after forest clearing had ceased. Our data indicate that this land clearing is still affecting the Abbott's Booby – more than 20 years after clearing ceased – as these birds are less likely to occupy habitat within or near a disturbed area, because such sites lack emergent, high-canopy trees suitable for nesting.

One impact of edge-induced canopy turbulence is that adult Abbott's Booby abandon traditional nest sites and seek new ones (Brett 1989, Reville *et al.* 1990). Our island-wide survey data indicate that Abbott's Booby have begun occupying areas that traditionally have been avoided, such as the eastern third of the island and the western edge of South Point (compare Fig. 2 with Nelson 1971, Nelson & Powell 1986, Yorkston & Green 1996). Whether these habitats have improved or the birds are now using suboptimal habitat remains unknown but should be the focus of future research. In addition, our results showing increasing likelihood of occupancy with increasing distance from disturbance

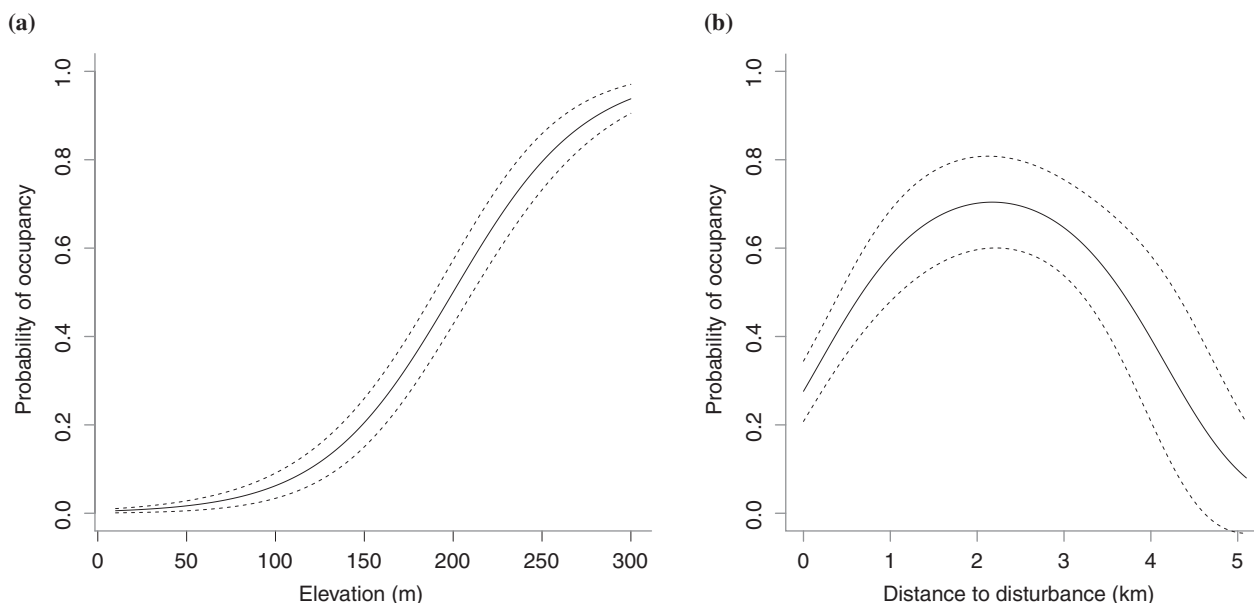


Fig. 3. Predicted relationship between occupancy by Abbott's Booby and elevation (a) and distance to the nearest disturbed area (b), mean model-averaged estimate and 95% CI (dashed lines).

suggest that areas surrounding disturbed habitats continue to represent suboptimal habitat for Abbott's Booby.

In 2000, Christmas Island National Park embarked on a program to control the spread of high-density Yellow Crazy Ant colonies by baiting with Presto (active ingredient: fipronil). Nonetheless, by 2002, more than 2 500 ha (or about 25%) of the island's forest was invaded by high-density Crazy Ant colonies, which were treated by a large-scale heli-baiting campaign in September 2002. Over the ensuing seven years, Crazy Ant infestations began to gradually reappear, requiring a second heli-baiting campaign across 784 ha in September 2009 (Boland *et al.* 2011). Our data do not support the idea that the presence of these high-density Crazy Ant infestations has negatively affected the distribution of Abbott's Booby on Christmas Island. Indeed, if anything, Abbott's Booby was more likely to occupy sites near Crazy Ant infestations (negative but non-significant relationship between occupancy and distance to nearest high-density Crazy Ant colony). However, our results are based upon presence/absence data, and detailed population studies may identify a negative impact yet to be detected by our survey protocol. Lag effects associated with high-density Crazy Ant infestation and control (i.e. changes in vegetation communities) may be detected in future surveys.

Our results suggest that the approach taken here provides reliable mapping of Abbott's Booby nesting habitat on Christmas Island. If data are collected regularly (e.g. during the biennial island-wide survey), they should provide natural resource organisations on the island with timely indications of significant change. However, this survey approach is not a substitute for detailed study of the species' demography and breeding behaviour; rather, in combination with other information, the survey approach will allow managers to detect and better understand broad changes in distribution over time. The attraction of this approach is that it provides sound census information at a low cost, adding value to an existing program.

However, our approach has limitations. Abbott's Booby forage at sea and, accordingly, may be detected simply moving through an area and, conversely, may be missed when individuals are away from their nests. Both of these factors would reduce detection probabilities (our estimate was 0.65) and could lead to some degree of overestimation of occupancy. With continued surveying, our understanding of the species' distribution and its variability should improve. Such surveys will help to determine the need for management action in the future.

Should major changes in the distribution of Abbott's Booby be detected, management actions would be justified. What degree of decline should trigger a management response, and what that management response should be, are yet to be determined by the appropriate natural resource management agencies. However, it is clear from this and previous work that any new disturbance will further restrict a limited and reduced habitat resource upon which the species depends.

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THE ROLE OF FORAGING ECOLOGY IN THE CONTRASTING RESPONSES OF TWO DARK TERNS TO A CHANGING OCEAN CLIMATE

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SUMMARY

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The Bridled Tern *Onychoprion anaethetus* and Brown Noddy *Anous stolidus* meta-populations breeding off southwestern Australia have shown contrasting responses to changes in the regional ocean climate. Bridled Terns have expanded their distribution southward, founding 40–50 frontier colonies up to 1 400 km from the edge of their historical range (pre-1900) at the Houtman Abrolhos islands. Some of these frontier colonies are amongst the largest recorded for this species anywhere. Conversely, the Brown Noddy's response to recurrent poor breeding performance at the Houtman Abrolhos has been limited dispersal and the establishment of only one frontier colony, at Lancelin Island, 280 km south of its stronghold on Pelseart Island. Egg-laying has started progressively later at the Bridled Tern frontier colony on Penguin Island, probably tracking a shift in the seasonal peak in sea temperature. The start of egg-laying in the Brown Noddy colony on Lancelin Island is significantly correlated with the long-term trend in the Southern Oscillation Index (SOI), with earlier breeding during *La Niña* periods when the Leeuwin Current is flowing strongly. The converse was the case in the Bridled Tern, which started breeding earlier during protracted *El Niño* periods. We present long-term trends in the timing of breeding of both species in relation to the *El Niño* Southern Oscillation. We also review the foraging ecology of the two species off southwestern Australia and discuss the role that differences in foraging ecology between the two species may have in accounting for contrasting population responses to a changing ocean climate.

Key words: Bridled Tern, Brown Noddy, foraging ecology, changing ocean climate, southwestern Australia

INTRODUCTION

At least eight seabird species populations of tropical origin have undergone southward shifts in breeding distribution off southwestern Australia over the last century, but particularly over the last 4–5 decades (Dunlop 2009). The poleward movement of tropical species is in line with observations and predictions in relation to global warming (Chambers *et al.* 2011). However, individual species respond differently, and the observed shifts in distribution may have very different implications for long-term population size (Wormworth & Şekerciöglu 2011).

There have been marked oceanographic changes in shelf and oceanic waters off southwestern Australia in recent decades. These changes include a general weakening of the Leeuwin Current due to the increasing frequency and duration of *El Niño* events, a background rise in mean sea temperature of up to 0.9 °C since the 1950s and a delay in the annual peak in sea temperature of 10–20 days over a similar period (Pattiararchi & Buchan 1991, Pearce & Feng 2007, Feng *et al.* 2009, Caputi *et al.* 2010). These changes in ocean climate and associated shifts in marine productivity have been implicated in the establishment of frontier colonies of tropical seabirds south of the Houtman Abrolhos islands off southwestern Australia (Dunlop 2009); for the locations of the species discussed, see Fig. 1. Trends in the timing of breeding and in the number of breeding Noddies (Brown Noddy *Anous stolidus* and Lesser Noddy *A. tenuirostris*) and Sooty Terns *Onychoprion fuscata* at the

Abrolhos islands over the last 2 decades appear to indicate a long-term decline in marine productivity (Surman & Nicholson 2009a).

Three “dark” tern species were amongst the tropical seabirds involved in the observed southward redistribution of colonies in the region: Bridled Tern *Onychoprion anaethetus*, Sooty Tern and Brown Noddy (Dunlop 2009). The Lesser Noddy, the fourth member of the tropical pelagic tern guild in this region, has not as yet established any frontier colonies south of its stronghold in the Houtman Abrolhos islands (Surman & Wooller 1995, Surman & Wooller 2003). This may be attributable to a lack of suitable tree-nesting habitats (e.g. mangroves) on the islands further south.

Here, we synthesize various previously reported aspects of the foraging ecology of the Bridled Tern and Brown Noddy in the region, summarize previously reported changes in geographical distribution and present additional analyses on the timing of breeding in these species. We suggest that the differences in foraging ecology between the two dark tern species explain contrasting responses to changes in ocean climate off southwestern Australia.

METHODS

Timing of breeding

The timing of the first egg laid in each breeding season was determined for the Bridled Tern colony on Penguin Island for 24

of the 26 years from 1986 to 2011. First laying dates were also determined for the Brown Noddy colony on Lancelin Island over an 18-year period between 1994 and 2011. The laying date for the first egg was determined by the observation of a freshly laid egg, from weight loss (Wooller & Dunlop 1980, Dunlop & Goldberg 1999, Garavanta & Wooller 2000), from observation of first hatching or from early chick growth. When a range of methods was utilized during a season, the earliest resulting date was selected. The first laying dates for each year for both species/colonies are plotted, along with the 3-year rolling mean annual Southern Oscillation Index (SOI) in Fig. 2 for those years (from 1994 onwards) when there were complete and comparable data sets. The mean annual SOI was calculated by adding the monthly SOI values for each year (Australian Bureau of Meteorology) and then producing a rolling 3-year average of the annual sums. The data were explored for correlations with the

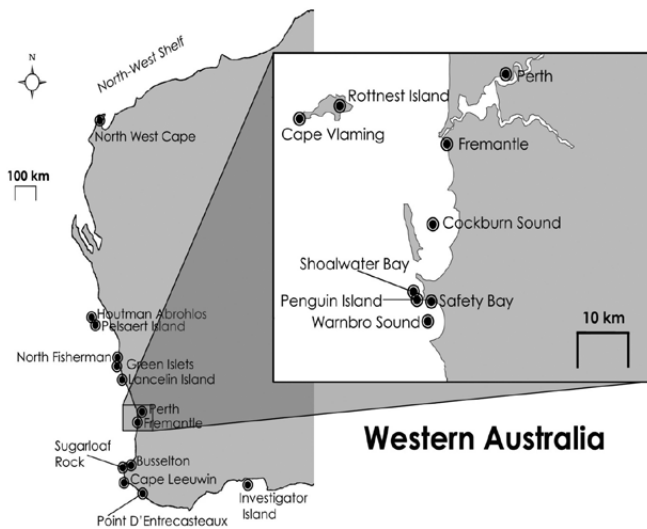


Fig. 1. Locality map for seabird islands of southwestern Australia.

mean annual SOI in the breeding year, and the rolling mean annual SOI with the previous year, previous 2 years and previous 3 years. There was no correlation with the current year, marginal significance with the 2-year rolling average, highly significant correlations after 3 years, and declining correlations after 4 years.

RESULTS

Foraging ecology

Our current knowledge of aspects of the foraging ecology of Bridled Terns and Brown Noddies breeding on islands of southwestern Australia is summarized in Table 1.

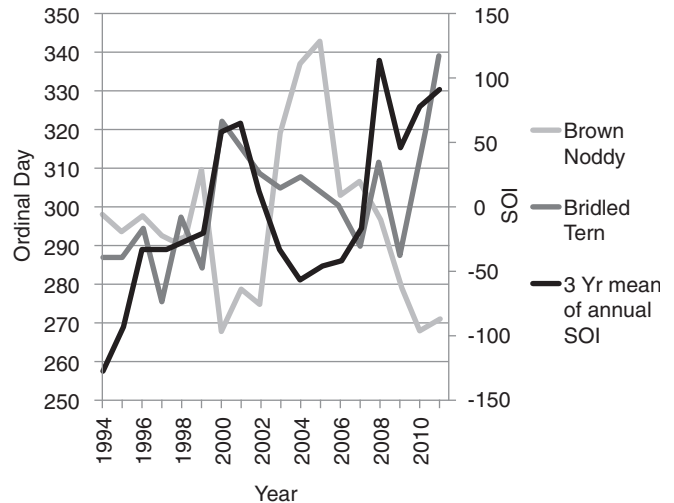


Fig. 2. First laying dates for the Bridled Tern colony on Penguin Island and the Brown Noddy colony on Lancelin Island between 1994 and 2011. Also plotted is the 3-year mean annual Southern Oscillation Index (SOI) for the same period.

TABLE 1
Comparative summary of foraging ecology in the Bridled Tern and Brown Noddy off southwestern Australia

| Aspect of foraging ecology | Bridled Tern | Brown Noddy |
|---|---|--|
| Prey capture | In-flight contact dipping (Dunlop 1997, Surman & Wooller 2003) | In flight-contact dipping (Surman & Wooller 2003) |
| Foraging range | 20–80 km (Dunlop 1997) | >100 km (Surman & Wooller 2003) |
| Relationship with foraging predatory fish | Facultative, in the absence of competition from other dark terns, particularly Black or Lesser Noddies (Dunlop 1997, Dunlop 2011) | Near obligate with small, surface-feeding tuna (Catry <i>et al.</i> 2009, Hulsman 1988, Gaughan <i>et al.</i> 2002, Jaquemet <i>et al.</i> 2004 & 2007, Surman & Wooller 2003, Ramos <i>et al.</i> 2006) |
| Prey types | Post larval fish and crustaceans, as well as insects (Dunlop 1997) | Post larval fish and squid (Gaughan <i>et al.</i> 2002, Surman & Wooller 2003, Surman & Nicholson 2009 a & b) |
| Prey length | Multi-modal, high proportion under 10 mm (Dunlop 1997) | Mean fish 51 mm, squid 39 mm (Gaughan <i>et al.</i> 2002) |
| Prey diversity | Spread over 20+ taxa (Dunlop 1997) | Concentrated in 2–3 taxa (Gaughan <i>et al.</i> 2002) |
| Prey shifts within breeding season | In pre-laying and late chick-rearing periods (Dunlop 1997, Aurélie Labbé unpublished data) | None (Gaughan <i>et al.</i> 2002, Surman & Nicholson 2009b) |
| Foraging habitat | Offshore on continental shelf (Dunlop <i>et al.</i> 1988, Dunlop 1997) | Oceanic, shelf edge, canyons and beyond (Gaughan <i>et al.</i> 2002, Surman & Nicholson 2009b) |
| Water mass productivity | Oligotrophic (Dunlop 2011) | Higher in inorganic nitrogen (Dunlop 2011) |

Bridled Terns forage offshore over oligotrophic, continental shelf waters, utilising a wide range of prey types and sizes, a proportion of which are taken from floating rafts of seaweed or associated with other flotsam. Bridled Terns switch prey types within and between seasons. Brown Noddies forage largely beyond the continental shelf in relatively productive environments probably at shelf edge upwellings or in Leeuwin Current eddies. Tuna associated with these localized productive areas are probably important in making prey available to Brown Noddies. Unlike Bridled Terns, the Brown Noddies in this region take a narrow range of prey species, and have not been observed switching prey types during the breeding season.

Changes in distribution

Bridled Tern

Bridled Terns were observed breeding at the Houtman Abrolhos islands in 1843 (Storr *et al.* 1986) but were not recorded further south (at Rottnest Island) until 1889 (Fig. 1). They were the first tropical seabird species to establish frontier colonies south of their original recorded distribution in the region. They were observed in the Safety Bay area south of Fremantle in 1901 and breeding on the smaller islands in Shoalwater Bay (32°18'S) by 1921. Bridled Terns were breeding on the islands around Cape Leeuwin (34°23'S) by 1956 (Dunlop 2009). There were unpublished reports of the species breeding along the western portion of the south coast of Western Australia near Point D'Entrecasteaux (34°50'S, 116°01'E; Fig. 1) in the late 1990s.

In January 2008 a small group of Bridled Terns was recorded on Haul-Out Rocks (34°42'S, 118°39'E) east of Albany, and in December 2007 Bridled Terns were observed on Investigator Island (34°05'S, 120°52'E; Fig. 1) on the eastern portion of the south coast, indicating that the species may have reached the western edge of the Recherche Archipelago. An expedition to Investigator Island in late January 2008 confirmed a successful breeding colony of around 400 pairs that may have been present for at least a decade (Dunlop 2009). Surman & Wooller (2000) recorded Bridled Terns in the area in December 1995. Recent unconfirmed reports suggest that there is now a colony of Bridled Terns on Termination Island, due south of Esperance in the western Recherche Archipelago. Overall, the breeding range of the Bridled Tern has shifted south and then east about 1 400 km since the late 19th century, expanding rapidly along the south coast of Western Australia over the last 2 decades.

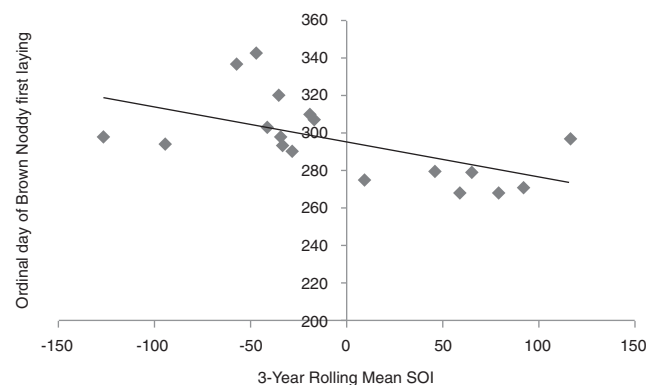


Fig. 3. Relationship between first laying dates in the Brown Noddy colony on Lancelin Island and the 3-year rolling mean annual Southern Oscillation Index (SOI) $R^2 = -0.571$, $P < 0.01$.

Recent decades have also seen remarkable growth in the size of some colonies south of the Houtman Abrolhos islands (e.g. North Fishermen [Johnstone 1978], Lancelin [pers. obs.], Penguin [Dunlop & Jenkins 1994] and Rottnest Islands) and a general infilling of the southern breeding areas with the occupation of additional breeding sites (Dunlop & Wooller 1990, Dunlop & Jenkins 1994). There are now 40–50 colonies (occupied islands) south of the Houtman Abrolhos islands. Some of these islands support several thousand pairs (e.g. Penguin Island [Dunlop & Jenkins 1994], Lancelin Island, North Fisherman Island [Burbidge *et al.* 1996]). These are large colonies compared with most of those reported from other Indian Ocean regions (Cramp 1985, Diamond 1976, Nature Seychelles 2003) or from the Houtman Abrolhos islands (typically in the tens to a few hundred pairs per island; Fuller *et al.* 1994). Large colonies of several thousand pairs do occur in the Pilbara region off northwestern Western Australia (e.g. at Bridled Island in the Lowendal Group 20°38'S, 115°23'E; Dunlop 1996). Bridled Terns breeding off southwestern Australia are present at their colonies between September and April and winter in the northwest Sulawesi Sea (between 4°N and 7°N between June and August; Dunlop & Johnstone 1994).

Brown Noddy

Brown Noddies had not been recorded breeding south of Pelsaert Island in the Houtman Abrolhos islands (28°54'S) before 1991/92 (Fig. 1). In that year, five pairs were discovered nesting on Lancelin Island (31°00'S; Fig. 1), a southward extension of breeding range of approximately 280 km.

The Lancelin colony grew exponentially between 1994/95 and 1997/98 and had reached about 900 pairs in 1998/99 (Dunlop & Mitchell 2001). It was estimated that net immigration ceased around 2002, but the colony continued to grow gradually through natal recruitment (Dunlop 2005, 2009). It was estimated at about 1 300 pairs in 2010 (Dunlop pers. obs.). In the 2003/04 season, Brown Noddies began prospecting Penguin Island (32°S, approximately 450 km south of Pelsaert Island) and continued to do so during late December and January in 2004/05, 2005/06 and 2006/07 (Dunlop pers. obs.). None was recorded there in 2007/08, but the pattern of visitation resumed between 2008/09 and 2011/12.

Brown Noddies breeding off southwestern Australia are migratory, being present at or around their colonies from September to April and absent from May to August. These birds are thought to winter in the subtropical Indian Ocean (Dunlop 2011).

Changes in the timing of breeding

The first laying dates of the Brown Noddies at Lancelin Island were not strongly correlated with the annual monthly Southern Oscillation Index (SOI). However, a relationship was evident with the longer-term SOI trend (Fig. 2) with egg-laying occurring earlier in *La Niña* (+ SOI) years and later under prolonged *El Niño* conditions. A significant negative correlation was found between the first laying date and the 3-year rolling mean annual SOI (Fig. 3, $R^2 = -0.571$, $P < 0.01$).

There was a positive correlation between first laying date and the 3-year rolling mean annual SOI in the Bridled Tern (Fig. 4, $R^2 = 0.643$, $P < 0.025$) over the same period (1994–2011). Bridled Terns therefore tended to lay later in *La Niña*-dominated periods

versus *El Niño* periods, the opposite pattern to that observed in the Brown Noddy. The longer-term Bridled Tern data contains a *La Niña* period from 1986–88 that appears to be an exception to this trend. There is, therefore, more uncertainty in the relationship between timing of breeding and the *El Niño*–Southern Oscillation (ENSO) for the Bridled Tern than for the Brown Noddy.

First laying dates in Bridled Terns have become significantly later over the last 25 years (Fig. 5, $R^2 = 0.645$, $P < 0.005$). No long-term chronological pattern is evident in the laying dates of the Brown Noddies at Lancelin Island.

DISCUSSION

The Bridled Tern and Brown Noddy, along with the Lesser Noddy and Sooty Tern, are members of a “contact-dipping” guild of dark-plumaged tropical terns. This paper documents the marked contrast in the observed responses of the Brown Noddy and Bridled Tern to a changing ocean climate off southwestern Australia in relation to our current understanding of their foraging ecology (Table 1). Changes in geographical distribution and timing of breeding have also been observed in the Sooty Tern in the region (Dunlop 2009, Surman & Nicholson 2009 a & b).

Bridled Terns forage over the continental shelf for a diversity of mainly small prey items, including post-larval fishes and crab megalopae associated with floating rafts of *Sargassum* and other flotsam (Dunlop 1997). Their preferred prey types are associated with the oligotrophic waters typical of the mid-shelf conditions over much of the region (Dunlop 2011). The spectacular southward expansion in the distribution of the Bridled Tern, spanning about 6° of latitude or 1 400 km of coastline, is probably attributable to a shift in suitable prey resources in response to rising background sea temperature. Many marine species, including their larval and post-larval stages, occur and persist further south when sea temperatures in this region are elevated (Pearce & Hutchins 2007, Caputi *et al.* 2011). The changing temperature regime may effectively lengthen the period when suitable (mostly tropical) prey species are available, with the peak in abundance occurring later. Weak Leeuwin Current conditions reduce cross-shelf mixing and productivity (Feng *et al.* 2009), potentially increasing the foraging area for a species adapted to clear-water oligotrophic conditions and the avoidance of competitors.

The Bridled Tern’s adaptable foraging ecology (Table 1) may contribute to its ability to exploit new opportunities and geographical

areas. The inability of the other dark terns to follow may have also released the Bridled Tern from competition within its guild, particularly with the similarly sized Lesser Noddy, with which it probably has the highest degree of niche overlap (Surman & Wooller 2003). This competitive release provides a explanation for the relatively large population sizes now observed at the frontier colonies south of the Houtman Abrolhos islands.

Devney *et al.* 2009 report greater sensitivity to *El Niño* events in pelagic (oceanic) species than inshore foraging species. The same trend is clearly evident off southwestern Australia (Surman *et al.* 2012), particularly when these species are also migratory. Although not strictly an inshore forager, the Bridled Tern’s foraging grounds over the continental shelf may be relatively buffered against ENSO-induced changes in oceanic productivity due to the availability of resources supplied by benthic food chains. Flotsam foraging represents a form of benthic–pelagic coupling.

It is unclear why Bridled Terns breed earlier during *El Niño* periods. The observed delay in Bridled Tern laying dates may be tracking the receding peak in sea temperature observed in the region (Pearce & Feng 2007), indicating that this tern is adapting its timing of reproduction to the changes in ocean climate. Breeding success is very difficult to estimate in Bridled Terns on Penguin Island because the chicks are mobile and difficult to trace consistently under the dense vegetation cover. However, in years when laying is extremely late, few fledglings are produced (Dunlop pers. obs.).

The large (130 000 pair) Brown Noddy colony on Pelsaert Island in the Houtman Abrolhos islands has frequently suffered low breeding performance, or complete failure, over at least the last 2 decades as a result of low prey availability (Surman & Nicholson 2009a & b). Historically, these poor breeding seasons were generally associated with *El Niño* events, although in recent years they have become decoupled from the ENSO cycle (Surman & Nicholson 2009a & b).

Breeding failure at core colonies in the region is thought to have driven dispersal in pre-breeders and the initiation of frontier colonies south of the former breeding range (Dunlop 2009). However, the Brown Noddy has at this stage established only one frontier colony, at Lancelin Island 280 km south of Pelsaert Island. Prospecting Brown Noddies have been recorded at Penguin Island (400 km south of Pelsaert Island) during late December and January in most years since 2003, but breeding has not been initiated there. Information from stable isotope analyses indicates that the dominant

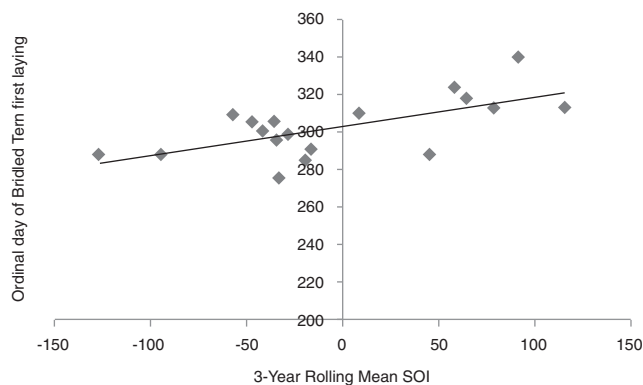


Fig. 4. Relationship between first laying dates in the Bridled Tern colony on Penguin Island and the 3-year mean annual Southern Oscillation Index (SOI) $R^2 = 0.643$, $P < 0.025$.

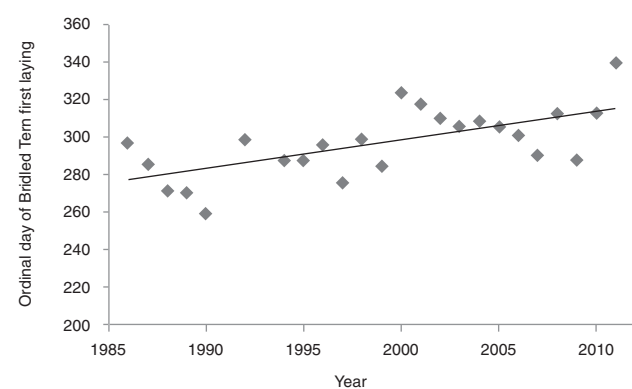


Fig. 5. Relationship between first laying dates in the Bridled Tern colony on Penguin Island and year over a 26-year period $R^2 = 0.645$, $P < 0.005$.

prey species taken by Brown Noddies in the region grow in relatively productive water masses with elevated levels of inorganic nitrogen (Dunlop 2011). Such water masses would also attract tuna (Jaquemet *et al.* 2007), which are probably important in forcing the prey species to surface, where they become available to foraging Brown Noddies. Given the Noddy's foraging range, these relatively productive areas with a higher probability of tuna aggregation are likely to be over or beyond the shelf edge. *La Niña* conditions are associated with a stronger eddy structure in the Leeuwin Current, increased mixing and higher productivity (chlorophyll *a*) at the shelf edge and beyond (Feng *et al.* 2009). Brown Noddies would therefore be expected to have higher reproductive output during *La Niña* periods.

The timing of laying in the frontier Brown Noddy colony on Lancelin tracks the long-term ENSO cycle, with earlier, and potentially more successful, breeding occurring under *La Niña* or neutral conditions. Historically, there was also higher Brown Noddy breeding success during *La Niña* years at the Abrolhos islands (Surman & Nicholson 2009 a & b, Surman *et al.* 2012), and this was associated with a proportionally high intake of the preferred fish prey (*Gonorrhynchus greyii*). However, this relationship has been breaking down over recent years (Surman *et al.* 2012). Early breeding has been associated with higher breeding success at the Abrolhos islands (Surman & Nicholson 2009 a & b). There has been a significant trend towards Brown Noddies laying later at the Abrolhos islands over the last 20 years (Surman & Nichollson 2009a) associated with reduced reproductive performance.

Interestingly, the cost to the adults of previous breeding seasons apparently influences subsequent laying dates for up to 3 years. The stress of attempting to breed during periods of low food availability can be considerable in seabirds (Kitaysky *et al.* 2007) and may influence recovery times preceding subsequent breeding attempts. It would appear that at Lancelin Island, in contrast to the recent situation at the Abrolhos islands, the ENSO cycle continues to control marine productivity in the foraging area.

Brown Noddy, Lesser Noddy and Sooty Tern populations are all showing evidence of decline at the Abrolhos islands (Surman & Nicholson 2009 a & b, Surman unpublished data). Unlike the Bridled Tern, the Brown Noddy's diet is dominated by a few prey species and shows little capacity for prey switching, within or between breeding seasons (Dunlop 1997, Surman & Nicholson 2009b). This concentration on two or three prey species and on particular, small-scale, oceanographic features with relatively enhanced productivity may explain the comparatively conservative re-distribution observed in the Brown Noddy population. Extensive areas of Brown Noddy breeding habitat (Nitre Bush *Nitraria billardieri*) remain available on Lancelin Island but potential breeding islands, with suitable foraging areas within reach, may be few and far between south of the Abrolhos islands. This may also explain the inability of prospecting Brown Noddies and Sooty Terns to establish colonies at Penguin Island over the last 8 years.

Overall, we predict that species-specific responses to changes in ocean climate will result in a significant decline in Brown Noddy, and probably Lesser Noddy and Sooty Tern populations, in the region. However, the re-distribution of the Bridled Tern has already resulted in an increase in abundance such that southwestern Australia, south of the former breeding range, is now a global stronghold for this species.

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SPATIAL DISTRIBUTION OF NEARSHORE FORAGING SEABIRDS IN RELATION TO A COASTAL MARINE RESERVE

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SUMMARY

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The Vandenberg State Marine Reserve (VSMR) was established in 1994 with the primary goal of protecting fishes and invertebrates targeted by fisheries. However, studies of other reserves have shown that effects cascade and benefit species at several trophic levels. We tested the hypothesis that the VSMR would provide benefits to nearshore foraging seabirds. We measured the foraging rates (mean number of individuals observed per hour) of seabirds at four plots (two inside and two outside the VSMR) over six years to test the hypothesis that foraging rates are greater inside the reserve than outside. The VSMR spans a coastal promontory, and we controlled for promontory effects by selecting plots at windward and leeward sites. All species showed either no difference or higher rates outside the reserve than inside. The consistency of our results over the six-year period illustrates predictable foraging behavior in these species. Piscivorous species foraged more in leeward plots than windward plots, while the benthic invertebrate specialist foraged more in windward plots. Our results reflect reported differences in community structure around coastal promontories; namely, windward habitats enhance biomass of suspension-feeding invertebrates while leeward habitats provide refuge for fish recruitment. Our results suggest that the VSMR is not protecting significant foraging habitat for nearshore foraging seabirds and that coastal geography should be considered when designing marine reserves to protect these species.

Key words: coastal promontory, marine reserve, nearshore foraging, seabird foraging, Brandt's Cormorant, Pelagic Cormorant, Pacific Loon, Surf Scoter

INTRODUCTION

Although seabirds are not directly targeted by fisheries, they can benefit from fisheries management. Tasker *et al.* (2000) describe fisheries impacts on seabirds as direct or indirect. Direct impacts include bycatch and disturbance to breeding colonies (especially where fishing is close to shore), whereas indirect impacts include competition for food resources. Marine reserves offer a means to address both direct and indirect fisheries impacts. Here we focus on the indirect impacts.

There is growing evidence that “no take” reserves can protect ecosystem diversity and even alter the community structure of fished areas, especially when developed within the context of other management schemes (Allison *et al.* 1998). Intense fishing practices have cascading effects on community structure, altering predator–prey relationships and even removing entire trophic groups (Sumaila *et al.* 2000). “No take” reserves offer a potential way to reverse such effects because they protect all ecosystem components (Bohnsack 2000). In theory, a well-designed marine reserve should protect not only commercially valuable species, but their predators as well. Here we evaluate the hypothesis that upper-trophic-level predators can benefit from the protection provided by a marine reserve established in central California, USA. Alternatively, if the benefits of reserve protection are overshadowed by regional physical processes (e.g. interannual variability in coastal upwelling), then foraging distribution should reflect the geography and oceanography influencing prey distribution.

The reserve we studied is located along a large coastal promontory. There is therefore a potential for prey abundance to differ between the windward and leeward sides of this promontory. Recent research has shown that coastal promontories influence the flow of nearshore currents, especially during upwelling events (e.g. Mace *et al.* 2006). In the California Current System (CCS), alongshore winds create Ekman transport that drives coastal upwelling. The net flow of this transport is offshore, carrying the planktonic larvae of fishes and invertebrates away from nearshore habitats (Cury & Roy 1989). However, circulating structures, termed “upwelling shadows,” are formed in the lee of coastal promontories, providing refuge for planktonic larvae against offshore transport (Wing *et al.* 1995, 1998). This, in turn, increases the probability that larvae settle into habitats adjacent to the upwelling shadow. Additionally, upwelling shadows retain nutrients and phytoplankton for long periods of time (Graham & Largier 1997), thereby enhancing primary productivity and potentially attracting nektonic organisms such as schooling fishes and squid. It is therefore important to study both sides of the promontory when addressing questions about this marine reserve.

Based on a six-year dataset on two resident and two migrant seabird species, collected during spring and summer, we investigated whether the presence of a marine reserve and coastal promontory influenced the distribution of foraging seabirds; whether reserve effects were consistent for leeward and windward sites; whether promontory (and associated upwelling shadow) effects were consistent within and outside the reserve; and whether observed effects were consistent across years.

STUDY AREA

The Vandenberg State Marine Reserve (VSMR) is located along the Point Arguello Promontory (34°34'38"N, 120°39'03"W) in central California, USA (Fig. 1). During the upwelling season, near-surface currents over the continental shelf flow equatorward and offshore (Dever 2004, Ohashi & Wang 2004, Dong & Oey 2005). Trainer *et al.* (2000) and Robinette *et al.* (2007) provided evidence of a small, nearshore upwelling shadow created in the lee of Point Arguello during upwelling events. This shadow has since been confirmed (J. Largier pers. comm.).

The VSMR was established in 1994 under the California Marine Resources Protection Act of 1990. It is a "no take" reserve, protecting waters adjacent to Vandenberg Air Force Base, and is enforced by Air Force game wardens. The VSMR extends 8.4 km along the coastal boundary of the promontory and offshore to the 18 m isobath (Fig. 1). It has an average offshore width of 1.0 km and total area of 6.2 km². Bottom habitat in and around the reserve is primarily sand with scattered rocks and small rocky reefs. Data obtained from the California Fisheries Information System (CFIS) show 785 tonnes of fishes and invertebrates were taken from ~85 km² of nearshore habitat around the reserve over our six-year study period.

METHODS

Study species

We analyzed the foraging distributions of the four seabirds observed most frequently during surveys (Table 1); other species were not observed consistently enough to be included. Brandt's Cormorants *Phalacrocorax penicillatus* and Pelagic Cormorants *Phalacrocorax pelagicus* are year-round residents and breed at Point Arguello and Rocky Point (Fig. 1). Brandt's Cormorants forage on schooling, mid-water and demersal fishes in multiple bottom habitats, ranging from rock to sand, at depths from 10 m to 120 m (Wallace & Wallace 1998). Pelagic Cormorants forage predominantly on bottom fishes

within the same bottom habitats as Brandt's Cormorants, but in waters from intertidal to 36 m in depth (Hobson 1997). Pacific Loons *Gavia pacifica* and Surf Scoters *Melanitta perspicillata* are spring migrants that pass through the area on their way to northern breeding grounds. Pacific Loons typically forage on nearshore schooling fishes in aggregations of mixed seabird species (Russell 2002). However, all of our observations were of non-aggregated foraging individuals, likely taking mid-water species such as the surfperch (Embiotocidae) reported by Palmer (1962). Surf Scoters forage on sessile invertebrates in waters less than 9 m deep (Savard *et al.* 1998).

Data collection

We collected data using a paired design, selecting two sites within the VSMR and two sites just outside the northern or southern boundaries. One pair of sites was located on the windward side of the promontory and the other pair on the leeward side (Fig. 1). At each site, we defined a rectangular area of observation (approximately 0.17 km²) based on easily recognizable coastal landmarks. We made observations within this area using binoculars and a 20–60× spotting scope. We conducted weekly surveys from April through July (breeding season for seabirds and marine mammals) in 2000–2005. We surveyed each site once a week during one of the following time periods: 06h00–09h00, 09h00–12h00, 12h00–15h00, or 15h00–18h00 PDT, rotating sites among the four time periods per week. Because it was not possible to follow each individual bird within a study site for three hours, we divided the observation period into 15 min blocks. We recorded the maximum number of foraging individuals for a given species during each time block. We considered a bird to be foraging if it was observed actively diving for prey. Birds rafting on the water or in transit through the area were not recorded.

Data analysis

We averaged counts for 15 min blocks over each 3 h period for each species at each site. Data for a given 15 min block were not analyzed if the entire site was not visible during the observation period, usually due to fog or rain. The dependent variable in each analysis was the number of individuals recorded per 15 min block.

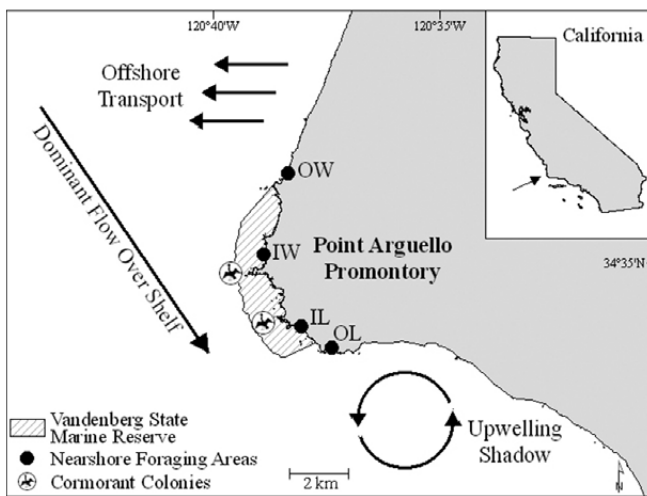


Fig. 1. Map of the Point Arguello Promontory showing the location of the Vandenberg State Marine Reserve and the four observation sites (OW = outside, windward; IW = inside, windward; IL = inside, leeward; OL = outside, leeward). Also shown are the locations of Brandt's and Pelagic Cormorant nesting areas and dominant nearshore currents during the upwelling season.

TABLE 1
Local diet and seasonal occurrence
of the four seabirds selected for this study

| Species | Diet | Seasonal occurrence |
|--------------------|--|--|
| Brandt's Cormorant | Opportunistic on bottom, mid-water and pelagic fishes ^a | Resident Breeds Apr-Aug ^a |
| Pelagic Cormorant | Predominantly bottom fishes ^b | Resident Breeds Mar-Aug ^b |
| Pacific Loon | Predominantly pelagic fishes and squid, but also mid-water fishes ^c | Spring migrant Peak numbers Apr-May ^c |
| Surf Scoter | Benthic invertebrates, predominantly bivalves ^d | Spring migrant Peak numbers Apr-Jun ^d |

^a Wallace and Wallace (1998)

^b Hobson (1997)

^c Russell (2002)

^d Savard *et al.* (1998)

We analyzed data using negative binomial regression (nbg), an especially appropriate analytic method for count data (Hilbe 2007). Nbg is an example of a generalized linear model with log link and over-dispersed Poisson residuals. We used a hierarchical approach for the analysis, first determining the within-season trend to the data by analyzing “week” as a quantitative variable, distinguishing among linear, quadratic and cubic trends. Quadratic models included linear and quadratic terms; cubic models included lower-order terms as well, where “week” varied from one to 16. We selected the model corresponding to the highest-order term that was significant at $P < 0.05$. We also used Akaike’s information criterion (AIC) to select models with the best fit. All statistical tests used the likelihood-ratio statistic.

We then examined the effects of reserve (inside or outside) and of promontory (windward vs. leeward), as well as the interaction of reserve and promontory, while controlling for “week” as determined above. We examined the interaction of year, treated as a categorical variable, with reserve (in/out) and with promontory (windward/leeward) to determine whether reserve and/or promontory effects were consistent over the six years. Significance was set at $P < 0.05$. STATA 8.2 statistical software was used for all analyses (STATA Corp. 2005).

Controlling for abiotic influences

Wind speed and wave height during an observation period can affect foraging behavior, independent of the underlying prey distribution. Furthermore, wind and wave effects should differ between windward and leeward sides of the promontory. To disentangle the effects of prey distribution from those of wind and wave effects, we conducted the reserve and promontory analyses with and without controlling for wind speed and wave height. A change in the apparent effect of reserve or promontory as a result of controlling for wind speed and wave height would indicate that physical conditions are influencing foraging behavior directly, in addition to possible influences of the underlying prey distribution. Tidal height can also affect foraging behavior, but the effects should not differ between windward

and leeward sides of the promontory. Thus, confounding was not expected between reserve or promontory and tidal height; tidal height was therefore controlled for in all analyses.

Hourly wind speeds (m/s) and wave heights (m) were downloaded from the National Oceanic and Atmospheric Administration’s (NOAA) weather buoy station 46023 moored at 34°42'50"N, 120°58'00"W, approximately 17 nm northwest of Point Arguello (NOAA 2007). Tidal heights for Point Arguello were obtained using the online tide predictor program XTide (2007). Tidal height was calculated in meters and averaged over each observation hour.

RESULTS

Within-season trends in predator abundance

All species except Brandt’s Cormorants showed a significant within-season trend in abundance (Table 2). Pelagic Cormorants showed a slight linear decrease in abundance with date (Fig. 2), consistent with their post-breeding dispersal from colony sites. The two spring migrants also showed a decrease in abundance with date, as would be expected for birds that breed outside our study area. Pacific Loons showed a cubic trend, with peak abundance between the first and 10th week of our study period, whereas Surf Scoters showed a linear trend.

Effects of marine reserve and promontory on foraging patterns

There were significant reserve effects for all seabirds except Surf Scoters and significant promontory effects for all seabirds except Pacific Loons (Table 3). The promontory effect was marginally significant for Pacific Loons ($P = 0.093$). Results were similar whether or not we controlled for wind and wave height, suggesting that wind and wave height were not confounded by promontory location or inside vs. outside the reserve. Thus, spatial patterns of foraging seabirds were more likely driven by prey distribution than by environmental conditions during our observations. We therefore report our results without controlling for wind and wave height.

TABLE 2
Comparison of within-season models for each species, derived by negative binomial regression analysis

| Species | Model ^a | | | | Best fit ^b |
|--------------------|-----------------------|---|--|--|-----------------------|
| | Constant | Linear | Quadratic | Cubic | |
| Brandt’s Cormorant | (882.61) ^c | (883.95) LRS = 0.65 $P = 0.419$ | (885.87) LRS = 0.08 $P = 0.774$ | (887.60) LRS = 0.27 $P = 0.605$ | Constant |
| Pelagic Cormorant | (668.37) | (663.54) LRS = 10.77 $P = 0.001$ | (669.27) LRS = 0.21 $P = 0.643$ | (674.76) LRS = 0.45 $P = 0.502$ | Linear |
| Pacific Loon | (439.76) | (419.46) LRS = 22.29 $P < 0.001$ | (417.09) LRS = 4.38 $P = 0.036$ | (405.74) LRS = 13.35 $P < 0.001$ | Cubic |
| Surf Scoter | (1183.19) | (1118.38) LRS = 66.81 $P < 0.001$ | (1120.26) LRS = 0.12 $P = 0.729$ | (1121.00) LRS = 1.26 $P = 0.261$ | Linear |

^a Each model is being compared with the model to its left

^b Results of likelihood ratio statistics comparing all four models (constant, linear, quadratic, cubic; six pairwise comparisons)

^c Akaike’s information criterion (AIC) is shown in parentheses for each model

Brandt's Cormorants, Pelagic Cormorants and Pacific Loons foraged mostly outside the reserve at leeward sites (Fig. 3). Surf Scoters foraged mostly at windward sites. There was a marginally significant interaction between reserve and promontory for Brandt's Cormorants ($P = 0.095$), with a larger difference between inside and outside of the reserve at leeward sites than at the windward sites. The majority of Brandt's Cormorant foraging occurred at the leeward site outside the reserve. There were no significant interactions between reserve and promontory for any other species.

With the exception of Surf Scoters, there were no reserve \times year or promontory \times year interactions for any of species, indicating that foraging patterns were consistent for the duration of our study (Table 4). Surf Scoters showed both reserve \times year and promontory \times year interactions, although the latter was due mostly to variable use of windward plots and persistent non-use of leeward plots (Fig. 4). The interaction between year and reserve for this species illustrates alternating use of plots inside and outside the reserve on the windward side.

DISCUSSION

In this study, seabirds did not forage inside the VSMR more than in adjacent areas, as would be expected if their prey were more abundant or available inside the protected area. In fact, the three piscivorous species (Brandt's Cormorant, Pelagic Cormorant and Pacific Loon) foraged more outside the reserve than inside. Also, the foraging distributions of these three species were consistent over our six-year study period. Thus, these species were not responding to stochastic events, but rather cuing into a static resource. Our evidence suggests that potential reserve effects are overshadowed by geographic and oceanographic factors influencing prey distribution.

The three piscivorous predators in our study preferred foraging in leeward areas over windward. Robinette *et al.* (2007) showed differences in diet between leeward-foraging and windward-foraging Pigeon Guillemots (*Cepphus columba*) at Point Arguello. The leeward diet was less variable among years and had a higher incidence of the dominant prey, sanddabs (*Citharychthys* sp.), suggesting that sanddabs were more available in leeward waters and more stable overall than in windward waters. Such increased availability of demersal fishes likely attracts their predators to leeward waters. Furthermore, Trainer *et al.* (2000) documented an algal bloom in the lee of Point Arguello that lasted more than three weeks. Such prolonged primary productivity of an upwelling

TABLE 3
Effects of reserve, promontory, and reserve \times promontory interaction on the foraging behavior of each species, evaluated by negative binomial regression

| Species | Variable (model with all variables compared with model lacking variable) | | |
|--------------------|--|-----------------------------|-----------------------------|
| | Reserve | Promontory | Reserve \times promontory |
| Brandt's Cormorant | LRS = 42.05 $P < 0.001$ | LRS = 141.73 $P < 0.001$ | LRS = 2.78 $P = 0.095$ |
| Pelagic Cormorant | LRS = 9.66 $P = 0.002$ | LRS = 33.23 $P < 0.001$ | LRS = 2.34 $P = 0.126$ |
| Pacific Loon | LRS = 8.55 $P = 0.004$ | LRS = 2.83 $P = 0.093$ | LRS = 0.54 $P = 0.463$ |
| Surf Scoter | LRS = 2.56 $P = 0.110$ | LRS = 186.31 $P < 0.001$ | LRS = 0.09 $P = 0.766$ |

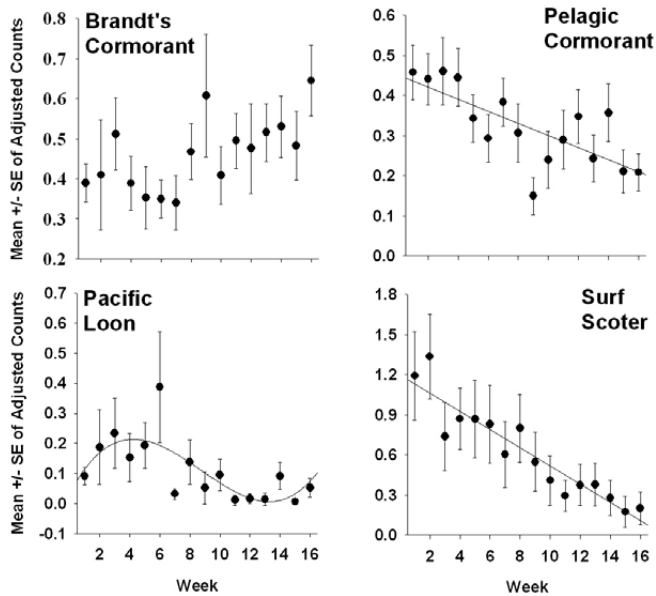


Fig. 2. Within-season trends in the weekly abundances of foraging seabirds using all data from 2000–2005. Values plotted are the means +/- SE of adjusted counts, controlling for tide and observation site.

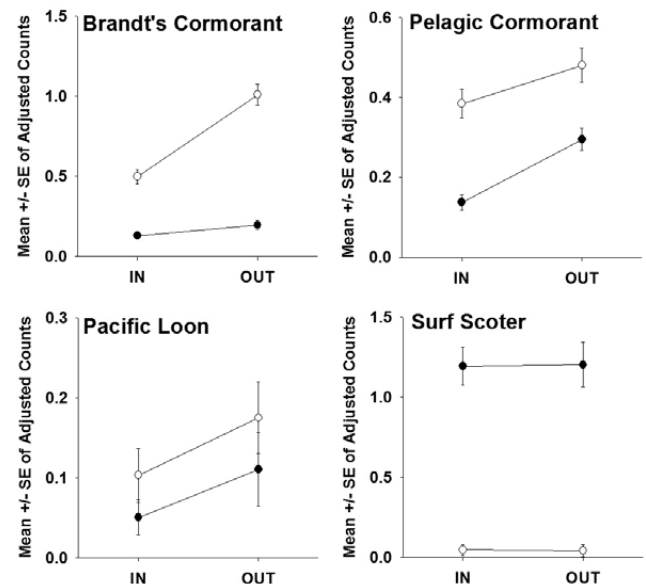


Fig. 3. Reserve \times Promontory interaction plots showing the mean abundance of seabirds foraging in each observation site. Values plotted are the means +/- SE of adjusted counts incorporating the within-season models shown in Fig. 2 and controlling for tide. Means were calculated for observation sites inside (IN) and outside (OUT) the marine reserve over the duration of our study, 2000–2005. Open circles represent leeward sites and filled circles windward sites.

shadow would attract planktivorous organisms and their predators to leeward waters.

An alternative interpretation of these results is that the reserve is protecting large fishes that compete with seabirds for their prey. Brandt's Cormorants typically take fishes <20 cm in length (Wallace & Wallace 1998), and Pelagic Cormorants take fishes <10 cm in length (Hobson 1997). Four of the fisheries adjacent to the VSMR (representing 26% of groundfish catch for the area) have minimum size restrictions that range from 25 cm to 61 cm total fish length (California Code of Regulation 14 CA ADC §28.15, §28.27, §28.28; California Fish and Game Code 8588). For these species, the smallest individuals are being protected both inside and outside the reserve, whereas the largest individuals are protected only within the reserve. The abundance of small fishes might be higher outside the reserve, where they are protected by legal size limits and provided a refuge from the larger fishes taken by fishers. Such shifts in community structure have been documented in other areas where fishing pressure has changed (Scheffer *et al.* 2005, Mumby *et al.* 2006). However, the large fishes, likely benefitting from the VSMR, have movement ranges that span the reserve's boundaries. Movement patterns of the fish groups mentioned above can range from 0.8 km to 20 km, with larger individuals typically moving farther than smaller individuals (Lowe & Bray 2006). The VSMR would need to be much larger in order to protect large fish and produce the hypothesized shift in

community structure. We therefore feel this alternative argument is not compelling and that the VSMR is not protecting important foraging habitat for piscivorous seabirds.

Surf Scoters were the only predator showing no difference between inside and outside sites. Surf Scoters foraged more at the two windward sites. At both sites, they foraged in the surf zone over the low intertidal (during high tide) and shallow subtidal habitats. Inside the reserve, scoters foraged in both rocky and sandy habitats, but outside the reserve, they were limited mostly to sandy habitat. Scoters in our study were likely taking infaunal invertebrates such as small clams and polychaete worms from sandy habitats as well as mussels (likely *Mytilus californianus*) from rocky habitats, as found in diet studies of scoters foraging in these habitats (Stott & Olson 1973, Savard *et al.* 1998).

The distribution of foraging Surf Scoters likely reflects differences in invertebrate community structure. Invertebrate communities are markedly different between windward and leeward habitats, with windward habitats generally being dominated by competitively dominant, wave-resistant species such as mussels (Lubchenco & Menge 1978). Growth rates and overall biomass of filter feeders such as mussels, clams and polychaetes are greater at exposed habitats because waves quickly replenish the planktonic prey as they are filtered from the water (McQuaid & Branch 1985, McQuaid & Lindsay 2000). Our observations on Surf Scoter foraging distributions are consistent with observations that filter-feeding invertebrate biomass is greater at exposed habitats. Furthermore, the alternating use of inside and outside windward sites by Surf Scoters is consistent with the high among-year variability in prey distribution typically observed in windward habitats (McQuaid & Lindsay 2000).

To our knowledge, this is the first study to test the efficacy of a coastal marine reserve in protecting the foraging habitat of nearshore foraging seabirds. Although it is reasonable to expect that "no take" reserves would benefit upper-trophic-level predators, it is important to consider size and location, especially in relation to physical features that may concentrate prey, when designing reserves to protect all trophic levels of a community. Although the predators in our study did not appear to respond to the boundaries of the marine reserve, consistency in their foraging distributions over six years suggests the reserve could provide benefits if the boundaries were redrawn to protect more foraging habitat. Our results suggest the VSMR would be more effective at protecting foraging habitat if it were 1) increased in overall size and 2) expanded to protect more leeward habitat.

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TABLE 4
Reserve × year and promontory × year interactions,
evaluated by negative binomial regression analysis

| Species | Reserve × year | Promontory × year |
|--------------------|--------------------------|--------------------------|
| Brandt's Cormorant | LRS = 6.81 P = 0.235 | LRS = 2.68 P = 0.749 |
| Pelagic Cormorant | LRS = 5.53 P = 0.354 | LRS = 1.33 P = 0.932 |
| Pacific Loon | LRS = 2.85 P = 0.724 | LRS = 4.20 P = 0.521 |
| Surf Scoter | LRS = 55.27 P < 0.001 | LRS = 17.60 P = 0.004 |

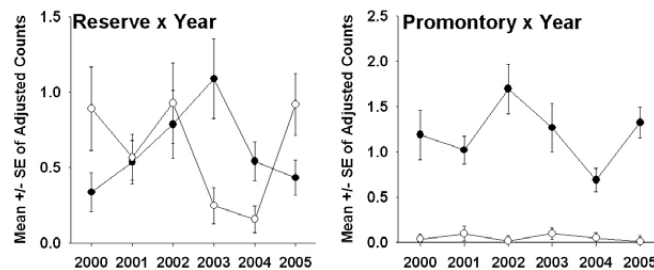


Fig. 4. Reserve × year and promontory × year interaction plots for Surf Scoters, the only species in this study to show significant year interactions (see Table 4). Values plotted are the means +/- SE of adjusted counts incorporating the within-season models shown in Fig. 2 and controlling for tide. Means were calculated over each year for each site category (inside vs. outside for reserve or windward vs. leeward for promontory). Filled circles represent inside or windward sites and open circles represent outside or leeward sites.

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KITTLITZ'S MURRELET *BRACHYRAMPHUS BREVIROSTRIS* POPULATION TREND IN PRINCE WILLIAM SOUND, ALASKA: IMPLICATIONS OF SPECIES MISIDENTIFICATION

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SUMMARY

HODGES, J.I. & KIRCHHOFF, M.D. 2012. Kittlitz's Murrelet *Brachyramphus brevirostris* population trend in Prince William Sound, Alaska: implications of species misidentification. *Marine Ornithology* 40: 117–120.

Suspected population declines of the Kittlitz's Murrelet *Brachyramphus brevirostris* led to selection of the species as a candidate for listing under the Endangered Species Act (USFWS 2004). Kittlitz's Murrelet is currently classified by the International Union for the Conservation of Nature as critically endangered under criterion A4 on the basis of an estimated and projected decline of at least 80% over a period of 36 years (three generations) stretching from 24 years in the past to 12 years in the future (1986–2022) (Taylor 2011). In this paper we evaluate Kittlitz's Murrelet survey data for the initial time frame, from 1986 through present, for Prince William Sound, Alaska. We show that Prince William Sound had factors that would cause the population estimates to be sensitive to misidentification of species. We present evidence that misidentification occurred, and re-analyze the population trend censoring two years with suspected misidentification. We enhance the time series analysis by incorporating two additional years of survey from Kuletz *et al.* (2011a) – the intensive surveys of 2001 and 2009 – designed specifically for Kittlitz's Murrelets. We also present a non-linear weighted least squares regression, excluding the same two outlying years as Kuletz *et al.* (2011a) and including their intensive surveys. These analyses indicate no significant decline of Kittlitz's Murrelets in Prince William Sound.

Keywords: Kittlitz's Murrelet, Marbled Murrelet, misidentification, trend, Alaska, Prince William Sound, *Brachyramphus*, population

POPULATION ESTIMATES FOR KITTLITZ'S MURRELETS IN PRINCE WILLIAM SOUND ARE SENSITIVE TO MISIDENTIFICATION

Kittlitz's Murrelets *Brachyramphus brevirostris* co-exist in Prince William Sound with the more abundant and phenotypically similar Marbled Murrelets *B. marmoratus*. The two species cannot be readily differentiated in the field, and this leads to difficulty in monitoring (Kirchhoff 2011, Kuletz *et al.* 2011a). When misidentification occurs, and the species ratios are highly skewed, the errors will greatly inflate population estimates of the rarer species. For example, from 1996 to 2007, the average number of Marbled Murrelets in Prince William Sound was roughly 20 times greater than the number of Kittlitz's Murrelets (Kuletz *et al.* 2011a). If we assume that 100% of the birds in a hypothetical sample were identified to species, but 2% of both species were misidentified as the other species, then the Kittlitz's Murrelet population estimate would be inflated 36% by misidentification and the Marbled Murrelet population estimate would be deflated 2%.

The bias is also sensitive to the proportion of murrelets identified to species in the field. For example, in Prince William Sound, in 1993, only 11% of the sampled birds were identified to species. If observers had the same identification error rate as in the previous example (2%), but identified just 11% of the birds to species, the prorated population estimate for Kittlitz's Murrelet would be

inflated by a factor of 4.3. The partial identification of the sample would have greatly amplified the effect of misidentification, resulting in a very high population estimate. In fact, the population estimate was very high in 1993 (Fig. 1).

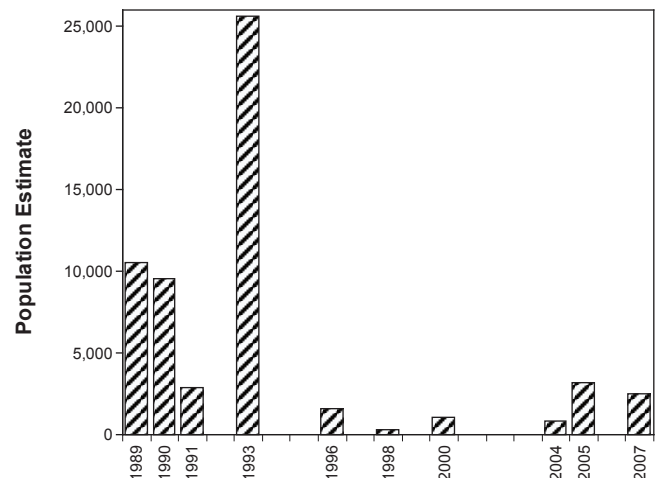


Fig. 1. Population estimates for Kittlitz's Murrelets in Prince William Sound. The unidentified birds were prorated to species by assuming the same species ratio as in the field-identified birds. This differs from the figures in Kuletz *et al.* (2011a), which display only the field-identified birds.

FURTHER EVIDENCE OF SPECIES MISIDENTIFICATION IN 1993

In Prince William Sound, the Kittlitz's Murrelet is found mainly in glacial-influenced marine habitat (Day *et al.* 2003, Kuletz *et al.* 2003). Indeed, during the period 1996–2007, just 12% of Kittlitz's Murrelets were found outside of their core areas (Kuletz *et al.* 2011a). In contrast, Marbled Murrelets were distributed abundantly throughout Prince William Sound (Aglar *et al.*, 1998, Day *et al.* 2003, Piatt *et al.* 2007). If Kittlitz's Murrelets were found in substantial numbers on transects outside of their core areas, this would be a reason to suspect misidentification of Marbled Murrelets as Kittlitz's Murrelets. In 1993, 65% of the identified Kittlitz's Murrelets were located outside of their core areas (Fig. 2).

Kuletz *et al.* (2011a) suggested that the abnormally high numbers of Kittlitz's Murrelets in 1993, abnormally distributed throughout Prince William Sound, could have been due to an influx of Kittlitz's

Murrelets from other regions. If immigration was the cause, it represented at least 15 000 displaced birds, and it never happened again at even a reduced level (Fig. 2). We believe it is more likely these abnormalities reflect species misidentification.

There is additional reason to suspect misidentification in 1993. Lower Cook Inlet data had the same anomalous results in 1993 (Kuletz *et al.* 2011b). The Kittlitz's Murrelet population estimate was extraordinarily high, and the percent identified to species was extraordinarily low (18%). As a result, Kuletz *et al.* (2011b) corrected the Lower Cook Inlet Kittlitz's Murrelet population estimate for 1993 by substituting the average percent Kittlitz's Murrelets seen by more experienced observers in later survey years. Kuletz *et al.* (2011b:88) explained the adjustment as follows: "The survey crews during 1996–1999 had experienced murrelet observers, crew members were fairly consistent across years, protocols were identical, and observers achieved a higher rate of species identification (77% across all years)." However, the

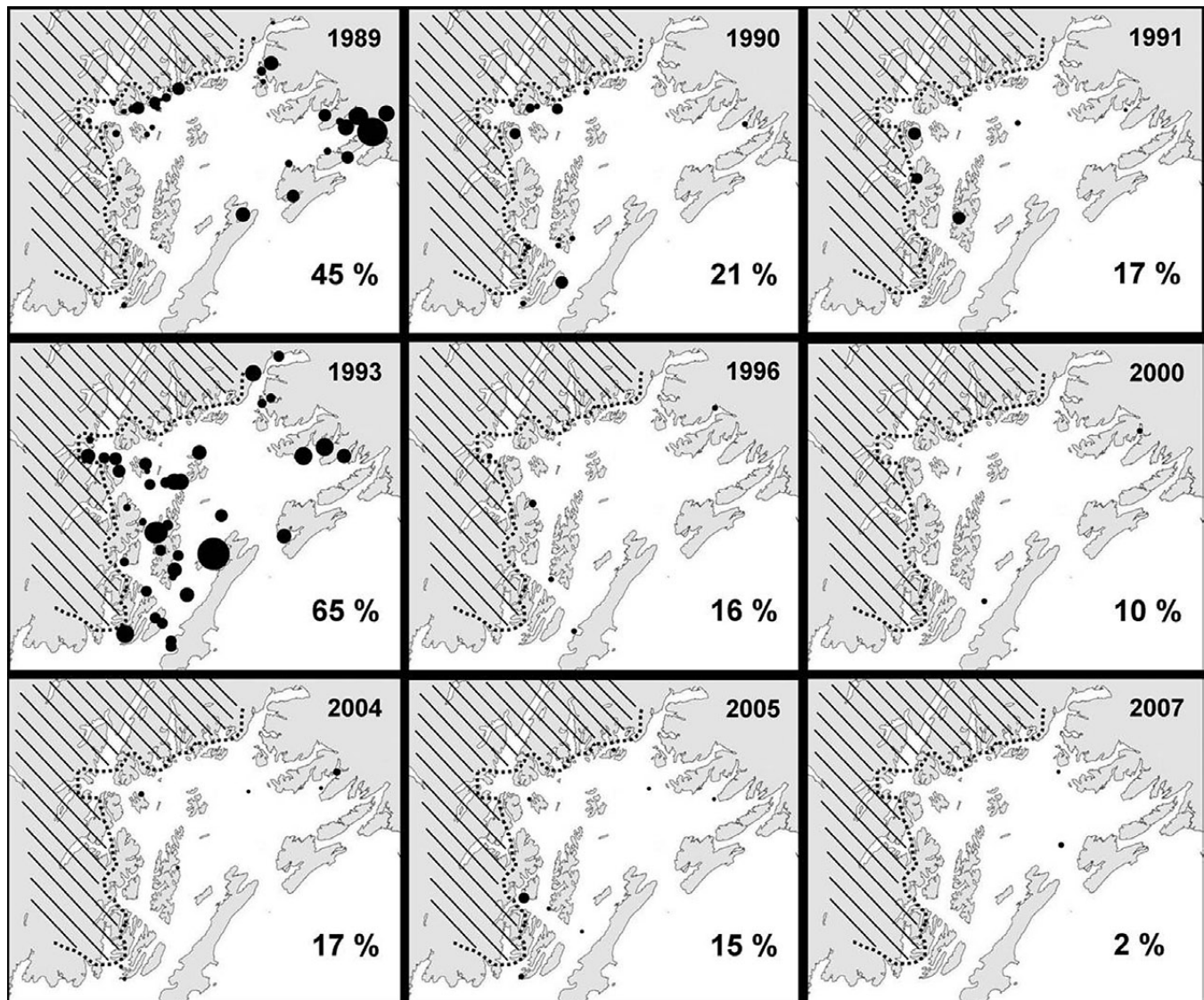


Fig. 2. Distribution of observations outside of core Kittlitz's Murrelet habitat. Hatched area is the core Kittlitz's Murrelet habitat as delineated by the intensive surveys of Kuletz *et al.* (2011). Circle size is scaled (range 1 to 150 birds) to include unidentified birds, prorated to species. Percentages represent the proportion of Kittlitz's Murrelet found outside of the core Kittlitz's Murrelet habitat.

observers in Lower Cook Inlet in 1993 were the same observers as in Prince William Sound that year. Therefore, their observations in Prince William Sound would have the same need for correction.

MISIDENTIFICATION WAS LIKELY IN 1989

Inspection of the distribution maps in Fig. 2 reveals that misidentification of species likely also occurred in 1989. An unusual percentage of Kittlitz's murrelets (45%) were seen outside of their core habitat (Fig. 2), as defined by the intensive survey area (Kuletz *et al.* 2011a). The Exxon Valdez oil spill in 1989 does not explain why so many Kittlitz's Murrelets would move out of the relatively undisturbed and non-oiled core areas (Kuletz *et al.* 2011a) into an area teeming with vessel traffic. The clustering of misidentified birds in the southeast region could be explained by misidentification within a single survey crew responsible for this area.

INTENSIVE SURVEYS PROVIDE ADDITIONAL POPULATION ESTIMATES FOR KITTLITZ'S MURRELETS

Recognizing that the surveys of Prince William Sound had allocated little effort to Kittlitz's Murrelet habitat, intensive surveys were conducted in 2001 and 2009, focusing on "core areas" or fjords in Prince William Sound where Kittlitz's Murrelets were known to occur at the highest densities (Kuletz *et al.* 2011a). The survey transects were therefore located in core Kittlitz's Murrelet habitat (delineated in Fig. 2, see also Day *et al.* 2003). These intensive surveys contained roughly 10 times as many pelagic transects (>200 m from shore) in the core Kittlitz's habitat as the previous Prince William Sound-wide surveys. Consequently, the intensive surveys were far more precise (average coefficient of variation [CV] of 0.18) than the Prince William Sound-wide surveys (average CV of 0.50). The two intensive surveys showed a statistically significant increase in population from 2001 to 2009 (Kuletz *et al.* 2011a). However, they were not included in the Kuletz *et al.* (2011a) trend analysis.

These minimum population estimates provide valuable information and two additional data points. They can be adjusted to represent Prince William Sound after applying a small correction factor for the Kittlitz's Murrelet population outside the intensive survey areas.

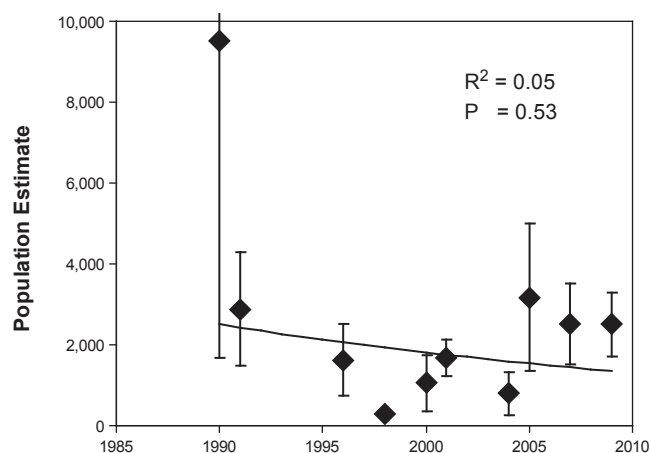


Fig. 3. Re-analysis of population estimates (with standard errors) for Kittlitz's Murrelets in Prince William Sound (trend curve based on exponential regression analysis), showing stable population over the 20-year period 1990–2009.

As mentioned earlier, the four Prince William Sound-wide surveys from 2000 to 2007 found an average of 12% Kittlitz's Murrelets outside of the intensive survey areas (Fig. 2). Thus, the intensive surveys represented an estimated 88% of the Prince William Sound-wide population. We therefore adjusted the intensive survey results by a factor of 1.14 to be comparable to the Prince William Sound-wide surveys. We also prorated the small number of unidentified birds (5% in 2001 and 6% in 2009) to species, as is the accepted practice (Kirchoff 2011). The resultant Kittlitz's Murrelet population estimates are 1 676 in 2001 and 2 513 in 2009.

THE TWO-GENERATION (1986–2010) KITTLITZ'S MURRELET TREND ANALYSIS USING AN EXPONENTIAL REGRESSION

Kuletz *et al.* (2011a), in their summary, reported a population decline rate of -13% per annum (confidence limits -7% to -19%) from 1989 to 2007. We find a much different trend estimate over that time period by including the two intensive survey years (2001 and 2009) and excluding the two years of probable misidentification (1993 and 1989). In this analysis, the exponential trend (Fig. 3) is not statistically significant ($P = 0.53$). Hence, we cannot reject the possibility of a stable population, for which the best estimate is the mean of 2 605 Kittlitz's Murrelets.

THE TWO-GENERATION (1986–2010) KITTLITZ'S MURRELET TREND ANALYSIS USING LEAST SQUARES NON-LINEAR REGRESSION WITH WEIGHTING INVERSELY PROPORTIONAL TO VARIANCE

Our analysis used weighted least squares non-linear regression of Kittlitz's Murrelet population estimates. Kuletz *et al.* (2011a) used a similar regression analysis, which additionally incorporated Marbled Murrelets into their models. Our population estimates included the unidentified birds prorated to each species based on the ratios among the field-identified birds. We assumed the CVs were the same for the prorated estimates as the field estimates. We weighted the least squares regression using the inverse of the variance (SE squared). We removed the two outliers (1993 and 1998), which Kuletz *et al.* (2011a) also removed individually in two of their models. At this point, our trend estimate would be nearly identical to that produced by the Kuletz *et al.* (2011a) model. However, we incorporated two additional data points (the intensive surveys of 2001 and 2009), which Kuletz *et al.* analyzed separately from their regression models. Our weighted least squares regression yields a decline rate of -0.1% per annum, or -2% for the 20-year period from 1989 to 2009, not significantly different from a stable population.

CONCLUSIONS

The high population estimate in 1993 could have been caused by misidentification or by immigration. We believe the simplest and most likely explanation for 1993 was misidentification. It simultaneously explains the extraordinarily high population estimate and the atypical distribution pattern. Misidentification was possible in 1989 as well, based on large numbers of Kittlitz's Murrelets recorded outside of their core habitat.

The influence of misidentified and unidentified murrelets has been underappreciated as a factor that can inflate population estimates of rare species like the Kittlitz's Murrelet. Misidentification was most likely to occur in the earlier years, when there was less emphasis

on accurately identifying a high percentage of murrelets to species. It may be difficult to know whether misidentification problems occurred in other years in the Prince William Sound, or in other areas of their range, but it should be considered as one of the possible sources of bias.

We suggest that previous population trends of Kittlitz's Murrelet in Prince William Sound were driven by two early surveys that suffered from low identification rates and suspected higher-than-usual species misidentification. When the questionable data are censored, and the two years of intensive Kittlitz's Murrelet surveys are added, the population of Kittlitz's Murrelets in Prince William Sound shows no sign of a significant decrease since 1989. A weighted non-linear regression also showed no significant decline.

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THIRD CONFIRMED RECORD OF THE RED-FOOTED BOOBY *SULA SULA* FROM SRI LANKA

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On 27 April 2011, the authors were informed of a large gull-like bird found by a local fisherman around 06h00 in Eththukala (7°14'N, 79°47'E), Negombo, in the Gampaha District of Western Province, Sri Lanka. The bird had been found in the sea about 3 km from the shore. It was alive but exhausted and unable to fly when caught.

We retrieved the bird and kept it in captivity for several days. From Ali and Ripley (1978), the bird was identified as an immature Red-footed Booby. The Red-footed Booby (*Sula sula*) is a pantropical resident (Howard & Moore 1980, Le Corre 1999). Adults are polymorphic, with three recognized major adult plumage types (white, white-tailed brown and brown) and several intermediates, including golden white, black-tailed white, and white-headed white-tailed brown (Nelson 1978, Del Hoyo *et al.* 1992).

The bird had generally grayish-brown plumage, with paler underwing coverts and the a lighter throat, with the breast and belly clearly darker (Figure 1). The bare skin around the eye and the bill was ocean-blue. The iris was bright yellow. The head was dusky white, fading into the body color on the nape. The bill was dark brown except for the pinkish base of the lower mandible. Some parts of the bill were much paler, but the tip was black. Legs and



Fig. 1. Immature white color morph of Red-footed Booby *Sula sula* at Eththukala, Negombo, Sri Lanka. (Photograph by C. J. Amarasinghe)

feet were flesh-colored; the feet were webbed, with claws dusky white in color. The tail was pointed with 14 tail feathers. The head-to-tail length was 685 mm; the wingspan 1.45 m; weight 0.900 kg; culmen 80.0 mm; gape 101.6 mm; tarsus 38.1 mm; the middle toe (without claw) was 76.2 mm. The bird fed voraciously in captivity, swallowing fish whole. On occasion, it attacked aggressively, raising the feathers on its head.

The dark bill, yellow eye, and pale-colored legs and feet all identify this bird as an immature. The commonest morph of Red-footed Booby in the Indian Ocean, including all extant breeding colonies (Le Corre 1999), is all white except for black primaries and secondaries. The specimen recorded by de Silva (1985) was also a white morph. The other morphs are largely brown (Diamond 1971). Juveniles cannot usually be assigned to a particular morph, but the much whiter head of this bird suggests it might have been beginning transition to the adult plumage of a white morph.

The Red-footed Booby is a vagrant to Sri Lanka, previously known from only two confirmed records (Kotagama & Rathnaweera 2010). The first specimen was captured somewhere in Ceylon and brought to the Colombo Museum on 2 July 1936 (Henry 1955). The second record is from Dehiwala (6°50'N, 79°52'E), in the Colombo District of Western Province (de Silva 1985). However, de Silva (2011) also reported the species as a visitor, in very small numbers, to the western and southern coasts of Sri Lanka. He also reported that the *Seabird Watch (Sri Lanka)* has a few records of this species during the southwest monsoon (May/September), and moreover he has observed two specimens off the western coast during December/January (northeast monsoon).

Weather conditions in the area for the 24 hours before the bird was found could explain its origin. The sky was mostly overcast, and afternoon thundershowers with light winds were reported during the period. Strong southwest winds gusting to 78 km/h were recorded from 14h45 that day, lasting for about one hour in the particular area, and may have blown the bird near the shore. At around the same time that the Red-footed Booby was found, many Sooty Terns (*Sterna fuscata*) were storm-blown to the area, including three banded in the Seychelles or Juan de Nova, to the southwest of Sri Lanka (M. LeCorre and C.Feare, in litt. to editor); this booby may have been affected by the same extreme weather event. The largest colonies of Red-footed Boobies in the region lie to the southwest of Sri Lanka: Chagos archipelago (5°59'N, 71°59'E), Aldabra Atoll (9°24'S, 46°21'E) and Ile Europa (22°21'S, 40° 21'E); although the closest of these (Chagos) is over 1600 km away.

The bird was kept in captivity for eight days. During this time it ate well. After this period, it began to flap its wings and attempted to escape. On release we marked the bird with a plastic label (numbered 48) on the right leg and released it from the coast of Eththukala. This is the first detailed observation of Red-footed Booby from Sri Lanka in the last 25 years.

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RARE COLOUR ABERRATION IN THE GUANAY CORMORANT *PHALACROCORAX BOUGAINVILLII*

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The occurrence of aberrant colorations such as melanism, leucism or albinism is rare in birds (Sage 1962, 1963). In seabirds, mainly melanism or leucism (also described as isabellinism) have been reported (Thompson *et al.* 2000, Everitt & Miskelly 2003, Bried & Mougeot 2004, Bried *et al.* 2005, Mancini *et al.* 2010). Albinism (*sensu* van Grouw 2006), a complete loss of all pigment in plumage and other body parts, is the most severe aberration in plumage patterns. It results in birds with white plumage and lack of pigment in soft parts (Sage 1962, Gross 1965) and is very rarely recorded in natural populations (Sage 1962, 1963, Gross 1965). Here, we report the first observation of an albino Guanay Cormorant *Phalacrocorax bougainvillii*, a near threatened species on the IUCN Red List (Birdlife International 2010).

Our observations were made on Isla Pescadores (11.775°S, 77.265°W), a small island located 7.5 km off the central coast of Peru, during fieldwork on Guanay Cormorants between 9 November and 2 December 2011. Guanay Cormorants were breeding in large colonies on the island (an estimated 61 000–80 600 breeding pairs, scientific staff of Agrorural, government service for rural development pers. comm.) incubating or rearing small to large chicks.

While we were on the island, we viewed and photographed colonies of cormorants twice a day from a fixed point (lighthouse), to avoid disturbing them. The albino individual was noticed while checking

breeding colonies with binoculars. Its plumage was pure white, without any pigmentation (Fig. 1). The bill and the legs lacked any pigmentation, resulting in a pink colour. The individual was a chick, 5–6 weeks old, with sibling and parents presenting the classical (white and black) plumage of the species. The individual seemed in good condition. We observed regular begging behaviour followed by feeding by parents, and did not note any obvious conflict between this albino individual and its conspecifics.

To our knowledge, our observation represents the first reported case of albinism (pure albinos *sensu* van Grouw 2006) for this species (Sage 1963, Gross 1965, Nelson 2005), despite the permanent field presence and weekly visits to the large Guanay Cormorant colonies by wardens of the island over many years (Murphy 1936, Vogt 1942, Duffy 1983, Tovar *et al.* 1987). This is the first case reported for the Isla Pescadores and the second for the Peruvian colonies (A. Melo & L. Dávila, pers. comm.); both observations involved chick or juvenile individuals. Adult albinos have not been reported for the species, nor is there any mention of albinism in the Guanay Cormorant in the literature, suggesting that this trait is very uncommon. The rarity of albinism may result from a higher mortality rate from predators and difficulty in obtaining a mate (Sage 1963). Furthermore, albino individuals can be difficult to detect due to very large size of the colonies (Fig. 2).

Among Phalacrocoracides, albinism has been reported for the Great Cormorant *Phalacrocorax carbo* (Goula & Parchas 2012), the

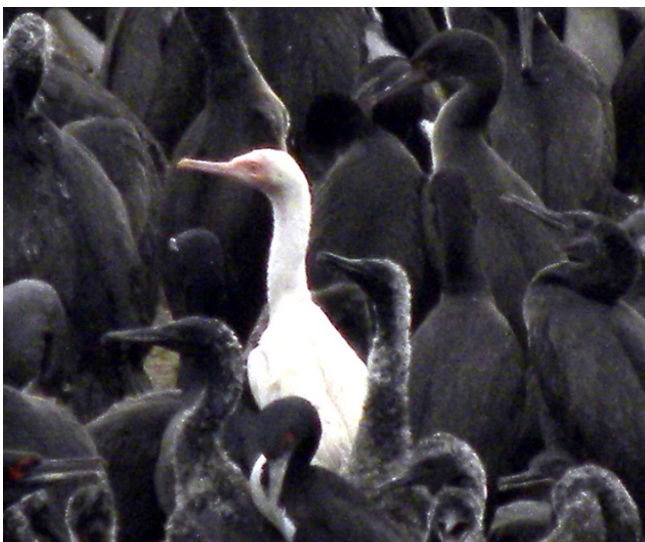


Fig. 1. Close-up of the albino Guanay Cormorant (*Phalacrocorax bougainvillii*) chick on Isla Pescadores, Peru. (November 2011, Karine Delord).



Fig. 2. General view of a small part of the colony of Guanay Cormorant with the albino on Isla Pescadores, Peru. (November 2011, Karine Delord).

Bank Cormorant *Phalacrocorax neglectus* (Nelson 2005) and the Cape Cormorant (Cook *et al.* 2012). The cause of variation in the incidence of albinism among families is unknown but “it ... appears to be in species that are both social in their breeding habits and also fairly sedentary” (Sage 1962), conditions that increase the chances of mating between individuals heterozygous for albinism. Albinism is known to have a genetic basis, and others factors such as diet or trauma are of minor significance (Sage 1962). Moreover, diet or trauma are unlikely to have been involved in this case because of the age of the bird and the condition of conspecifics observed in the colony. There was no obvious sign of malnutrition, and we observed feeding events by both parents. A more plausible explanation is that both parents possessed an albino allele, as hereditary albinism is generally a recessive character (Sage 1962).

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NEW LIFE-SPAN RECORDS OF THE BROWN BOOBY *SULA LEUCOGASTER*

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Seabirds are exposed to a highly variable marine environment in which prey availability is unpredictable, patchy and ephemeral (Ashmole 1971, Hunt & Schneider 1987, Shealer 2002). Consequently, seabirds have evolved a number of distinct life history traits to cope with those conditions, such as low fecundity, deferred maturity and high adult survival (e.g. Furness & Monaghan 1987, Weimerskirch 2002). An important life history trait of seabirds is their longevity. Seabirds can reach extremely old ages and are able to reproduce during this long life span, increasing their chances to project their genes into future generations under the challenging conditions of their marine habitat.

Despite the general acknowledgement of seabird longevity and its evolutionary importance, the life spans of many seabird species are unknown. As age determination in birds is difficult, following banded birds over time is the most common method used to age them. However, seabirds' life spans often exceed the duration of particular research programs, and hence maximum longevity often remains unknown. However, knowledge of life span is crucial for modelling and predicting processes concerning demography and population dynamics as well as for conservation.

The Brown Booby (*Sula leucogaster*) is an abundant, medium-sized member of the Sulidae. It breeds in large numbers in the tropical and sub-tropical waters worldwide (Nelson 1978, Carboneras 1992). Until now, the life span of this species has been unknown and was only roughly estimated based on the life span of other, better studied members of the sulid family (Marchant & Higgins 1990, Carboneras 1992, Nelson 2005). Here, we report on several band resightings that provide new and direct information on the life span of this species.

METHODS AND RESULTS

Three re-sightings of banded adult Brown Boobies were made at two locations:

(1) A female Brown Booby banded as a fully fledged young at Raine Island, Coral Sea (11.6°S, 144.0°E) on December 02, 1986, was re-sighted at the same place on November 30, 2010, 23 years, 11 months and 28 days after banding. The bird had also been re-encountered at this location several times previously.

(2) An adult Brown Booby (sex unknown) banded as a nestling at Raine Island on December 21, 1984, was resighted on December 6, 2009, 24 years, 11 months and 15 days after banding. This is the oldest age known for this species in Australia and, to the authors' knowledge based on literature surveys, worldwide.

(3) On May 10, 2009, a dead bird with a leg ring was found in the Brown Booby colony at the "Dales", Christmas Island, Indian Ocean (10.5°S, 105.6°E). The bird was already decomposed to bones and feathers, but the carcass was complete, and the bones were still largely held together by ligaments. It had been banded at approximately the same location on August 16, 1985. Time and cause of death are unknown but, given the condition of the carcass, it seems likely that the bird died of a natural cause several weeks before the finding. The time from banding to recovery was 23 years, 8 months and 24 days. Making the most conservative assumption, i.e. the bird was banded as a chick and died at the start of the rainy season at the beginning of November 2008, the minimum life span of this individual was ca. 23 years and 3 months.

Our findings show that Brown Boobies can reach old ages and longer life spans than previously assumed. Information on the longevity of booby species is sparse, which is generally the case in the long-living seabirds. The life span of the Red-footed Booby (*S. sula*) was determined to be 22 years (Carboneras 1992, Nelson 2005). The life spans of Abbott's Boobies (*Papadusa abbotti*) and Masked Boobies (*S. dactylatra*) are estimated to be 30–35 years (Nelson 2005) and over 23 years (Carboneras 1992), respectively. For the other booby species, including the Brown Booby, no data are available. The life span of Brown Boobies determined in this study (almost 25 years) matches well with the life spans of Red-footed and Masked Boobies. Animals with similar life histories, body sizes and habitats, generally have similar life spans (cf. Roff 1992, Stearns 1992). The substantially longer life span of Abbott's Booby can most likely be attributed to the different life-history of this species compared to all other boobies (Nelson 1978).

In all three cases, the birds we report here were re-encountered at approximately the same location where they were banded as young birds. This suggests that they spent their entire (reproductive) life close to the location where they hatched and had a life-long fidelity to their natal colony, behaviour often observed in seabirds. Upon reaching maturity, brown boobies return to their natal colony for breeding and do not change colonies anymore as high site fidelity from one reproductive season to the next has been observed in adult birds (Nelson 1978, Carboneras 1992).

Although numerous censuses were conducted at both islands, only one of the birds was re-sighted repeatedly while the other two were not. That may be because Brown Boobies do not always breed seasonally (i.e. they can have breeding cycles shorter than 12 months and hence "escape" seasonal yearly counts), because adults might skip reproduction when conditions are unfavourable and/or because adults

that do not breed spend extended periods away from their breeding site (Nelson 1978, Marchant & Higgins 1990, Carboneras 1992).

Both birds of Raine Island were still alive and might be re-sighted again. In addition, other individuals banded on Raine and Christmas Island in the late 1980s and early 1990s might be re-encountered in future censuses and increase sample size as well as perhaps setting new records of longevity for this species.

In conclusion, our findings provide information on the life span of brown boobies that should allow more accurate modelling of population dynamics and demography. Our findings also emphasize the importance of long-term studies in seabird research and of national bird banding schemes as long-term data collection, storage and access are crucial to providing information on longevity for many seabird species.

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LONGEVITY RECORDS OF FLIGHTLESS CORMORANTS

PHALACROCORAX HARRISI

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The Flightless Cormorant *Phalacrocorax harrisi* is endemic to the Galápagos Islands, Ecuador (Harris 1973). This species is morphologically and behaviorally unique among extant species of cormorants (Phalacrocoracidae) because of its flightlessness and sequential polyandrous mating system (Valle 1994, Kennedy *et al.* 2009, Valle 2009). The IUCN listed the Flightless Cormorant as endangered (EN) until 2010, but changed its listing in 2011 to vulnerable (VU) “because evidence suggests that the population is stabilizing and the recorded fluctuations during the last three decades have not been extreme” (IUCN 2011). However, its small population size, with numbers fluctuating between 700 and 1 900 individuals during the last three decades (Jiménez-Uzcátegui 2010) as well as its restricted distribution range around Fernandina and the Isabela islands (except the southern and southeastern parts) make the species vulnerable to the impact of recurrent El Niño events (Valle & Coulter 1987, Valle 1995), increases in pathogens (Travis *et al.* 2006, Merkel *et al.* 2007, Deem *et al.* 2010) and introduced predators, such as rats *Rattus* spp. and feral cats *Felis catus*, that prey especially on chicks and juveniles (Valle 1986, 1995).

Of 38 species of cormorants worldwide (Johnsgard 1993), the oldest longevity records for the two species genetically closest to the Flightless Cormorant are 22.6 years for the Double-crested Cormorant *P. auritus*, and 11.9 years for the Neotropic Cormorant *P. brasilianus* (Lutmerding & Love 2011). These two species are considered of least concern (LC) because they have a large

distributional range with large and increasing populations of mature individuals (IUCN 2011).

On 8 April 2006, the monitoring team of one of us (FHV) captured a female Flightless Cormorant *Phalacrocorax harrisi* that was at least 17.2 years old at Zone 4 (0°19'S, 91°23'W) on the northeastern coast of Fernandina Island, Galapagos Archipelago, Ecuador. This cormorant had a metal ring No. 100-029 and had been banded as an adult by one of us (CAV) on 10 July 1990 on South Colony, approximately 3 km southwest of Punta Espinosa, Fernandina Island (Valle 1994); this indicated an actual banded age of 15.9 years. At the time of banding, this bird was sexually mature, therefore at least 17 months old (Valle 1994, 1995, Larrea 2007). This finding establishes the longest life span ever recorded for a Flightless Cormorant. We also provide four additional longevity records for this species based on birds banded by one of us (CAV) between 1989 and 1991 (Table 1).

At present, we are unable to assess whether ages of more than 10 years for Flightless Cormorant are the exception or the norm in their population. As these records were established between 1989 and 2006 (Table 1), we conclude that these individuals are survivors of the last strong El Niño-famine event in 1997–1998. Like many seabird species, Flightless Cormorants have low reproductive levels and depends directly on food availability, which, in turn, depends on oceanographic conditions (Harris 1979, Tindle 1984,

TABLE 1
Longevity records of Flightless Cormorants *Phalacrocorax harrisi*, Galápagos Islands

| Identification | | | Banding | | | | | Re-capture | | | | Age (years) | |
|----------------|----------|------------------|-------------|------------------|------------------|--------------|-------------------------------|-------------|-----------------|-----------|-------------------------------|-------------|-----------|
| Pit-tag | Band No. | Sex ^a | Date | Age ^b | Breeding Status | Locality | Coordinates | Date | Breeding Status | Locality | Coordinates | Banded | Estimated |
| 53812301 | 100029 | F | 10-Jul-1990 | A | Courtship | South Colony | 0°17'12.08'S 91°25'5.58'W | 08-Apr-2006 | Incubation eggs | Zone 4 | 0°19'45.30'S 91°23'41.64'W | 15.9 | 17.2 |
| 53512101 | 100035 | F | 26-Jul-1990 | A | Nesting chicks | Espinoza | 0°15'50.61'S 91°26'40.52'W | 02-Oct-2003 | Solitary | Serrano | 0°17'12.08'S 91°25'5.58'W | 13.3 | 14.8 |
| 42023011 | 100060 | F | 21-Nov-1991 | J | Solitary | Valle | 0°15'38.55'S 91°27'34.27'W | 08-Apr-2006 | Solitary | Valle | 0°15'38.55'S 91°27'34.27'W | 14.5 | 14.7 |
| 53380633 | 100043 | M | 28-Jul-1990 | A | Nest building | South Colony | 0°17'12.08'S 91°25'5.58'W | 26-Aug-2003 | Solitary | Serrano | 0°17'12.08'S 91°25'5.58'W | 13.1 | 14.6 |
| 42045262 | 100130 | M | 29-Jun-1989 | A | Nesting juvenile | Valle | 0°15'38.55'S 91°27'34.27'W | 22-Apr-2001 | Solitary | Escondida | 0°15'45.25'S 91°28'7.21'W | 11.1 | 12.6 |

^a F: Female, M: Male

^b A: Adult, J: Juvenile

Valle 1994). Hence, the protection of adult cormorants surviving El Niño events should be top priority, as they have the potential to reproduce and restore the diminished populations immediately after such extreme climatic events. These records also reinforce the importance of preventing cumulative increases in adult mortality from disease, predation, entanglement in fishing gear and other anthropogenic threats. Therefore, we recommend maximizing survival of adult cormorants as a protection measure to achieve long-term conservation goals for the species.

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EFFECTS OF A STORM ON COLONIES OF SEABIRDS BREEDING AT THE FALKLAND ISLANDS

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Seabirds of the order Procellariiformes are particularly well adapted to strong winds, which they use to facilitate long-distance foraging for patchily distributed food resources (Davies *et al.* 2010). On land, albatross colonies are often distributed to maximise exposure to the prevailing winds, thus making it easier for birds to get airborne. At sea, most seabirds either use storm conditions to aid their movements, or avoid severe weather effects by flying away from a storm (e.g. Culik *et al.* 2000, Catry *et al.* 2004). It is when seabirds are on land, at their breeding sites, that they are most vulnerable to the effects of extreme weather events. Severe weather conditions can affect seabird

colonies both directly, by causing the loss of eggs and chicks (e.g. Randall *et al.* 1986, Anderson & Cruz 1998, Hennicke & Flachsbarth 2009), or indirectly, by inhibiting adult feeding and thus reducing provisioning rates of chicks (Schreiber 2002).

Located in the southwest Atlantic Ocean, the Falkland Islands archipelago experiences a temperate oceanic climate, dominated by westerly winds; strong winds are frequent throughout the year, reaching and exceeding Force 8 on the Beaufort Scale (>63 km/h, 34 knots) 5–8% of the time from September to May (Upton & Shaw 2002). Storm conditions are not rare, but there have been no previous reports of storms having caused extensive damage to seabird colonies. Here we report the impacts of a storm event in mid-December 2010 on seabirds breeding at Beauchêne and Steeple Jason islands, in the south and north-west of the archipelago, respectively (Fig. 1). Both of these sites support globally significant seabird populations, including the two largest Black-browed Albatross *Thalassarche melanophris* colonies in the world (Agreement on the Conservation of Albatrosses and Petrels 2010). Although Beauchêne Island is rarely visited, two of the authors (ACW and SC) were on the island at the time of the storm; the other author (AMMB) was at Steeple Jason Island during the storm event. As part of a Falkland Islands archipelago-wide survey, a census of Black-browed Albatrosses, Rockhopper *Eudyptes chrysocome* and Gentoo Penguins *Pygoscelis papua* breeding at Steeple Jason Island and Beauchêne Island was conducted from 23 October to 14 November 2010 (Baylis 2012), approximately one month before the storm.

On the afternoon of 13 December 2010, a deep low pressure system of 95.0–95.5 kPa (950–955 mb) that had been building up from the Drake Passage reached the Falkland Islands. Wind speeds of 111–120 km/h (60–65 knots) were measured at the Mount Pleasant Complex, East Falklands (UK Meteorological Office, Mount Pleasant Complex, unpubl. data). Although wind speeds were not measured on Beauchêne Island, it was estimated that on the afternoon and night of 13 December, the wind speed had increased to an estimated 130–148 km/h (70–80 knots, Force 11 Beaufort Scale: violent storm conditions), resulting in open ocean swells in excess of 10 m. The wind and swell came from the southwest, making the south and west coasts of the island – where the majority of the seabirds nest – especially exposed (Fig. 1). Storm conditions persisted throughout the night. By the morning of 14 December, the wind speed had dropped considerably, but the sea remained very rough until 16 December.

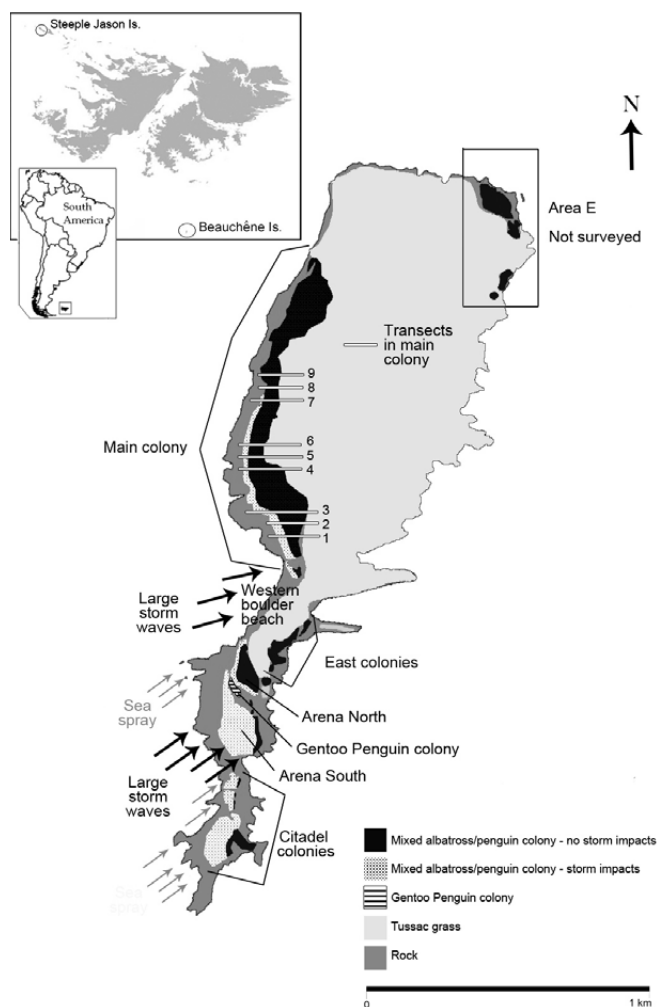


Fig. 1. The distribution of seabird colonies at Beauchêne Island, in the Falkland Islands archipelago, illustrating the relative impacts of the storm event on 13 December 2010.

As the wind increased in strength on 13 December, albatrosses nesting at Beauchêne Island were observed bracing their wings against the nests to anchor themselves down. By the evening of

13 December, waves breaking on the western coast had reached some of the nesting seabirds on the southern and western side of the island. A single wave was observed breaking over an area containing about 100 Black-browed Albatross nests, a similar number of Rockhopper Penguin nests, and about 30 Imperial Shag *Phalacrocorax atriceps* nests, pulling out to sea most of the adult nesting birds in the process. The landing sites along the western coast of the island, normally used by thousands of Rockhopper Penguins returning from foraging trips, were completely underwater, and being battered by large breaking waves. At the time of the storm, breeding Black-browed Albatrosses were either incubating eggs or brooding recently hatched chicks. Most Rockhopper and Gentoo Penguin nests contained small chicks, ranging in age from one to three weeks; Imperial Shag nests contained eggs.

From 14 to 19 December 2010 we conducted rapid assessments of the main seabird colonies at Beauchêne Island to examine the effects of the storm on the island's breeding seabirds. Based on the extent of abandoned eggs, chicks and empty nests, we estimated (Fig. 1) roughly the proportion of nests that had failed for each colony, and related this to the number of breeding pairs estimated during the archipelago-wide census that took place approximately five weeks before the storm.

The extent of breeding failure was significant, amounting to more than 22 500 failed Black-browed Albatross nests and 14 000 failed Rockhopper Penguin nests (Table 1, Fig. 1), but was not uniform across Beauchêne Island. On the basis of our observations, we

assumed that the failure rates within the mixed colonies of Black-browed Albatrosses and Rockhopper Penguins were the same for both species. Even within colonies, the extent of breeding failure and loss of nest sites varied. For example, a small area on the southwestern (seaward) margin of the main colony (Fig. 1) was completely washed away by waves, and on the morning of 14 December was devoid of albatrosses and penguins. Large boulders had been shifted around, and the nests, guano and mud had been scoured from the area. To examine the variation in breeding failure in the main colony, which contains more than 100 000 nests (Table 1), we conducted nine transects across the width of the colony in which we counted active and failed nests in 20 m by 2 m contiguous strips from the coast inland. The proportion of total nests that were active ranged from 0% to 87%, increasing with distance from the coast and towards the north (Table 2). After considering likely breeding failure due to factors other than the storm, we estimated the overall storm-related breeding failure in the main colony to be between 5% and 10% of the number of pairs that attempted breeding (Table 1). The largest impact was in the Arena South colony, where we estimate about 90% of the nests failed due to the storm event (Table 1). The albatross and Rockhopper Penguin nests that survived the storm were located in elevated areas, mostly on the eastern side of the colony.

We recorded 251 dead or severely injured adult Black-browed Albatrosses at Beauchêne Island, mostly in the Arena South colony (Table 1). Of the birds found dead in the colony, 24 were pinned under boulders that had presumably been moved by large

TABLE 1
Estimated impacts of the 13 December storm event on seabirds at Beauchêne and Steeple Jason islands

| Site | Black-browed Albatross | | | | Rockhopper Penguin | | | | Gentoo Penguin | Imperial Shag |
|-----------------------------|------------------------|-------------------------|--------------------|---------------------------|-----------------------|-------------------------|--------------------|---------------------------|---------------------------|---------------------------|
| | 2010 census estimates | Proportion nests failed | Total nests failed | No. dead & injured adults | 2010 census estimates | Proportion nests failed | Total nests failed | No. dead & injured adults | No. dead & injured adults | No. dead & injured adults |
| Beauchêne Island | | | | | | | | | | |
| Main colony | 103 338 | 5–10% | 5 167– 10 334 | 24 | 79 567 | 5–10% | 3 978– 7 957 | 0 | | |
| East colonies | 2 382 | <2% | | | 2 553 | <2% | | | | |
| Arena South | 14 903 | 90% | 13 413 | 142 | 9 083 | 90% | 8 175 | 14 | 4 | 2 |
| Arena North | 6 225 | 25% | 1 556 | 19 | 3 874 | 25% | 969 | 4 | | |
| Citadel colonies | 4 727 | 50% | 2 364 | 0 | 1 927 | 50% | 964 | 0 | | |
| Area E ¹ | 7 761 | ns | | | 8 439 | ns | | | | |
| Cliff ¹ | 462 | ns | | | 169 | ns | | | | |
| Pond ¹ | 0 | ns | | | 166 | ns | | | | |
| Boulder beach | na | | | 66 | na | | | 0 | | |
| TOTAL | 139 798 | | 22 499– 27 666 | 251 | 105 778 | | 14 085– 18 064 | 18 | 4 | 2 |
| Steeple Jason Island | | | | | | | | | | |
| All colonies | 214 203 | 15–30% | 32 130– 64 261 | 113 | 121 396 | 15–30% | 18 209– 36 419 | 0 | | |

¹ not surveyed after the storm (ns)

waves (Fig. 2). Smaller numbers of adult Rockhopper and Gentoo Penguins and Imperial Shags were also found dead in the Arena South colony (Table 1). In the days following the storm, some adult albatrosses, clearly exhausted and many waterlogged, were observed attempting to take off from the boulder beach, but were unable to gain sufficient height to fly over the large breaking waves. These birds were inevitably battered by the large waves, and some were observed being washed up on the shore of the western boulder beach, either dead or with broken wings. Seventeen of the injured or dead birds along the western boulder shore were entangled in kelp, wedged under *Poa flabellata* tussock bogs or under stranded *Nothofagus* tree trunks. The majority of severely injured birds that we were able to individually identify later died. However, we did not systematically search every section of each colony for dead and injured birds. Therefore the number of dead and severely injured birds recorded represented an unknown proportion of the total mortality. In addition, some dead birds, unrecorded by us, were probably washed out to sea. We do not know how many of the nesting Black-browed Albatrosses that we observed being washed out to sea on the evening of 13 December later died. Southern Giant Petrels *Macronectes giganteus* were observed mobbing

weak albatrosses and scavenging albatross carcasses approximately 30 m offshore from the western boulder beach until 19 December, at which time we left the island. Compared with Black-browed Albatrosses, the substantially lower numbers of adult Rockhopper Penguin mortalities is not surprising, given their greater robustness and superior ability to swim in rough sea conditions, especially being able to dive under breaking waves.

The only Gentoo Penguin colony at Beauchêne Island is located in the area between Arena South and North (Fig. 1) and comprises *ca.* 680 pairs (Falklands Conservation 2011). During a survey of the area on 14 December, it appeared that this colony had suffered complete breeding failure; large numbers of dead chicks had been moved to an area about 30–40 m north of the colony. During a subsequent visit to Beauchêne Island from 15–19 March 2011, three large Gentoo Penguin chicks, close to fledging, were recorded at the colony.

At Steeple Jason Island, 2 637 incubating Black-browed Albatrosses were counted at three study colonies from 6 to 16 November 2010 (one month before the storm). Subsequent counts on 14 December revealed that 90 chicks remained within these study colonies after the storm, a failure rate of 97%. Opportunistic observations and a crude assessment of the remaining colonies at Steeple Jason revealed that, as with Beauchêne Island, the storm-related impacts were greatest in the lower-lying coastal areas of the island. Some colonies, including two of the study colonies, experienced 100% breeding failure, whereas others were little affected. Overall, we estimate that roughly 15–30% of the Black-browed Albatrosses and Rockhopper Penguin nests at Steeple Jason failed due to the storm, equivalent to a minimum of about 18 200 and 32 100 nests, respectively (Table 1). One of the study colonies contained 852 ringed adult breeders. After the storm 13 (1.5%) of these ringed birds were recovered dead in the colony. In total, 113 dead adult Black-browed Albatrosses were recorded at Steeple Jason Island. Given the spatial variation in the storm impacts and the extent of the colonies surveyed, we do not know what proportion of the total mortality this figure represents.

Although severe impacts of storms and cyclones on breeding seabirds are not unusual (Langham 1986, Schreiber 2002, Hennessey & Flachsbarth 2009), the impacts normally relate to reduced



Fig. 2. Adult Black-browed Albatrosses pinned under boulders at Beauchêne Island after a storm event on 13 December 2010.

TABLE 2
Proportion (%) of total nests that were recorded as active along nine transect counts conducted across the main colony at Beauchêne Island following the storm

| Location of 20 m section, moving inland | Contiguous 20 m section along transect | Direction of survey (south to north) and number of transect; % of total nests active after storm | | | | | | | | | |
|---|--|--|----|----|----|----|-------|----|----|----|----|
| | | South | | | | | North | | | | |
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | |
| ↓ | Coast | a | 16 | 15 | 13 | 21 | 0 | 54 | 85 | 78 | 70 |
| | | b | 44 | 57 | 52 | 23 | 29 | 42 | 83 | 78 | 76 |
| | | c | 73 | 63 | 72 | 50 | 42 | 75 | 83 | 84 | 84 |
| | | d | 72 | 70 | 83 | 79 | 74 | 87 | 84 | 71 | 81 |
| | | e | 71 | 80 | 74 | 81 | 78 | | | | |
| | Inland | f | 62 | 86 | 75 | | | | | | |

reproductive success (as reported here). Reports of storm events killing large numbers of adult seabirds are scarce (but see US Fish and Wildlife Service 2011, Heubeck 1999a, 1999b, Mallory *et al.* 2009). At Beauchêne Island, a minimum of about 300 adult Black-browed Albatrosses and 30 adult Rockhopper Penguins died after sustaining injuries caused primarily by large waves breaking close inshore and inundating sections of the breeding colony. At Steeple Jason Island, at least 113 adult Black-browed Albatrosses died, also due to injuries that we presume were brought about by wave action.

Although we did not observe the impacts directly, there was clear evidence from surveys carried out at Beauchêne Island on 14 and 15 December that waves had inundated large parts of the Arena South colony. The peak intensity of the storm during the darkness of night on 13 December, and early morning of 14 December, likely exacerbated the impacts, as the birds presumably had difficulties evading the waves. At Diego Ramirez Island in Chile, Black-browed Albatrosses have been observed sustaining injuries when they attempt to land in winds stronger than 120 km/h (65 knots; G. Robertson, pers. comm.), so it is possible that some of the deaths and injuries we recorded were due to the strong winds, rather than wave action. However, if this were the case, we would have expected to observe a greater number of dead and injured birds outside of the low-lying areas.

Although the lower-lying areas on the southern and western side of Beauchêne Island were most severely impacted, there was extensive breeding failure in the more elevated southern colonies of the Citadel (Fig. 1). In these colonies, we believe breeding failure was caused by exposure to strong winds and incessant salt spray. On 13 and 14 December large waves breaking against the offshore stacks and cliffs resulted in a constant deluge of salt spray over these colony areas. There were no dead adult birds found in the Citadel colonies, and large numbers of adults were still present, many occupying nests that were empty, or contained crushed eggs or dead, waterlogged, chicks. The impacts of the storm were likely exacerbated by the large numbers of newly hatched chicks, which would have been particularly vulnerable to the cold and wet conditions.

Although the loss of large numbers of eggs and chicks in the 2010/11 breeding season was substantial, these effects need to be considered in the context of high inter-annual variability in breeding success for Black-browed Albatrosses and Rockhopper Penguins (Prince *et al.* 1994, Catry *et al.* 2011, Falklands Conservation, unpubl. data), the two species most severely affected by the storm. Perhaps of greatest concern is the number of adult Black-browed Albatrosses that died as a consequence of the storm. As with other long-lived seabirds, adult survival of Black-browed Albatrosses is a critical parameter for long-term population viability (Catry *et al.* 2011). Although the proportion of the adult population that died following the storm is relatively small, a range of additional and ongoing factors may affect their population and conservation status, the cumulative effects of which need to be considered and assessed. These include fisheries mortality (Sullivan *et al.* 2006, Anderson *et al.* 2011), variability in the availability of prey (Croxall *et al.* 1998) and disease outbreaks (Uhart *et al.* 2004, Falklands Conservation, unpubl. data).

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(FIG). Access to Beauchêne Island was approved by FIG. Work on Steeple Jason Island was permitted by the Wildlife Conservation Society (WCS). We are grateful to Leiv Poncet and Yoann Gourdet for safely transporting the teams to and from Beauchêne Island, and to Michael Clarke for trips to and from Steeple Jason Island. Leigh-Anne Wolfaardt and Rachael Orben are thanked for their assistance with field work and observations at Beauchêne and Steeple Jason islands, respectively. We are grateful to J. Van Franeker, A.E. Burger, A.J. Gaston and an anonymous reviewer for their comments on an earlier version of this manuscript.

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SCIENTIFIC WRITING = THINKING IN WORDS

Lindsay, D. 2011. Collingwood, Australia: CSIRO Publishing. 122 pp., two black and white illustrations. Soft cover: ISBN 978-0-643-10046-6. AU\$29.95.

I do not mind if you think slowly.

I do mind, however, if you publish more quickly than you think.

—Wolfgang Pauli

At some point in their careers, most scientists discover that they're not only hypothesis testers and empirical observers but, in fact, writers. For the lucky, this discovery comes early, in a university science course where the professor assigns papers to be written in scientific paper format. For the less lucky, the discovery comes only after writing dozens of grant proposals and scores of papers, including rejected ones. Eventually, most scientists come to agree with Australian author David Lindsay, editors of virtually every scientific journal, and even character actor Stephen Tobolowski that "Science is not science unless you write down what you find."

Easier said than done, of course – which is where this book comes in. If you read nothing but the pulled-out quotations set in large type throughout the book, preferably in order, you will already have a pretty good sample of the fundamental principles of effective scientific communication. In the book's three main sections – "Thinking about Your Writing," "Writing about Your Thinking" (the heart of the book), and "Thinking and Writing Beyond the Scientific Article" – Lindsay explains how to apply these principles in formal journal articles, posters, oral presentations and theses.

Early on, Lindsay sets forth his core message: that a sound, well-structured scientific article "depends on a well-reasoned and clearly stated hypothesis." In the book's first section, Lindsay makes a basic case for why scientists must write and tries to calm scientists' fears that scientific writing is the very antithesis of what they know how to do. On the contrary, he argues: writing a paper is like doing the science itself. Both require planning for results, reasoning, presenting the results, and explaining the results; if you are clear and focused in how you think about your research results, you're in a good place to start writing about them.

In the second section, Lindsay takes you through the divisions of a standard research paper – Introduction, Materials and Methods, Results, Discussion, Summary, and "other bits" – and steps, including editing for readability and style, for getting a paper published. The book's last section offers "ways to cope" with reaching audiences other than readers of journal articles. Each section contains many helpful writing and presentation strategies, from presenting your most important research results first to how to arrange data within a table so that readers can most easily see a meaningful pattern, not just rows of numerals. Perhaps most helpful to the scientist-writer who has managed to write the first draft of a paper is a checklist on "editing for style and fluency" (p. 70).

Despite its load of good advice, helpful checklists, and a downright funny makeover of a poster presentation on piglets (pp. 93–94), I found myself annoyed when reading this book. To be fair, my

complaints center primarily on style rather than substance. For one, I find the analogy between an article's soundness and a well-reasoned hypothesis singularly unhelpful, particularly for marine ornithologists, who seldom base their research on conventional experimental hypotheses. Lindsay is really saying that an article should give its readers some reason to care about the topic: What are you telling me? Why should I care? Why would I keep reading? In other words, what's the point? I wish he'd just said that, instead of "So, there is little doubt that no other single statement in your paper is as important as the hypothesis . . . whatever you call it" (p. 24).

For another, Lindsay buries at the end of "Writing about Your Thinking" (pp. 64–70) the best writing advice for any profession: write in a way that matches how a reader reads. This advice comes from research in reader perceptions that was lucidly explained for scientist-writers in a 1990 article in *American Scientist* by George Gopen and Judith Swan; this article should be required reading for every scientist. The essence of the advice is that readers grasp information best when it begins with something they already know and builds bridges from old information to new information. In a piece of writing, this old-to-new principle means that every word needs to link to previous words within a sentence, which in turn needs to link directly to the next sentence and subsequent sentences in the same paragraph, which needs to link to the next paragraph and the next, and so on. These linkages build coherence, and, without them, readers lose their way fast.

My other complaint has to do with punctuation, usage and style. Editors are notorious for arguing over such matters, and I'm no exception; moreover, as a scientific and policy editor following American rules of punctuation, I may trip where Australian and Commonwealth readers would not. Still, I was annoyed by commas at every turn of phrase, as if dispensed from a shaker, even between subjects and verbs ("Despite the best of intentions, complying with the techniques of using size and position to convey impact vicariously, may not be always possible" [p. 44]). As this example illustrates, the author's own prose doesn't always float weightlessly off the page either. And why do so many sentences start with the tiresomely indirect "There is" or "There are" and contain so many variants of the verb "to be"? What happened to lively, vivid verbs and simple declarative sentences? This book is devoid of the love of language exemplified in so many other books on writing – even scientific writing.

All in all, though, this book is a handy guide for scientists anywhere in their careers who have not consciously recognized the positive feedback loop between thinking about science and writing about it. Writing is rarely easy for anyone, and it's never too early or too late to learn.

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SEABIRD ISLANDS: ECOLOGY, INVASION, AND RESTORATION

Mulder, C.P.H., Anderson, W.B., Towns, D.R. & Bellingham, P.J. (Eds.). 2011. Oxford, UK: Oxford University Press. 492 pp., 38 black and white illustrations. Hardcover: ISBN 978-0-19-973569-3. US\$79.95.

Many of the first island eradications of introduced predators and herbivores were initiated to save critically endangered species, often but not always seabirds. Throughout the last 40 years, the number of eradication attempts steadily grew and became more ambitious, with larger and larger islands successfully tackled. The New Zealanders pioneered most of the early island eradication techniques on islands around their homeland and in the subantarctic. By the 1990s, numerous islands around the globe were having non-natives removed, with a growing trend towards saving populations of seabirds rather than critically endangered seabird species, which in most cases had already been accomplished.

This trend continues today, now with global prioritization of target islands. Eradication attempts are becoming increasingly bolder and often more controversial, let alone exponentially more expensive. Early eradication efforts were sometimes hell-bent on succeeding, with little or no consideration of potentially disastrous ecosystem-level consequences. Lessons are being learned, however, and more caution is being exercised in planning eradication programs.

This book is not about seabirds – it is about the ecology of the islands they inhabit. In the process of discussing relevant ecological systems, the authors reiterate some facts we already know: that introduced predators are bad for seabirds, that seabirds play an important role in island ecosystems, and that public involvement is critical for eradication program success. Much of this could be considered a primer for seabird conservation, but the book contains important information well beyond this. The editors note that the book (three sections with 13 total chapters) is likely the first ever to address the big picture regarding critical interactions of seabirds with other island biota, and vice versa. They note that eradications must ultimately consider consequences for all island species and remind us that ecosystem restoration must be the ultimate goal.

The first section of the book deals with the natural history of seabird islands and details the role that seabirds play in their overall ecology.

The second section compares seabird island ecosystems around the globe, with the intent of determining which characteristics are common to all or, in some cases, common to certain geographically situated island settings, such as temperate, tropical or cold climate areas. The section also contains a chapter discussing indirect effects of introduced predators on seabird islands, an often-overlooked subject.

The third section of the book focuses on the restoration of seabird islands. Many lessons learned are discussed, and, perhaps more importantly, cautionary advice is given regarding the potential pitfalls of future eradication efforts. One of the key points of this section is that careful forethought and wide planning collaboration are essential. Too often, eradications have been rushed or conducted under a cloak of darkness and have ultimately failed. As the stakes for larger and more visible eradications and restorations increase, these important lessons cannot be ignored. Another volume with detailed case studies of failed eradications, or of unforeseen negative consequences of successful eradications, would be an extremely useful sequel.

There are minor editorial inconsistencies in the book, among which are missing captions (Figure 2.1) and inevitable typographic errors associated with using spell-checking utilities rather than conducting careful editorial review. These minor shortcomings do not detract from the value of this book. A less obvious but very useful value of the book is the extensive literature cited for each chapter.

This book should be mandatory reading for students who endeavor to become involved in seabird conservation or conservation research. It is indeed the current starting point for such learning. Above and beyond that, anyone already involved in island restoration on any level needs this book and the information contained therein.

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SHIFTING BASELINES: THE PAST AND THE FUTURE OF OCEAN FISHERIES

Jackson, J., Alexander, K. & Sala, E. (Eds.). 2011. Washington, DC: Island Press, 312 pp., figures. Hardcover: ISBN-10: 978-1-61-91-000-1. US\$70. Paperback: ISBN-13: 978-1-61091-000-9. US\$35.

In 1995 the eminent fisheries scientist Daniel Pauly observed that “each generation of fisheries scientists accepts as a baseline the stock size and species composition that occurred at the beginning of their careers, and uses this to evaluate changes” (Pauly 1995). Because fishing has depleted stock after stock, there has been a ratcheting down of that baseline from generation to generation – “a gradual accommodation of the creeping disappearance of resource species, and inappropriate reference for evaluating economic losses resulting from overfishing.”

Daniel Pauly’s now-famous shifting baseline syndrome is an interesting psychological and sociological phenomenon, but it wouldn’t exist without the serial depletion of resources, loss of biodiversity and wholesale transformation of ecosystems around the world. *Shifting Baselines: The Past and the Future of Ocean Fisheries*, edited by marine ecologists Jeremy B.C. Jackson and Enric Sala, and historian Karen E. Alexander, does not explore the syndrome but rather its drivers and is excellent background for anyone studying seabirds and their prey. The book addresses four aspects of the underlying problem: 1) the magnitude of human-caused depletion of fisheries, 2) the trajectories and tempo of the depletion, 3) documentation of the cause and effects and 4) use of this knowledge to “ameliorate the degradation.”

In the Introduction, Jackson and Alexander point out that the depletion of resources is not strictly a recent phenomenon. Historical documents have shown that the global depletion of fish began in the 15th century with the growth of the great maritime empires, and anthropological data have demonstrated the depletion of coastal resources as early as 10 000 years ago. They argue that, much as the expansion of humans out of Africa, which led to the colonization of every continent (except Antarctica) by the end of the last ice age, resulted in the extinction of the majority of large animals on those continents, the last few centuries have seen a similar trend in the oceans. They suggest that our baseline has been shifting for centuries and millennia, from which an inescapable conclusion is that we have only a fuzzy idea of what natural systems should look like. They caution that we need to understand the long-term pattern of degradation and not get distracted by short-term change.

Seabird ecologist-turned-ocean writer Carl Safina makes the case in the first chapter for extending our baselines back in time – “in nature conservation the past is the only rational guide to a better future” and suggests that we have so thoroughly transformed “every realm of nature” that, as we seek to understand the impact of our actions, the past is often the only control left.

Fisheries economist Rashid Sumaila and Daniel Pauly then systematically and concisely describe the depletion of fisheries and failures of governance and management around the world – what they call the “March of Folly”: the deliberate, institutionalized pursuit of overfishing for financial gain with full knowledge that it would lead to depletion and unsustainable resource extraction. They conclude by offering approaches that hold promise of an alternative, sustainable pathway.

Alex MacCall (Chapter 4), world expert on forage-fish population dynamics, reminds us that “sardine (*Sardinops* spp) and anchovy (*Engraulis* spp) populations around the world have exhibited extreme fluctuations, often varying a thousand-fold in abundance from one decade to the next.” Those fluctuations are likely inherent in the biology of these species in a highly variable environment subject to large shifts in oceanographic conditions on a decadal timescale. And, of course, those fluctuations have had devastating consequences for their predators – fish, squid, seabirds, marine mammals and humans. MacCall and David Field and colleagues (Chapter 5) use the extreme fluctuations in forage-fish populations – sardines and anchovies in the California Current and anchoveta in the Humboldt Current – to illustrate the difficulty of distinguishing the effects of fishing and other human activities from large-scale oceanographic shifts, or, more accurately, their relative contribution to the population dynamics of these species. While it may have been tempting at one point to ascribe the collapse of sardines in California or anchoveta in Peru to overfishing, we now know that such collapses in modern times are mostly likely the result of declines in ocean productivity coupled with excessive exploitation rates. The picture they describe suggests that, in this case, the shifting baseline syndrome effect is likely swamped by these large-scale dynamics operating on a similar scale. Field and colleagues note that changes associated with the warming of the planet complicate the problem and that much of our scientific knowledge of marine ecosystem dynamics has been acquired during a period of intense exploitation and depletion as well as disruption due to ocean climate change, further complicating the already-difficult problem of characterizing the original baseline.

Thomas Huxley famously claimed in 1883 that “probably all the great sea fisheries, are inexhaustible; that is to say, that nothing we do seriously affects the number of fish.” While the history of fishing has shown that Huxley seriously underestimated our capacity to exploit natural resources, present-day scientists have not been immune to similar miscalculations. Maritime historian W. Jeffrey Bolster and colleagues (Chapter 6) remind us that “only a generation ago marine scientists, fishery managers, and maritime historians shared the popular assumption that diminished fish stocks and damaged marine ecosystems were lamentable artifacts of the late twentieth century, of synthetic filaments, fish finding sonar, and electronic navigational systems.” In other words, although they knew that Atlantic cod had been subject to industrial fishing for hundreds of years, they felt it “unlikely that historic sailing fleets could have depleted naturally abundant fish populations with simple hooks, hemp line, and handmade nets,” and yet they did. Bolster and colleagues point out that “by 1675, there were reportedly 440 boats and about 1,300 men fishing the coast between Boston and eastern Maine, producing over 6 million pounds of dried salt cod annually.” A careful extraction of catch data from mid-19th century logbooks showed that the abundance (biomass) of cod on the Scotian Shelf then was likely three orders of magnitude greater than it has been in the last 40 years. Further, they noted that human exploitation was already driving right whales and the great auk toward extinction. Their historical analysis suggests that the shifting baseline syndrome is so potent that modern-day ecologists

and fishermen, largely unaware of this massive depletion of cod and other groundfish, apparently believed that pre-World War II conditions represented the pristine state or that the appropriate recovery target should be the abundance of the 1980s.

Bolster and colleagues convincingly demonstrate, in the case of cod, the necessity of historical analysis if we are to have any hope of understanding how far we have slid. In Chapter 7, Daniel Vickers, an early America and maritime historian, educates the reader on the difference between the past and history, on what happens when man is added to the ecological equation, and takes the reader through the maze of factors that can distort our view of the past and that must be taken into account by historical ecologists or ecological historians. Bolster and colleagues challenge ecologists to rethink their view of the past: "Integrating the *past* into ecology is one thing; integrating *history* into it is another."

Historical marine ecologist Heike K. Lotze and colleagues (Chapter 8) describe a wide range of disciplines and methods for extracting ecologically meaningful information and data from our history of the past. They conclude with a compilation of data gathered from prehistoric eras to the present that unambiguously show dramatic declines in marine birds, mammals, fish, invertebrates and habitats. Prominent marine population geneticist Stephen R. Palumbi (Chapter 9) uses new methods to address a vexing problem: What was the size of exploited whale populations before whaling? Traditionally, scientists have used whaling records to estimate the number of whales removed from the population. Palumbi offers an alternative method – an analysis of genetic diversity in the gene pool – which suggests pre-whaling population sizes of gray whales three to four times larger than previously estimated from analyses of whaling records. The same comparison for humpback whales yields roughly an order-of-magnitude difference. Palumbi concludes that needed improvements to the methods for reconstructing the past will enhance the diversity of perspectives we have, which is essential to understanding our ecological past.

Renowned fisheries scientist/manager and policy expert Andrew A. Rosenberg and colleagues (Chapter 10) bring the element of management into the picture, pointing out that management and its response to the evolution of fishing practices affects the course of population change, and that managers need to learn from history to avoid the mistakes of others: "The pattern of overfishing has been repeated again and again, as if learning by example were anathema." The fishing practices and management

systems form part of a fisherman's, manager's or scientist's baseline. Rosenberg and colleagues suggest that common sense makes it clear that slight reductions in fishing mortality are not going to return a biomass that is at 5% of what it was 150 years previously in a reasonable timeframe, if at all. They argue that "the shifting baseline paradigm challenges traditional perspectives on governance and scales of observation, refocusing management from single species to ecosystems, and acknowledging the role of humans as key species."

Marine ecologists Enric Sala and Jeremy B.C. Jackson (Chapter 11) illustrate the similarities in the processes that have led to the collapse of fisheries and ecosystems, foremost of which are the economic and social pressures to continue exploitation even in the face of obvious depletion to the point of extinction, and then relate the shifting baseline syndrome to changes on coral reefs around the world. Sala and Jackson propose five fundamental questions that need to be answered: 1) how variable were pristine ecosystems, 2) what are temporal patterns of degradation, 3) what causes collapse, 4) can collapse be anticipated, and 5) will degraded ecosystems recovery to their pristine state?

The well-supported message in *Shifting Baselines* appears to be that, because the restoration of resources and ecosystems requires a target, we cannot identify that target if we do not understand the dynamics of these ecosystems and resources, the history of human impacts and the resulting depletion and degradation. Missing from the book was much consideration of how the syndrome itself distorts our understanding of these processes and how that knowledge could be used to improve our understanding ecological history.

The editors conclude that "recognizing shifting baselines is the first step toward creating new ways of thinking that reintegrate the past, present, and future. Not to dwell on our past failures or to imagine returning to some idyllic pristine state, but to better envision ways of living that can heal the wounds of the natural world while improving people's lives."

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SEABIRD GENIUS: THE STORY OF L.E. RICHDALÉ, THE ROYAL ALBATROSS, AND THE YELLOW-EYED PENGUIN

Peat, N. 2011. Dunedin, NZ: Otago University Press. 288 pp. Black and white and color illustrations. Hardcover: ISBN 1877578118-10. NZ\$47. Soft cover: ISBN 978-1-877578-11-3. NZ\$27.50.

We stand on the shoulders of great seabird biologists; yet in today's modern world few are recalled. Neville Peat has written a long-sought-after biography of the New Zealand seabird researcher Lance Richdale in a loving portrayal of a life well lived and science well executed by a unique husband and wife team. This highly recommended biography reminds us of how in the last century, seabird science began with people motivated by the same marvel we experience today, except that they had no support, with only their drive to pursue the understanding of these marvelous marine creatures. Lancelot Eric Richdale is one such person. The "father" of albatross research, Lance had the great fortune to hail from New Zealand, the seabird capital of the world.

Lance Richdale first taught agricultural subjects and allied science disciplines in remote rural schools before trading them for Dunedin in the South Island of New Zealand. Dunedin is the only city in the world with an albatross colony, and it is thanks to his coming to the city in 1928 (his uncle was there in 1911 as Tairaroa head postmaster) that a Royal Albatross and a Yellow-Eyed Penguin colony exist there today.

Called the "Nature study-man" by his pupils, and known as a teacher and educator, Richdale began studying Royal Albatrosses at Tairaroa Head on the Otago Peninsula in 1936, but first he had to save them. Vandals had been killing birds and smashing eggs, leading Parliament to pass strict trespassing laws in 1942. Their passage had an effect, for five albatrosses fledged after that, and a chick that fledged in 1942 returned to nest in 1948, the first of the Tairaroa Head progeny to breed. Lance said: "The buildup is very slow and may take as long as 15 years." By observing what happened at the colony at Tairaroa Head, we can gain insight into what is happening with albatrosses at other breeding colonies such as the Short-tailed Albatross colony at Midway Island.

Richdale was the first to band seabirds systematically in New Zealand. He began his marking of birds by using a tram conductor's punch on their feet, and then he tried hand-making bands using #16 gauge aluminum. He finally used celluloid rings that he could read via a telescope at 40 m. His banding program for Royal Albatrosses provided information on their longevity, and the most famous testimony was a record made from the re-sighting of a female Royal Albatross ("Grandma"), a founder of the colony, 61½ years post-banding – a record matched only by "Wisdom," a Laysan Albatross at Midway Island. Researchers lost sight of Grandma in 2011 and assumed she died.

Few ornithologists worldwide have ever amassed as much data as Lance Richdale did. His research on Yellow-eyed Penguins started in 1936 and ran until 1954: an 18-year study with 800 visits by him. This work on penguins yielded the four volumes of *A Comprehensive History of the Behaviors of the Yellow-eyed Penguin*. This massive work was at first rejected by publishers because of reduced publishing volume in wartime but was printed and distributed after World War II. This tome added to his many published works in *Emu*, *the Condor*, *Auk*, *Wilson Bulletin*, *Ibis*, and *Bird Banding*.

Richdale pioneered that Holy Grail of seabird biology, long-term data sets. He had no patience for biologists who made remarks not backed up with data. His counter to a statement by R.C. Murphy that albatross parents deliberately starved their chicks for 3 months before fledging was to disprove it by research (Murphy, however, can be forgiven for his error by his statement: "I now belong to a high cult of mortals for I have seen the albatross").

In 1942, Richdale visited the muttonbirding camps (camps where people harvested Short-Tailed and Sooty Shearwaters for food, oil and feathers) and produced a detailed account of the practice. He also reported the decimating effects that feral cats had on the island's avifauna, eventually leading to their control.

Next to nothing was known of the breeding of the *Pterodromas* when he began a study on Whero Island where he and his wife Agnes studied four species. At the end of his research, much was known. It is safe to say Lance would not have achieved his status without Agnes – she typed his notes, drafts and correspondences throughout his career. Years later, at a Cooper's Meeting in Berkeley in 1951, Lance reported that a Sooty Shearwater banded at Whero in 1950 was found in Monterey California in 1957, the first evidence of a transpacific migration.

Richdale was awarded a Fulbright Fellowship at Cornell University and brought along Agnes. They met many different and key people there. The highlight of his sojourn at Cornell was meeting Margaret Nice, the song sparrow maven, whose systematic marking of birds was the first in the US. Lance had earlier claimed the title of the first person in the world to carry out systematic marking. In New York, Lance and Agnes dined with R.C. Murphy, an American ornithologist and curator of birds for the American Museum of Natural History, and his wife Grace, and at Cornell he became acquainted with Rosalie Barrow Edge, a conservationist, essayist and Women's Rights Activist who raised funds to buy Hawk Mountain in 1932 to save raptors from recreational hunters. While overseas in North America, the UK and Europe, Lance and Agnes were entertained by various keystone people of the 20th century, including Alfred Bailey, the American ornithologist and director of the Denver Museum; Olaus Murie, the wildlife biologist; David Lack, the British evolutionary biologist; Robert Storer, the American ornithologist known for his work on systematics and evolution; Bill Sladen, the Antarctic biologist; and Ronald Lockley, the Welsh naturalist and catalyst for the entire British Bird Observatory movement.

By 1972, Lance, in his early seventies, and slowing down after contracting Parkinson's disease, and Agnes retired and relocated to North Island. He continued to write with the co-authors John Warham and Christopher Robertson, who began to develop a keen interest in Lance's legacy and who inspired Neville Peat to write this book.

In 2011 at Tairaroa Head, 75 years after Richdale began his work, the population of Royal Albatrosses numbered about 200 birds and

24 nests. The 500th chick recently fledged, the last hatchling of Grandma. Forty-three percent of all the individuals that have ever nested on the colony (360) have been managed by rangers who have provided artificial incubation, supplemental feedings, fostering and first aid. No seabird colony has had such stewardship for so long.

Richdale's work with the other main species he studied, the Yellow-eyed Penguin, eventually led to the realization of a need for a trust fund, the Yellow-eyed Penguin Trust, that has purchased and set aside beach areas for nesting birds. These two protected areas have made Dunedin the wildlife capital of New Zealand, and it draws in NZ\$100 million a year from eco-tourism.

For his final honors, Dr. Lancelot Eric Richdale received the Queen's medal and the Order of the British Empire in his last year of life, dying on 19 December 1983, a fortnight shy of 84. Agnes lived over another decade and died at 98.

Was Lance a genius? If an infinite capacity for careful research and documentation, as well as an absorbing curiosity, define genius; if exceptional talent for researching seabirds, determination, and tolerance for privation and intensity of focus means genius; then yes, Lancelot Eric Richdale was indeed a seabird genius.

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