

A global assessment of the conservation status of the nominate subspecies of Eurasian Oystercatcher *Haematopus ostralegus ostralegus*

Martijn van de Pol^{1,2*}, Phil Atkinson³, Jan Blew⁴, Olivia Crowe⁵, Simon Delany⁶, Olivier Duriez⁷, Bruno J. Ens⁸, Bernd Hälterlein⁹, Hermann Hötker¹⁰, Karsten Laursen¹¹, Kees Oosterbeek⁸, Aevan Petersen¹², Ole Thorup¹³, Kathleen Tjørve¹⁴, Patrick Triplet¹⁵, Pierre Yésou¹⁶

¹Australian National University, Research School of Biology, Canberra, Australia. martijn.vandepol@anu.edu.au

²Netherlands Institute of Ecology NIOO-KNAW, Department of Animal Ecology, Wageningen, the Netherlands.

³British Trust for Ornithology, The Nunnery, United Kingdom

⁴Joint Monitoring Group of Migratory Birds in the Wadden Sea (JMWB) and BioConsult SH, Germany

⁵BirdWatch Ireland, County Wicklow, Republic of Ireland

⁶Delany Environmental, Rijnbandijk 22, 4043 JL Opheusden, The Netherlands

⁷Netherlands Institute for Ecological Research, Centre for Limnology, Maarssen, The Netherlands

⁸SOVON, Dutch Centre for Field Ornithology, Nijmegen, The Netherlands

⁹Nationalparkamt Schleswig-Holsteinisches Wattenmeer, Tönning, Germany

¹⁰Naturschutzbund Deutschland, Michael-Otto-Institut im NABU, Bergenhusen, Germany

¹¹Institute of Bioscience, Aarhus University, Denmark

¹²Brautarland 2, 108 Reykjavik, Iceland

¹³V. Vedsted, Ribe, Denmark

¹⁴Lista Bird Observatory Research Group, Borhaug, Norway

¹⁵Syndicat Mixte Baie de Somme, Abbeville, France

¹⁶Office National de la Chasse et de la Faune Sauvage, Nantes, France

*Corresponding author

van de Pol, M., Atkinson, P., Blew, J., Crowe, O., Delany, S., Duriez, O., Ens, B.J., Hälterlein, B., Hötker, H., Laursen, K., Oosterbeek, K., Petersen, A., Thorup, O., Tjørve, K., Triplet, P. & Yésou, P. 2014. A global assessment of the conservation status of the nominate subspecies of Eurasian Oystercatcher *Haematopus ostralegus ostralegus*. *International Wader Studies* 20: 47–61.

The nominate subspecies of Eurasian Oystercatchers *Haematopus ostralegus ostralegus* is the most abundant of all oystercatchers and the best studied. The main breeding and wintering areas are centered on the North Sea, but the distribution covers the European Atlantic coast to as far south as Ghana in western Africa. Population size increased strongly from the 1960s to 1990s to over one million birds. Although part of this expansion may have been caused by an ongoing successful adaptation to breeding inland, the main driving forces behind this increase are not well understood. Subsequently, the population size decreased substantially by about 200,000 individuals, mainly due to strong decreases in the Dutch-German-Danish Wadden Sea area. The decrease in the Netherlands is attributed largely to overexploitation by mechanical shell-fisheries; additional factors such as agricultural intensification and reduced eutrophication are likely to also have contributed. The causes for the decreases in Germany and Denmark are less well understood and urgently require further study. In other areas numbers are fairly stable or increasing, but good data for the Nordic countries are lacking. The global (and national) conservation status of *H. o. ostralegus* is classified as of 'Least Concern'. We discuss other threats, such as habitat loss, climate change, hunting and human disturbance, and make prioritized recommendations for research and management.

TAXONOMIC STATUS

Haematopus ostralegus ostralegus is the nominate subspecies, the three other subspecies being *H.o. longipes* (Eastern Eurasia), *H. o. osculans* (East Asia), *H.o. finschi* (New Zealand) (Hockey 1996). Sometimes, two additional subspecies are distinguished *H.o. malacophaga* (Iceland and Faeroe) and *H.o. occidentalis* (United Kingdom and Ireland), but here these are grouped within *H. o. ostralegus* (cf. Sibley

& Monroe 1990). In former times, the Icelandic population was considered a separate subspecies (Timmermann 1935).

LIFE-HISTORY

The Eurasian Oystercatcher, subspecies *ostralegus*, is a medium-sized Oystercatcher of the pied form. Males and females are sexually monomorphic and form long-term



Photo A. Three colour-marked adult Eurasian Oystercatchers in a piping ceremony involving a territorial border dispute between a breeding pair and a neighbour on Schiermonnikoog, the Netherlands. The bird on the right also carries a GPS-tracker (<http://www.uva-bits.nl/species/oystercatcher>) (photo: Jeroen Onrust).



Photo B. Adult Eurasian Oystercatcher feeding an earthworm to a small chick in meadow in the Netherlands, May 2006 (photo: www.vogeldagboek.nl).



Photo C. A fledged chick with its Eurasian Oystercatcher parents in their territory in the polder of Ameland, the Netherlands (photo: Tom Voortman).

socially and mostly also genetically monogamous pair bonds (although polygyny is known to occur, Heg & van Treuren 1998). Pair members together defend nesting and feeding territories and take about equal shares in parental care (Safriel *et al.* 1996) [Photo A], in winter pairs may split up. Individuals show extreme site-fidelity to their summer breeding area. Site-fidelity to winter areas is also strong, but nonetheless individuals can move substantially within estuaries and during severe cold spells individuals might also move between estuaries. In exceptionally harsh winters large groups of birds can move more southerly than normal, resulting in mass migration (Camphuysen *et al.* 1996). Birds seem less prone to migrate *en masse* as a result of food shortages (Atkinson *et al.* 2003). Although most populations are migratory and migrate over longer distances than other Oystercatcher species do, sedentary populations also exist.

Young are semi-precocial and even after fledgling parental care is prolonged for several months (Safriel *et al.* 1996) [Photos B & C]. In the first two years of life juveniles exhibit low site-fidelity. Juveniles are thought to become sexually mature at the age of three, as this is the youngest age of first breeding recorded. Delayed reproduction is common due to habitat saturation (Ens *et al.* 1995, van de

Pol *et al.* 2007) and can be delayed up to the age of 16 years, but most individuals start to breed at the age of six or seven years (Harris 1970, Schnakenwinkel 1970, van de Pol *et al.* 2006a). Natal and breeding dispersal is usually limited to some tens of kilometers, but large scale dispersal (>500km) is known to occur (Dare 1970, Bakken *et al.* 2006).

First year survival (from fledging) is around 0.5 and second year survival about 0.8 (van de Pol *et al.* 2006b). From that age on survival is probably age-independent (Schnakenwinkel 1970) and is around 0.9–0.95 in normal years (Atkinson *et al.* 2003, Oosterbeek *et al.* 2006, van de Pol *et al.* 2010a). Nonetheless, in occasional years with severe winters and/or low food stocks adult survival be as low as 0.7 (Camphuysen *et al.* 1996, Nève and van Noordwijk 1997, Atkinson *et al.* 2003, van de Pol *et al.* 2010a). Maximum recorded lifespan is 43 years (Staav & Fransson 2006), making it one of the longest-lived waders. Generation time is about 11–13 years (Burfield & van Bommel 2004, van de Pol *et al.* 2011). Breeding success is low with *ca.* 0.3–0.5 fledglings per pair per year; usually many years with virtually no reproduction are intermixed with the occasional very good year. Pairs lay up to four eggs and are single brooded, but (multiple) replacement clutches are common as predation risk is high.

Incubation period is 27–28 days; young fledge after *ca.* 35 days. Timing of breeding can vary considerably (by >6 weeks), and can even vary on a small geographical scale (Ens *et al.* 1996, Heg 1999, Yésou *et al.* 2001). There are no known latitudinal gradients in reproductive or survival rates, but birds from the north are usually larger.

HABITAT AND FOOD

H. o. ostralegus breeds in open habitat like saltmarshes [Photos D & E], agricultural arable and grasslands, beaches, dunes, rocky shores, but are also known to breed on roofs in residential areas. Although relatively little is known about the comparative success of breeders in different habitat, it has been suggested that saltmarsh is more productive than agricultural lands and that dunes are very non-productive (Dijksen 1980, Heg 1999, Hulscher & Verhulst 2003). Summer feeding habitat comprises estuaries, rocky shores, beaches and inland fields. In winter they aggregate primarily in estuaries along the coast, where they feed in the inter-tidal zone on sandy mudflats. Sometimes pastures near estuaries are also used in winter, especially when mudflats are inaccessible and/or intertidal food resources are insufficient (Goss-Custard & Durell 1994).

H. o. ostralegus has a wide prey spectrum; mussels *Mytilus edulis* and cockles *Cerastoderma edule* provide the staple food for most *H. o. ostralegus* (Hulscher 1996). In summer Baltic tellin *Macoma balthica* and the polychaetes ragworm *Nereis diversicolor* and lugworm *Arenicola marina* are also important. Locally other bivalve-, gastropod- and crustacean-species may be prominent in the diet, while in (agricultural) fields birds forage on earthworms *Lumbricidae* spp. and leatherjackets *Tipula* spp. Oystercatchers specialize in their feeding behavior, resulting in age and sex-dependent diet differences (Goss-Custard & Durell 1987, Durell *et al.* 1993, van de Pol *et al.* 2010b); different sexes and age-classes use somewhat different wintering areas (Durell & Atkinson 2004, Sutherland *et al.* 1996).

DISTRIBUTION

Currently, breeding and wintering areas barely overlap in distribution with its nearest conspecific *H.o. longipes* that lives in eastern Eurasia. Nonetheless, there is uncertainty about the subspecific status of the small numbers of breeding birds in Belarus, Ukraine, Romania, Bulgaria, Serbia & Montenegro, Albania, Greece, Italy and Turkey. Rusticali *et al.* (2002) considered these birds to be *H.o. longipes*, while Cramp & Simmons (1985) considered them to be *H. o. ostralegus*. Specifically Italian breeding birds are puzzling because they are morphologically closest to *H.o. longipes* in some traits (Rusticali *et al.* 2002), while some of them intermix in winter with *H. o. ostralegus* in France (N. Baccetti, pers. comm.). Here we included the Mediterranean breeding populations into *H. o. ostralegus* (see demarcation line in Fig. 1), but this decision will not affect the global conservation status of *H. o. ostralegus*, because these areas contain less than 0.5% of the total population. However, it should be noted that the underlying evidence for the chosen demarcation is not based on genetic data and is thus somewhat arbitrary.

Breeding areas cover most of the north-western European coastal areas (Fig. 1). In some areas, most notably United Kingdom, Netherlands, Germany and Denmark, breeding



Photo D. Optimal breeding habitat for Eurasian Oystercatchers – the edge of an eroding saltmarsh bordering the intertidal flats on the island of Schiermonnikoog, the Netherlands (photo: Bruno Ens).



Photo E. Nest of Eurasian Oystercatchers on the saltmarsh of Schiermonnikoog, the Netherlands, 30 May 2008 (photo: Bruno Ens).

areas extend up to 400 km inland (Goss-Custard *et al.* 1996). Wintering areas are generally more southerly than breeding areas. Wintering areas include the British Isles as well as most of the Atlantic coast from Denmark as far south as western Africa and can be as far north as Iceland (Fig. 1). Large parts of breeding and wintering areas overlap (Fig. 1), but this does not necessarily imply that birds are resident all year round in these areas; many migrate southward in winter (Fig. 2). In occasional severe winters sizeable number of birds move farther south than normal (mass migration), resulting in an atypical winter distribution. The global historical range is assumed not to have differed strongly from the present range, but data are limited. Notwithstanding, many inland breeding areas were colonized in the second half of the 20th century, caused by a successful adaptation to breeding on moist and well fertilized agricultural grasslands, which became available in this period (Briggs 1984, Goss-Custard *et al.* 1996). Furthermore, in Iceland *H. o. ostralegus* is suggested to have expanded its range between 1900 and 1950 due to climate change (Gudmundsson 1951), a trend which is continuing both during summer and winter (A. Petersen, pers. comm.).



Fig 1. Current breeding (yellow) and wintering (blue) distribution of *H. o. ostralegus*. Areas used for both breeding and overwintering are green (Jonsson 1993, Hulscher *et al.* 1996). The dashed black line depicts the demarcation between *H. o. ostralegus* and *H. o. longipes* used throughout this assessment. Solid black lines depict possible geographical barriers that limit natal and breeding dispersal and thereby the exchange of individuals between (sub)populations.

POPULATIONS: SIZES AND TRENDS

H. o. ostralegus is the most abundant Oystercatcher (sub) species [Photo F]. At the time of writing (2007), the most recent published estimate of midwinter counts (from the 1990s) estimated the total winter population to be around 1,020,000 individuals (Stroud *et al.* 2004). Therefore the official 1% level was set to 10,200 (Wetlands International 2006). However, we show that more recent surveys indicate that the total winter population is much lower nowadays around 817,000 (Table 1, p. 52). The most recently published estimate of the world breeding population is 366,000 pairs (mid-1990s); assuming roughly one-third of all individuals are non-breeding (juveniles and adult floaters) this would amount to 1,098,000 individuals (Thorup 2006). Because no more recent surveys on breeding numbers are available we cannot provide more up-to-date estimates (Table 1), however breeding numbers are likely to have declined similarly in recent years, see later.

Breeding is limited to Europe, with main breeding populations centered on the North Sea, specifically the United Kingdom (30%), the Netherlands (30%), Norway (11%) and Germany (9%) (Table 1). Smaller, but substantial breeding numbers exist in Iceland, Denmark, Sweden, Faeroes, Russia, Finland (all exceeding 1%). Main overwintering populations are in the United Kingdom (36%), northern Germany (21%) and the Netherlands (21%). Smaller but substantial

overwintering populations exist in Ireland (8%), France (6%) and Denmark (3%); no other country reaches the 1% threshold and in total less than 3% overwinter in Africa. Specific areas of international interest (>1% of flyway in winter as defined by the Ramsar convention) are the Wadden Sea (Netherlands-Germany-Denmark), Delta estuary (Netherlands), Morecambe Bay, Solway estuary, Dee estuary, Thames estuary, Ribble estuary, the Wash, Burry Inlet (all United Kingdom), Dundalk Bay (Ireland) and Baie de Mont St. Michel (France) (Delany *et al.* 1999, BTO website). Several of these sites reach the 1% threshold in occasional years, for example when winters are severe (see also Fig. 2, p. 53).

Although conservation issues are often dealt with at the national level, the biological concept of a population is not defined by country-borders, but by the amount of exchange between groups of individuals (e.g. van Treuren *et al.* 1999). Hulscher (1996) suggested on the basis of ring recoveries to distinguish Atlantic (Iceland, Faeroe, United Kingdom, Ireland) and Continental breeding populations. Hulscher (1996) suggested that relatively little exchange of individuals occurs across the North Sea. Although most Icelandic Oystercatchers overwinter on the British Isles (73%) substantial numbers (22%) are found in winter on the Continent (Petersen 1998). Norwegian birds might be another important exception to this rule because many of them overwinter in the United Kingdom (Hulscher 1996, O. Duriez unpubl. data, P. Atkinson unpubl. data; Fig. 2). Furthermore, there might also be some winter migration of British birds to France and Spain, especially in severe winters (Fig. 2). Nonetheless, these ring-recoveries were mainly in winter and therefore do not necessarily imply natal or breeding dispersal (i.e. genetic exchange) but only shows these birds overwinter there (Bakken *et al.* 2006).

Additional subpopulations might exist within the Atlantic and Continental populations (Wetlands International 2000, see also section on 'Taxonomic status'), but strong evidence for this is lacking. Nonetheless, given the typical short natal and breeding dispersal distance of *H. o. ostralegus* it seems plausible that several geographical barriers limit the gene flow and exchange of individuals within the Atlantic and Continental populations (Fig. 1). For example, the 2000km distance between Iceland and Britain-Ireland seems a sufficient barrier to separate these two breeding populations, although they mix freely in winter. This probably also hold for the Faeroese breeding population. Similarly, the channel connecting the North Sea and Baltic Sea might function as a barrier between Scandinavian birds and birds breeding in the Netherlands, Germany and Denmark. Finally, the small Mediterranean breeding populations in Spain, France and Italy might be separated from more northern breeding areas, although they do (at least in part) intermix with other northerly breeding populations in winter (N. Baccetti, pers. comm.). More generally it is important to emphasize that these possible barriers only separate breeding populations (i.e. limit natal and breeding dispersal, but not migration) as individuals from different breeding populations can use the same wintering areas.

Although the Eurasian Oystercatcher is a well studied species, data on long-term population trends are limited, especially before the 1980s. During the 20th century, total population size probably increased strongly, possibly as a result of its adaptation to breeding in a variety of agricultural land types which opened up vast areas of new inland habitat (Meltotte 1993, Goss-Custard *et al.* 1996). Breeding numbers are thought to have increased from the 1980s to the 1990s from an estimated 214,000–291,000 (Goss-Custard *et al.*



Photo F. A flock of roosting Eurasian Oystercatchers on the mud flats of Ameland, the Netherlands, during winter (photo: Tom Voortman).

1995, Hulscher 1997) to about 309,000–424,000 (Thorup 2006). Similarly, in the 1980s the world population in winter was estimated at 874,000 (Rose & Scott 1997) while in the mid 1990s this was estimated to have increased to 1,020,000 (Stroud *et al.* 2004). From 1990s to 2000s the total population size has decreased substantially by about 200,000 to 817,000 birds (Table 1), a result of the strong recent declines in the Dutch and German Wadden Sea (see next section). Good quality data on recent local trends are available for only a limited number of countries, but these largely include the most important breeding and wintering areas. In the United Kingdom breeding numbers have increased substantially over the last century, both in coastal as well as inland populations (Goss-Custard *et al.* 1996). Subsequently, breeding numbers decreased by 12% from 1994 to 2005 (Breeding Birds Survey UK; Fig. 3, p. 54). Wintering numbers in the United Kingdom (excluding Northern Ireland) increased from the mid 1970s up to the mid 1990s after which there has been a slight decrease of numbers, but the population is still larger than in the 1970s and seems to have stabilized (Rehfishch *et al.* 2003; Fig. 4, p. 54). In Ireland (including Northern Ireland) winter estimates doubled (possibly partly due to methodological issues) from 30,000–35,000 in the 1970s to about 70,000 in the 1980s and 1990s and have remained fairly constant since 2000 at about 65,000 - 68,000 (Crowe *et al.* 2008; Fig. 4). These birds are considered to be mainly Icelandic, Faeroese and also Scottish breeding birds or juveniles (Wernham *et al.* 2002). About half of these birds are likely to be Icelandic with an estimated 45,000 birds in the population (Gunnarsson 2009) and about 33,000 wintering in the UK. For Iceland and Faeroes no good data on recent trends are available (but see Jóhannsson & Guðjónsdóttir (2009) for a substantial region in north-west Iceland).

In the Netherlands both wintering and breeding numbers increased strongly between the 1960s and the 1980s and after a stable period in the 1980s declined between 1990 and 2003 (Blew *et al.* 2007; Figs. 3 & 4). The decrease in breeding numbers since 1990 has been over 3% per year, but nonetheless numbers are still larger than in the 1970s. In

Germany, breeding trends are similar to the Netherlands with a decline since the mid-1990s of more than 3% per year (Blew *et al.* 2007, Hötker *et al.* 2007; Fig. 3). In the Danish part of the Wadden Sea breeding numbers also strongly declined from 1996–2006 (Thorup *et al.* 2006; Fig. 3), however wintering numbers seem to be more stable there (Blew *et al.* 2007; Fig. 4). In total the winter estimates in the international Wadden Sea have decreased from almost 500,000 to 300,000 in the period 1987–2003. In France overwintering numbers in mild winters have gradually doubled from 1977 to 1997 (Triplet & Maheo 2000; Fig. 4). This increase is thought to have resulted from birds choosing to overwinter in France instead of the Wadden Sea and Delta area. However, the increase in France can only account for up to 10–20% of the total decrease in the Wadden Sea area. In cold winters the number of overwintering birds in France can be much higher due to the large influx of birds from more northerly areas (e.g. 1987 and 1997 in Fig. 4). Since 1997 numbers have stabilized in France, probably caused by a succession of mild winters.

In Norway Oystercatchers are thought to have increased over the last century (Hogstad & Øien 2001). Inland breeding seems to be a more recent phenomenon with breeding areas now up to 100 km inland. In recent decades breeding numbers were estimated to be 40,000 birds in 1979 (Kålås & Byrkjedal 1981) and 30,000–50,000 in the mid-1990s (Bakken *et al.* 2006). However, these later estimates were not based on new survey data and only the range of the estimate was adjusted to account for uncertainty as these estimates were based on counts in a small area that were extrapolated for the rest of Norway. Melfoite *et al.* (2006) stated that Norwegian breeding birds make up the majority of oystercatchers seen moving along the west coast of Denmark on autumn migration. Migrating numbers there were relatively stable from 1964 until the early 1990s and thereafter there has been a large decrease with only half the numbers observed on migration passage in the 2000s. Melfoite *et al.* (2006) suggested this might indicate that the Norwegian breeding population has decreased substantially.

Table 1. Most recent (mid)winter and summer population estimates as well as conservation status per country. The list of included countries may deviate slightly from other sources, depending on where to draw the demarcation line between *H. o. ostralegus* and *H. o. longipes* (see Fig. 1), but this does not strongly affect global estimates.

Country	Breeding pairs (min-max)	Survey year(s)	Source	Winter numbers	Survey year(s)	Source	Most recent status
Albania	10–15	1996–2002	Burfield <i>et al.</i> 2004	– ²	–	–	?
Algeria	0	–	Delany <i>et al.</i> 2006	70	1990s ⁴	Stroud <i>et al.</i> 2004	?
Belgium	1,050–1,150	2001–2002	Thorup 2006	2,250	1990s ⁴	Stroud <i>et al.</i> 2004	?
Denmark	10,000–14,500	1993–2001	Thorup 2006	26,000	2000–2003	Blew <i>et al.</i> 2007	Least concern
Faeroe Islands	10,000	1995	Thorup 2006	75	–	D. Bloch, pers. com.	?
Estonia	3,000–4,000	1998	Burfield <i>et al.</i> 2004	0	1990s ⁴	Stroud <i>et al.</i> 2004	?
Finland	4,000–5,000	1998–2002	Burfield <i>et al.</i> 2004	– ²	–	–	Least concern
France	1,000–1,200	1998–2002	Burfield <i>et al.</i> 2004	51,200	2002–2006	Wetlands International	Least concern
Gambia	0	–	Delany <i>et al.</i> 2006	50	1990s ⁴	Stroud <i>et al.</i> 2004	?
Germany	34,000–36,000	1996–2001	Thorup 2006	173,000	2000–2003	Blew <i>et al.</i> 2007	Least concern
Ghana	0	–	Delany <i>et al.</i> 2006	31	1990s ⁴	Stroud <i>et al.</i> 2004	?
Greece	30–60	1995–2000	Burfield <i>et al.</i> 2004	– ²	–	–	?
Guinea	0	–	Delany <i>et al.</i> 2006	1,000	1990s ⁴	Stroud <i>et al.</i> 2004	?
–	0	–	Delany <i>et al.</i> 2006	7,100	1990s ⁴	Stroud <i>et al.</i> 2004	?
Iceland	10,000–20,000	1990–2000	Burfield <i>et al.</i> 2004	2,400	2002–2006	Christmas Bird Counts	Least concern
Ireland	2,400–3,200	1988–1991	Thorup 2006	67,620 ³	1999–2004	Crowe <i>et al.</i> 2008	Green list
Italy	125	1999	Thorup 2006	15	1990s ⁴	Stroud <i>et al.</i> 2004	Endangered
Latvia	70–120	1992–1994	Thorup 2006	1	1990s ⁴	Stroud <i>et al.</i> 2004	?
Lithuania	20–40	1999–2001	Burfield <i>et al.</i> 2004	– ²	–	–	?
Mauritania	0	–	Delany <i>et al.</i> 2006	5,084	1990s ⁴	Stroud <i>et al.</i> 2004	?
Morocco	0	–	Delany <i>et al.</i> 2006	2,481	1990s ⁴	Stroud <i>et al.</i> 2004	?
Netherlands	90,000–130,000	1998–2000	Thorup 2006	171,000	2000–2005	SOVON	Least concern
Norway	30,000–50,000	1990	Thorup 2006	460	2002	Norsk Vinterfugle Atlas	Least concern
Poland	20–30	1997–2000	Thorup 2006	0	1990s ⁴	Stroud <i>et al.</i> 2004	?
Portugal	0	–	Delany <i>et al.</i> 2006	893	1990s ⁴	Stroud <i>et al.</i> 2004	?
Russia	3,110–10,052	1990–2000	Thorup 2006	– ²	–	–	?
Senegal	0	–	Delany <i>et al.</i> 2006	6,090	1990s ⁴	Stroud <i>et al.</i> 2004	?
Spain	52–64	1990–2001	Thorup 2006	1,985	1990s ⁴	Stroud <i>et al.</i> 2004	?
Sweden	12,000–18,000	1999–2000	Burfield <i>et al.</i> 2004	50	1990s ⁴	Stroud <i>et al.</i> 2004	Least concern
Tunisia	0	–	Delany <i>et al.</i> 2006	2,035	1990s ⁴	Stroud <i>et al.</i> 2004	?
Turkey ⁶	600–1,200	2001	Burfield <i>et al.</i> 2004	– ²	–	–	?
United Kingdom	98,500–127,000	2000	Thorup 2006	296,500 ³	1995–1999	Rehlfisch <i>et al.</i> 2003	Amber list ⁵
Total pairs	309,987–421,756	1988–2002					
Total individuals	929,961–1,265,268 ¹	1988–2002		817,390	1990–2006		Least Concern IUCN

¹ The number of individuals is estimated as the number of breeding pairs multiplied by three. ² No estimates available, but *H. o. ostralegus* is not expected to overwinter in these areas in substantial numbers. ³ For practical reasons the roughly 20,000 individuals in Northern Ireland are included in the Ireland and not in the United Kingdom estimate. ⁴ Numbers from Stroud *et al.* 2004, who state that these estimates are from the 1990s but do not give exact survey years. ⁵ Due to the importance of the United Kingdom population for global population. ⁶ Numbers from Turkey are not included in totals because they probably are composed of both *H. o. ostralegus* and *H. o. longipes*.

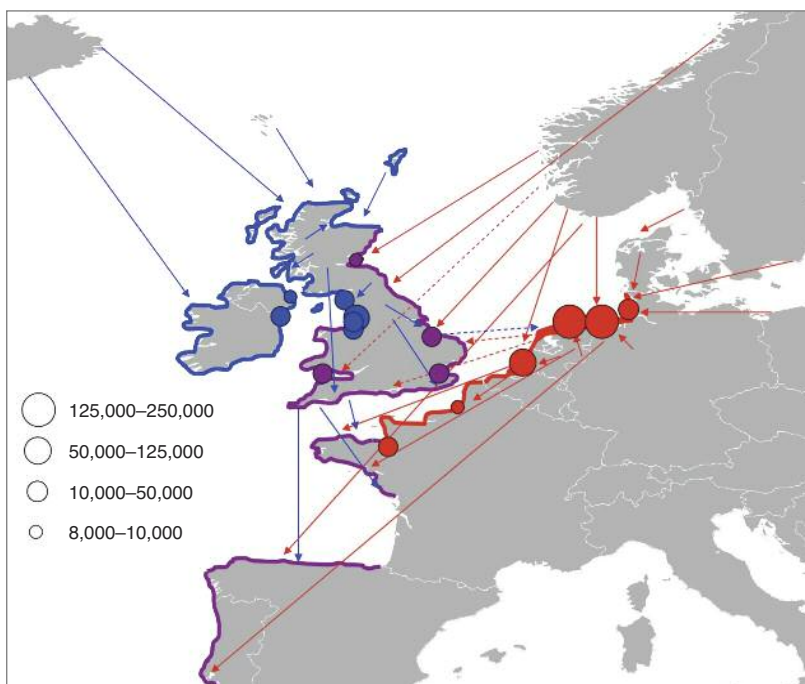


Fig 2. Schematic overview of the main migration routes to overwintering sites for the Atlantic (blue arrows) and Continental (red arrows) breeding population; less common migration routes are depicted by dashed arrows. Wintering areas of Atlantic breeding birds are in blue, while wintering areas of Continental breeding birds are in red; areas where both Atlantic and Continental breeding birds overwinter are in purple. The 16 most important wintering sites are depicted by circles, where the size of the circle depends on the maximum counted numbers at that site in recent years. These 16 key sites hold >75% of the total population; and most reach the official 1% threshold of 10,200 individuals in one or more years (although sometimes only in severe winters).

An alternative explanation is that many Norwegian breeding birds shifted their wintering grounds to the United Kingdom as a result of the low shellfish stocks in the Wadden Sea. However the hypothesis of Meltofte *et al.* (2006) is supported by another study in a Norwegian area of high breeding density (Tautra), where numbers have also approximately halved from 1970s to 2005 (Bollingmo, E. Tjørve & K.M.C. Tjørve, unpubl. data). Clearly new and more accurate estimates from Norwegian breeding numbers are much needed. Good data on trends of breeding numbers in the smaller, but nevertheless substantial, populations in Sweden, Finland & north-west Russia are also not available.

DEMOGRAPHIC AND MECHANISTIC CAUSES OF POPULATION CHANGE

The cause of the global increase in numbers in the 20th century is not well understood, but is usually ascribed to a successful adaptation to breeding inland on newly available (agricultural) grasslands (Meltofte 1993, Goss-Custard *et al.* 1996). However, long-term datasets from the United Kingdom, Netherlands, Germany and Denmark suggest numbers also increased in coastal areas throughout the 20th century (Goss-Custard *et al.* 1996). A between site comparison showed that hatching success was extremely high in the 1940s and 1950s and declined in later decades (Goss-Custard *et al.* 1996). Thus, it remains unclear to what extent numbers have increased because Oystercatchers have adapted to breeding inland, or whether inland breeding was a direct consequence of surplus productivity in coastal areas during most of the first part of the 20th century. Furthermore, little is known about productivity in inland areas and thus we cannot exclude the possibility that inland areas might

actually be sink populations. Declines in numbers seem to be most pronounced in low-quality habitat such as dunes (Ens *et al.* 2003).

Given the life-history of Oystercatchers (i.e. long-lived) it is expected that growth rates are more sensitive to changes in adult survival than in reproduction and therefore one could expect that Oystercatcher population dynamics would be primarily driven by variation in adult survival. However, the available evidence suggests differently. For example, a between site comparison showed that during the increase in numbers over most of the 20th century primarily the hatching success changed over time, while adult mortality was quite constant (Goss-Custard *et al.* 1996). In addition, recent population changes in breeding numbers in the Netherlands also seem to be largely driven by changes in reproduction rather than by changes in juvenile or adult survival (Hulscher & Verhulst 2003, van de Pol *et al.* 2006b). More specifically, in one population the decline in reproductive output was mainly caused by a reduced egg survival, probably as a result of poor food stocks (van de Pol *et al.* 2006b).

It is thought that the strong recent decrease in the Netherlands was ultimately caused by the large scale removal of the main prey species (mussels and cockles) by mechanical shellfisheries (see Main threats section). Food availability affects juvenile and adult survival, but primarily in cold winters. Furthermore, poor food stocks also reduce the body condition of birds in mild winters, which probably negatively affect their reproductive success as well (Heg 1999). In addition to shellfisheries changes in agricultural practices (mowing regimes) might have also reduced reproductive output, especially for inland breeding birds (Hulscher & Verhulst 2003). The causes of the large declines in the German and Danish Wadden Sea are not well understood & require further investigation.

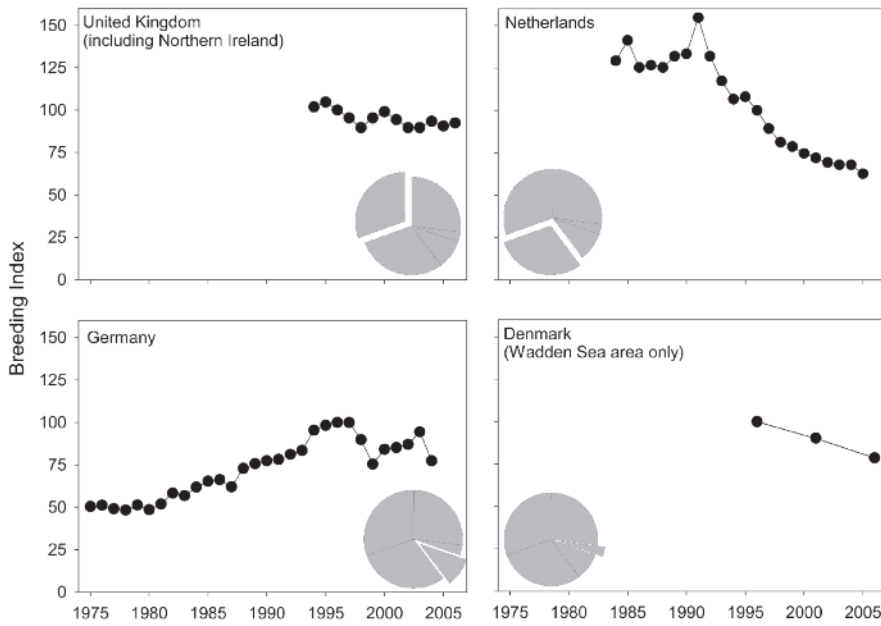


Fig 3. Changes in breeding indices over the last three decades for the years that accurate estimates are available (the year 1996 is set to 100). The size of the extracted slice in the inset pie chart represents the proportion of the world population that breeds in that country, as derived from Table 1. The four countries presented make up 73% of the world breeding population, however no accurate trend data are available for the breeding areas in Norway (>10% of world population), Iceland, Sweden, Faeroe, Russia and Finland (all >1% of world population). Sources: Breeding Birds Survey UK, SOVON, Hötker *et al.* 2007, Thorup *et al.* 2006.

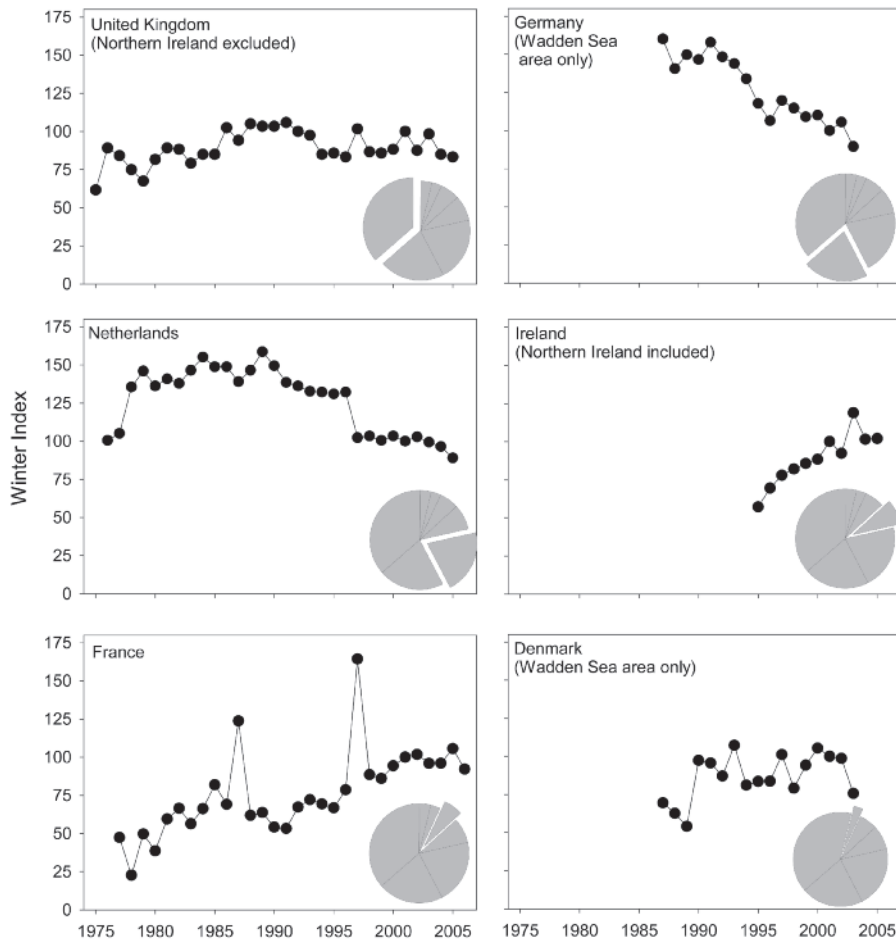


Fig 4. Changes in winter indices over the last three decades for the years that accurate estimates are available (the year 2001 [i.e. winter 2000/01] is set to 100). The size of the extracted slice in the inset pie chart represents the proportion of the world population that overwinters in that country, as derived from Table 1. The six countries presented make up 96% of the world wintering population. For Germany and Denmark indices are available only for the Wadden Sea area; however other areas in those countries are of only minor importance. Sources: British Trust for Ornithology, SOVON, Blew *et al.* 2007, Irish and UK Wetland Bird Surveys, Wetlands International France.

CONSERVATION STATUS

The global status of the Eurasian Oystercatcher was classified as being of Least Concern by the IUCN (Burfield & van Bommel 2004, BirdLife International 2004). This assessment is for the entire *H. ostralegus* species including the *ostralegus*, *longipes* and *osculans* subspecies (*finschi* is retained as a separate species). Nonetheless, the evidence for *H. o. ostralegus* suggests that the nominate subspecies is also of Least Concern, because the recent decreases are outweighed by earlier increases (the IUCN criteria of a >30% decrease in three generations (± 33 years) is far from being reached). The classification of the combined three subspecies of Eurasian oystercatcher by IUCN has an undesirable drawback. Namely, the nominate subspecies is by far the most abundant subspecies of Eurasian Oystercatcher (817,000 individuals), therefore even strong reductions in *H. o. longipes* (estimated at about 100,000–200,000 individuals) or *H. o. osculans* (estimated at about 10,000 individuals) will not result in a change of the status of the whole species when using current IUCN classification. Therefore, we suggest that in the future the IUCN classifies each of the three subspecies of Eurasian Oystercatchers separately.

In most countries the nominate subspecies is also listed as of Least Concern or a local equivalent thereof (Table 1). Only in Italy the species is listed as endangered, mainly because of the low (but stable) numbers. Nonetheless, for the international Wadden Sea area recent estimates are quite concerning, as numbers have declined with almost 40% in the last 17 years (Blew *et al.* 2007). However, recently the main cause of the decrease, mechanical shellfisheries, has been drastically restricted in the Netherlands and thus numbers are expected to improve again (but the recovery time may be on a scale of decades). For the German-Danish parts of the Wadden Sea the causes of the decline are not well understood and the future is uncertain.

THREATS

Mechanical shell-fisheries

Mechanical shell-fisheries are a major threat to *H. o. ostralegus*. The commercial removal of large amounts of edible mussels and cockles has resulted in food shortages for overwintering birds in the Netherlands and locally in the United Kingdom (e.g. Atkinson *et al.* 2003, 2006, Ens *et al.* 2004) [Photo G]. In the Dutch Wadden Sea this food shortage has resulted in mass mortality of *H. o. ostralegus* in winters with cold spells (Camphuysen *et al.* 1996, van de Pol *et al.* 2010a). However, in The Wash (United Kingdom) mass mortality also occurred in normal winters with poor food stocks (Atkinson *et al.* 2003). Interestingly, those years in The Wash with poor food stocks did not trigger mass migration to other estuaries; this suggests that *H. o. ostralegus* is not flexible to adverse food conditions. In addition, poor food stocks also reduce the body condition of surviving birds, which negatively affects their reproductive success (K. Oosterbeek *et al.* unpubl. data) and also increases the number of birds showing aberrant moult patterns (Atkinson *et al.* 2003). Mechanical shellfisheries also indirectly affect food stocks by disturbance of the soil, which makes the sediment less favourable for bivalve species (Piersma *et al.* 2001). Poor food stocks during the breeding season also reduce reproductive output (van de Pol *et al.* 2010a). In the



Photo G. A subadult Eurasian Oystercatcher with a mussel on a mussel bed in the Netherlands, March 2010 (photo: Jan van de Kam).

Westerschelde estuary (Dutch Delta) mechanized cockle fishery is estimated to have reduced the carrying capacity of *H. o. ostralegus* by about 30%, illustrating the huge impact of this industry (Rappoldt & Ens 2006).

Non-mechanical shell-fisheries

Non-mechanical shell fisheries are generally thought to be less detrimental as long as the scale is limited (Stillman *et al.* 2001, Atkinson *et al.* 2006). However there are serious concerns as, for example, removal of even limited amounts of cockles in the Burry Inlet led to reduced numbers of Oystercatchers in spring, a time when they need to increase mass to migrate and come into breeding condition (Norris *et al.* 1998).

Bait-digging

Bait digging, which involves the removal of large worms used in sports-fishing, can result in a strong local reduction of prey (Lambeck *et al.* 1996). Furthermore, bait-digging can severely increase mortality in cockle populations, a main prey species for *H. o. ostralegus* (Jackson & James 1979). Mechanical bait-digging (which involves the use of a boat) results in disturbance of a substantial part of the top-layer of the soil, which may change the composition of the sediment and thereby the composition of the benthic fauna (Lambeck *et al.* 1996). Finally, human presence during manual bait-digging disturbs feeding birds.

Agricultural intensification

Although agricultural intensification has opened up new habitat (fertilization increases food supply), too intense agriculture is detrimental to *H. o. ostralegus*. Frequent mowing of grasslands results in mortality of eggs and chicks; high cattle densities can result in trampling of nests (Beintema and Muskens 1987). While limited fertilization increases earthworm biomass, large amounts of fertilizers (manures) and pesticides tend to reduce soil invertebrate biomasses (including earthworms) (Edwards 1998, Duriez *et al.* 2005). Therefore food availability is likely to be poor in fields when agriculture is intense.

Eutrophication of estuaries

Eutrophication of water is generally decreasing and it has been suggested that this decrease in eutrophication results in lower shellfish productivity (Phillipart *et al.* 2007, Brinkman and Smaal 2004). In addition, in the Dutch Wadden Sea the declining shellfish stocks as a result of declining eutrophication are thought to have caused the fishermen to overexploit the littoral mussel beds, which caused the decline in the oystercatcher populations wintering there (Ens 2006).

Habitat loss

Over the last three centuries vast amounts of intertidal areas have been lost by human activities (Lambeck *et al.* 1996). For example, the building of a storm-surge barrier that closed of the Oosterschelde estuary (Dutch Delta) disturbed the geomorphological equilibrium of a large region. Restoration of the geomorphological equilibrium leads to erosion of the tidal flats. It was estimated that as a result of this erosion and sea level rise, the carrying capacity of the Oosterschelde will decline from 40,000 wintering Oystercatchers around the year 2000 to less than 10,000 in the year 2045 (Rappoldt *et al.* 2006). Nonetheless, with the establishment of protected areas and national and EU legislation future large scale habitat loss seems to be less likely; in fact there are considerable opportunities for habitat creation and restoration (e.g. Eertman *et al.* 2002). At the same time, sea level rise is resulting in increased erosion and habitat loss in some areas. This increased erosion is especially prevalent in the south-eastern parts of the United Kingdom and is happening for various reasons which include glacial rebound, the dynamic response of estuaries to being constrained by artificial boundaries and increased frequency of extreme climate events (Norris *et al.* 2004, Wolters *et al.* 2005). Currently, 0.2–0.7% of intertidal areas are lost each year in the United Kingdom, nonetheless the loss in Oystercatcher numbers may be less than proportional because the areas being lost do not constitute prime breeding or foraging areas for Oystercatchers. In the Wadden Sea autonomous geomorphological processes are expected to largely compensate for sea level rise by increased deposition. Nonetheless, flooding of nesting habitat due to extreme high tides seems to have become much more common in the Dutch Wadden Sea, probably due to climate change (van de Pol *et al.* 2010c).

Climate change

As in many other avian species, lay date has advanced from 1965–2005 in the United Kingdom (by about eight days), probably as a result of climate change (<http://www.bto.org/birdtrends2006/wcroyste.htm>). The population consequences are not known yet, but changes in lay date have been known to impact populations of other migratory species (e.g. Both *et al.* 2006). Furthermore, the population dynamics of the main prey species of *H. o. ostralegus* are sensitive to temperature; warmer winters in the future are expected to reduce the recruitment of bivalve stocks. At the same time cold winters, which can result in mass mortality of birds, are expected to become less common. Overall, the positive effect of warmer winters on survival is expected to outweigh any negative effects of lower food stocks on reproduction (van de Pol *et al.* 2010a, 2011). Climate change may also contribute (at least in part) to habitat loss via sea level rise (see previous section).

Hunting

Over most of its distribution the species is legally protected or not hunted since the mid 1980s. Nonetheless, hunting is still a major source of mortality for the *H. o. ostralegus* overwintering in France, where numbers of shot birds are substantial. From 1993–1999 numbers shot varied between 8,000 and 17,000 birds in severe winters when birds from more northerly estuaries visit France *en masse* (Trolliet 2000). In mild winters numbers shot are smaller (1,800–2,000 birds; Triplet 2000). Recently numbers of hunters are decreasing (P. Triplet pers. comm.) and severe winters will probably become less common due to climate change. Little is known about the impact of hunting on the population level, but its impact may actually be quite substantial on such a long-lived species.

Human disturbance / recreation

Human disturbance to roosting or feeding oystercatchers comes in two forms: deliberate (direct) such as walking towards a flock or shooting at birds and unintentional (indirect) disturbance from agricultural, military or leisure activities such as (dog) walking, surfing, birdwatching, boating, etc. (Lambeck *et al.* 1996, Koffijberg *et al.* 2003). Type of disturbance and estimated degree of threat can influence the extent of a disturbance effect (Kirby *et al.* 1993, E. Tjørve & K.M.C. Tjørve unpubl. data). For example, oystercatchers may become habituated to a non-threatening disturbance during the breeding season (e.g. regular traffic past breeding sites; E. Tjørve & K.M.C. Tjørve unpubl. data). The recovery time after human disturbance is much greater than that of natural disturbances (Kirby *et al.* 1993). As leisure activities on the coast have increased in recent decades (Lambeck *et al.* 1996), the influence of human disturbance on breeding and non-breeding Oystercatchers is likely to have increased. This can make areas previously suitable for roosting, feeding or breeding no longer profitable for *H. o. ostralegus* and can thus confound the problems caused by habitat loss.

Parasites and diseases

Parasites and diseases are still a major unknown. *H. o. ostralegus* can be infected with gut parasites by eating either free-living stages of parasites (notably Helminth spp.) or parasitized intermediate hosts (particularly bivalves and annelids) in both summer and winter (Borgsteede *et al.* 1988, Goss-Custard *et al.* 1993, Norris 1999). Although infestation rates may be high the effects on reproduction and survival and thereby population dynamics, are not known (van Oers *et al.* 2002). Avian influenza has not been found in *H. o. ostralegus* (Munster *et al.* 2007).

Predators

H. o. ostralegus breeding in the Netherlands on mainland saltmarshes are declining and this could be due to an increase in the fox *Vulpes vulpes* population (Willems *et al.* 2005).

Competitors

The Pacific oyster *Crassostrea gigas* is a non-native invasive species that has recently become very abundant in

the Oosterschelde (Dutch Delta) and is increasing in the Dutch Wadden Sea. The species is (with a few recorded exceptions) not eaten by *H. o. ostralegus* nor by any other species and is apparently taking over mussel beds. Furthermore, the Pacific oyster may directly compete for the same food resources as cockles and mussels or even eat their larvae. At the same time it has been suggested that Pacific oyster-beds may facilitate the re-establishment of new mussel beds by offering a solid substrate (Cadée 2007). Thus, although Pacific oysters are potentially a major threat, relatively little is still known about the consequences of this recent invader on Oystercatchers.

RECOMMENDATIONS FOR RESEARCH (IN ORDER OF PRIORITY)

- 1. Mechanistic causes of decline in Germany and Denmark.** We need to gain insight into the strong declines of both the breeding and migratory populations in the German and Danish Wadden Sea. Suggestions are to stimulate ringing studies, look at chick survival and food quality for breeding birds. With regard to migratory birds, local trends should be related to habitat quality or food availability and quality.
- 2. Climate change.** Existing models should be used to quantify the effects of sea level rise and habitat loss for *H. o. ostralegus* on a population scale (e.g. Goss-Custard *et al.* 1995, Sutherland 1996, Rappoldt *et al.* 2004, van de Pol *et al.* 2010c).
- 3. Meta-population structure and population dynamics.** We need to improve our knowledge about the meta-population structure of breeding and overwintering populations in order to better identify which subpopulations exist. Such identification is crucial to investigate which subpopulations are under threat and in which winter or breeding areas the causes for potential declines should be sought. Long-term standardized research using ringing and monitoring on breeding grounds (like in the Netherlands) should be continued and extended to other main breeding sites (United Kingdom, Norway, Germany, Denmark, Faeroe, Iceland). Furthermore, there should be more focus on the role of inland breeding sites and what role they play in source-sink dynamics. Winter-based research should not be neglected and long-term ringing and monitoring on wintering sites, like the Exe, Wash and Delta estuary in the 1980s, should be extended. We lack recent ringing programs in winter from the Dutch Delta, Germany, Denmark, Ireland and France. Winter counts are insufficient to infer the origin of birds, color ringing as well as radio or satellite tracking is needed to better understand movements in winter. For survival analyses Euring data is currently inadequate because this database only includes birds that have been resighted/recaptured/recovered. The inclusion of ringing data of birds that are not recovered into the EURING database is required. An alternative non-exclusive approach is to analyze the genetic structure of different populations to make inferences about the meta-population structure (*cf.* van Treuren *et al.* 1999).
- 4. Recreation.** Further research is required to determine the exact influence of human disturbance on breeding and non-breeding oystercatchers, in addition to determining the potential for habituation to disturbances and possible disturbance thresholds (Goss-Custard *et al.* 2006).
- 5. Demographic causes of population change.** Most studies on Oystercatcher population dynamics have either focused on what happens in winter and how this affects survival, or have focused on what happens in summer and how this affects reproduction. However, there can be important feedbacks between overwinter conditions and reproductive output or between density dependent winter survival and breeder recruitment (Goss-Custard *et al.* 1996, Bruinzeel *et al.* 2006, van de Pol 2006, Duriez *et al.* 2012, Oosterbeek *et al.* unpubli data). The existence of such feedbacks advocates the need for demographic population models which include both the winter and breeding stage. Furthermore, such demographic models can clarify to what extent changes in numbers are primarily caused by changes in reproduction, juvenile or adult survival (van de Pol *et al.* 2010a).
- 6. Skewed sex-ratios and effective population size.** It has been suggested that many of the winter populations are substantially male biased (Durell & Atkinson 2004, Durell 2006), which has important consequences for estimates of effective population sizes. Nonetheless, most of the evidence is based on biometric sex-discrimination, while this method might be biased (van de Pol *et al.* 2009). Furthermore, the mechanism by which sex-ratio might become skewed is unknown. Thus, it is important to sample the sex ratio of fledglings and adults on a large scale using DNA analysis.
- 7. Taxonomic status of Mediterranean breeding populations.** The taxonomic status of the very small Mediterranean breeding (sub)population needs to be resolved in order to allow a more accurate assessment of its conservation concern. Currently evidence is mixed, as in some traits they are morphologically more similar to *H.o. longipes* (Rusticali *et al.* 2002), while their wintering distribution overlaps with *H. o. ostralegus* (N. Baccetti pers. comm.) and their coastal breeding is also typical for *H. o. ostralegus*. A comparison between Mediterranean Oystercatchers, *H. o. ostralegus* and *H. o. longipes* based on genetic structure is needed.

RECOMMENDATIONS FOR MANAGEMENT (IN ORDER OF PRIORITY)

- 1. Shell-fisheries.** Mechanical shell-fisheries are known to negatively affect Oystercatchers in many ways. Sustainable coexistence of mechanical shell-fisheries and Oystercatchers is almost never attained. Furthermore, the creation of small protected areas (by allowing mechanical shellfisheries in only parts of an area) is not a solution to this problem, as *H. o. ostralegus* exhibit high site-fidelity and do not redistribute themselves to protected areas (Verhulst *et al.* 2004). Only restricted non-mechanical shell-fisheries seem to have limited effects on *H. o. ostralegus*.

2. **Hunting.** In France substantial numbers of *H. o. ostralegus* are shot, especially in years with cold winters when thousands of extra birds overwinter in France. Currently, hunting is usually forbidden after a period of several days of continuing frost. However, international agreements should be made to temporarily stop hunting as soon as a cold spell is detected in northern Europe & the interdiction should last one–two weeks after the cold spell to let birds recover their body condition and return to their usual wintering grounds.
3. **Improve surveys.** More accurate and frequent population surveys are needed for the Nordic countries. This may involve the development of new techniques more suitable for these sparsely populated and vast breeding areas. Especially new and better estimates of breeding numbers in Norway (which harbours 11% of the total population) are critical to confirm whether or not this population is decreasing, or has changed wintering areas.
4. **Recreation.** With the ever increasing pressure on coastal zones for building houses and for leisure activities, it is crucial to preserve some areas within the distribution of *H. o. ostralegus* in a relatively undisturbed form as a reference (e.g. by the restriction of human activities in nature reserves).

ACKNOWLEDGEMENTS

We thank John Atle Kålås, Svein-Håkon Lorentsen, Even Tjørve, Ingar Øien and the people at the Norsk Ornithologisk Forening for help with interpreting Norwegian data and literature. We thank Dorete Bloch for information about Faeroese Oystercatchers, Hans Meltofte for references on Oystercatchers migrating through Denmark & Nicola Baccetti for data on recovery patterns of Italian Oystercatchers. Finally, we thank all delegates to the La Rochelle 2007 workshop on ‘Conservation status of Oystercatchers around the world’ for feedback.

REFERENCES

- Atkinson, P.W., N.A. Clark, S.G. Dodd & D. Moss. 2006. Changes in fisheries practices and Oystercatcher survival, recruitment and body mass in a marginal Cockerle fishery. *Ardea* 93: 199–212.
- Atkinson, P.W., N.A. Clarke, M.C. Bell, P.J. Dare, J.A. Clark & P.L. Ireland. 2003. Changes in commercially fished shellfish stocks and shorebird populations in the Wash, England. *Biological Conservation* 114: 127–141.
- Bakken, V., O. Runde & E. Tjørve. 2006. Norsk Ringmerkingsatlas. Stavanger Museum, Stavanger.
- Beintema, A.J. & G.J.D. M. Muskens. 1987. Nesting success of birds breeding in Dutch agricultural grasslands. *Journal of Applied Ecology* 24: 743–758.
- BirdLife International. 2004. *Haematopus ostralegus*. IUCN Red List of Threatened Species.
- Blew, J., K. Günther, K. Laursen, M. van Roomen, P. Südbeck, K. Es-kildsen & P. Potel. 2007. Trends of waterbird populations in the International Wadden Sea 1987–2004 – an update. In: B. Reineking & P. Südbeck, *Seriously Declining Trends in Migratory Waterbirds: Causes-Concerns-Consequences*. Proceedings of the International Workshop on 31 August 2006 in Wilhelmshaven, Germany. Wadden Sea Ecosystem No. 23. Common Wadden Sea Secretariat, Wadden Sea National Park of Lower Saxony, Institute of Avian Research, Joint Monitoring Group of Breeding Birds in the Wadden Sea, Wilhelmshaven, Germany.

- Borgsteede, F.H.M., E. van Broek & C. Swennen. 1988. Helminth parasites of the digestive tract of the Oystercatcher *Haematopus ostralegus*, in the Wadden Sea, the Netherlands. *Netherlands Journal of Sea research* 22: 171–174.
- Both, C., S. Bouwhuis, C.M. Lessells & M.E. Visser. 2006. Climate change and population declines in a long-distance migratory bird. *Nature* 441: 81–83.
- Briggs, K. 1984. The breeding ecology of coastal and inland Oystercatchers in North Lancashire. *Bird Study* 31: 141–147.
- Brinkman, A.G. & A.C. Smaal. 2004. Onttrekking en natuurlijke productie van schelpdieren in de Nederlandse Waddenzee in de periode 1976–1999. Wageningen, Alterra. Alterra report 888.
- Bruinzeel, L.W., M. van de Pol & C. Trierweiler. 2006. Competitive abilities of Oystercatchers (*Haematopus ostralegus*) occupying territories of different quality. *Journal of Ornithology* 147: 457–463.
- Burfield, I. and F. van Bommel. 2004. *Birds in Europe: population estimates, trends and conservation status*. BirdLife International, Cambridge.
- Cadée, G.C. 2007. Vervangen de recente Japanse oesterriffen de vroegere oesterbanken? *De Levende Natuur* 108: 62–65.
- Camphuysen, C.J., B.J. Ens, D. Heg, J.B. Hulscher, J. van der Meer & C.J. Smit. 1996. Oystercatcher *Haematopus ostralegus* winter mortality in The Netherlands: the effect of severe weather and food supply. *Ardea* 84A: 469–492.
- Crowe, O., G.E. Austin, K. Colhoun, P.A. Cranswick, M. Kershaw & A. J. Musgrove. 2008. Estimates and trends of waterbird numbers wintering in Ireland, 1994/95–2003/04. *Bird Study* 55: 66–77.
- Dare, P.J. 1970. The movements of Oystercatchers (*Haematopus ostralegus* Linnaeus) in the British Isles. *Fishery Investigations* 25: 1–137.
- Delaney, S. & D. Scott. 2006. *Waterbird population estimates*, 4th edition. Wetlands International, Wageningen.
- Delany, S., C. Reyes, E. Hubert, S. Phil, E. Rees, L. Haanstra & A. van Strien. 1999. Results from the International Waterbird Census in the Western Palearctic and Southwest Asia 1995 and 1996. *Wetlands International* 54: 1–178. Wageningen, Wetlands International.
- Dijkzen, L. 1980. Enige gegevens over broedseizoen en broedsukses bij scholeksters (*Haematopus ostralegus* L.) in de duinen. *Watervogels* 5: 3–7.
- Durell, S.E.A.L.V.d. 2006. Possible existence of large-scale brood sex-ratio manipulation in Eurasian Oystercatchers. *Functional Ecology* 20: 486–490.
- Durell, S.E.A.L.V.d. & P.W. Atkinson. 2004. Differential distribution of Oystercatchers *Haematopus ostralegus* overwintering on the Wash, east England. *Bird Study* 51: 76–82.
- Durell, S.E.A.L.V.d., J.D. Goss-Custard & R.W.G. Caldow. 1993. Sex-related differences in diet and feeding method in the oystercatcher *Haematopus ostralegus*. *Journal of Animal Ecology* 62: 205–215.
- Duriez, O., Y. Ferrand, F. Binet, E. Corda, F. Gossmann & H. Fritz. 2005. Habitat selection of the Eurasian Woodcock in winter in relation to earthworm availability. *Biological Conservation* 122: 479–490.
- Duriez, O., Ens, B.J., Choquet, R., Pradel, R. & Klaassen, M. 2012. Comparing the seasonal survival of resident and migratory oystercatchers: carry-over effects of habitat quality and weather conditions. *Oikos* 121: 862–873.
- Edwards, C.A. 1998. *Earthworm Ecology*. CRC press, Boca Raton.
- Eertman, R.H.M., B.A. Kornman, E. Stikvoort & H. Verbeek. 2002. Restoration of the Sieperda Tidal Marsh in the Scheldt Estuary, the Netherlands. *Restoration Ecology* 10: 438–449.
- Ens, B.J. 2006. The conflict between shellfisheries and migratory waterbirds in the Dutch Wadden Sea. In: G.C. Boere, C.H. Galbraith & D.A. Stroud (eds), *Waterbirds around the world*, pp. 806–811. The Stationery Office, Edinburgh.
- Ens, B.J., K.B. Briggs, U.N. Safrieli & C.J. Smit. 1996. Life history decisions during the breeding season. In: J.D. Goss-Custard (ed.), *The Oystercatcher: from individuals to populations*, pp. 186–218. Oxford University Press, Oxford.
- Ens, B.J., L.W. Bruinzeel, T. Bult, L. Haanstra, J.B. Hulscher, B. Koks, M. van de Pol, C. Rappoldt, W. Teunissen & S. Verhulst. 2003. Where have the oystercatchers gone? A synthesis of current insights in the population dynamics of Oystercatchers in the Netherlands. *Limosa* 76: 34–38.
- Ens, B.J., A. Smaal & J. de Vlas. 2004. The effects of shellfish fishery on the ecosystems of the Dutch Wadden Sea and Oosterschelde. Final report on the second phase of scientific evaluation of the Dutch shellfishery policy (EVA II). Alterra report 1011, Wageningen.

- Ens, B.J., F.J. Weissing & R.H. Drent. 1995. The despotic distribution and deferred maturity: two sides of the same coin. *American Naturalist* 146: 625–650.
- Goss-Custard, J.D., P. Triplet, F. Sueur & A.D. West. 2006. Critical thresholds of disturbance by people and raptors in foraging wading birds. *Biological Conservation* 127: 88–97.
- Goss-Custard, J.D., A.D. West & S.E.A.L.V.d. Durell. 1993. The availability and quality of the mussel prey *Mytilus edulis* of Oystercatchers *Haematopus ostralegus*. *Netherlands Journal of Sea Research* 31: 419–439.
- Goss-Custard, J.D., R.T. Clarke, K.B. Briggs, B.J. Ens, K.M. Exo, C. Smit, A.J. Beintema, R.W.G. Caldow, D.C. Catt, N.A. Clark, S.E.A.L.V.d. Durell, M.P. Harris, J.B. Hulscher, P.L. Meininger, N. Picozzi, R.P. Prys-Jones, U.N. Safriel & A.D. West. 1995. Population consequences of winter habitat loss in a migratory shorebird. I. estimating model parameters. *Journal of Applied Ecology* 32: 320–336.
- Goss-Custard, J.D. and S.E.A.L.V.d. Durell. 1994. Feeding ecology, winter mortality and the population dynamics of the oystercatchers on the Exe Estuary. In: P.R. Evans, J.D. Goss-Custard & W.G. Hale (eds), *Coastal Waders and Wildfowl in winter*. Cambridge University Press, Cambridge.
- Goss-Custard, J.D., S.E.A.L.V.d. Durell, R.T. Clarke, A.J. Beintema, R.W.G. Caldow, P.L. Meininger & C.J. Smit. 1996. Population dynamics: predicting the consequences of habitat change at the continental scale. In: J.D. Goss-Custard (ed.), *The Oystercatcher: from individuals to populations*, pp. 352–383. Oxford University Press, New York.
- Goss-Custard, J.D. and S.E.A.L.V.d. Durell. 1987. Age-related effects in Oystercatchers *Haematopus ostralegus* on mussels *Mytilus edulis*. III. The effect of interference on overall intake rate. *Journal of Animal Ecology* 56: 549–558.
- Cramp, S. & K.E.L. Simmons. 1985. *Handbook of the birds of Europe, the Middle East and North Africa*. Oxford University Press, London.
- Gudmundsson, F. 1951. The effects of the recent climatic changes on the bird life of Iceland. Proceedings of the International Ornithological Congress 10, 502–514.
- Gunnarsson, T.G. 2009. Iceland – A shorebird maternity unit. In: J. Wilson & M. Carmody. *Shorebirds of Ireland*, pp. 56–69. The Collins Press, Cork.
- Harris, M.P. 1970. Territory limiting the size of the breeding population of the Oystercatcher (*Haematopus ostralegus*) – a removal experiment. *Journal of Animal Ecology* 39: 707–713.
- Heg, D. 1999. Life-history decisions in oystercatchers. PhD thesis, University of Groningen, Groningen.
- Heg, D. & R. van Treuren. 1998. Female-female cooperation in polygynous oystercatchers. *Nature* 391: 687–691.
- Hockey, P.A.R. 1996. *Haematopus ostralegus* in perspective: comparisons with other Oystercatchers. In: J.D. Goss-Custard (ed.), *The Oystercatcher: from individuals to populations*, pp. 251–288. Oxford University Press, New York.
- Hogstad, O. and I.J. Øien. 2001. Endringer i norsk fuglefauna – hva har skjedd i løpet av de siste hundre år? *Vår Fuglefauna* 24: 54–66.
- Hötter, H., H. Jeromin & J. Melter. 2007. Development of populations of meadow waders breeding in Germany – results of a new monitoring approach for scarce bird species. *Vogelwelt* 128: 49–65.
- Hulscher, J.B. 1997. Oystercatcher *Haematopus ostralegus*. In: W. Hagemeyer & M.J. Blair (eds), *The EBCC Atlas of European Breeding Birds: their distribution and abundance*, pp. 246–247. T. & A.D. Poyser, London.
- Hulscher, J.B. 1996. Food and feeding behaviour. In: J.D. Goss-Custard (ed.), *The Oystercatcher: from individuals to populations*, pp. 7–29. Oxford University Press, New York.
- Hulscher, J.B., K.-M. Exo & N.A. Clark. 1996. Why do Oystercatchers migrate? In: J.D. Goss-Custard (ed.), *The Oystercatcher: from individuals to populations*, pp. 155–185. Oxford University Press, Oxford.
- Hulscher, J.B. and S. Verhulst. 2003. The rise and fall of the breeding population of oystercatchers in Friesland 1966–2000. *Limosa* 76: 11–22.
- Jackson, M.J. & R. James. 1979. The influence of bait digging on cockle, *Cerastoderma edule*, populations in North Norfolk. *Journal of Applied Ecology* 16: 671–679.
- Jóhannsson, J.H. & B. Guðjónsdóttir. 2009. The breeding population of Oystercatcher in western Húnaflói, NW-Iceland. *Bliki* 30: 65–69. [In Icelandic with English summary.]
- Jonsson, L. 1993. *Birds of Europe*. Wahlstrom & Widstrand, Stockholm.
- Kålås, J.A. & I. Byrkjedal. 1981. Vadefuglenes hekkestatus I Norge med Svalbard. Proceedings of the 2nd Nordic Congress of Ornithology, pp. 57–74.
- Kirby, J.S., C. Clee & V. Seger. 1993. Impact and extent of recreational disturbance to wader roosts on the Dee estuary, some preliminary results. *Wader Study Group Bulletin* 68: 53–58.
- Koffijberg, K., J. Blew, K. Eskildsen, K. Gunther, B. Koks, K. Laursen, L.M. Rasmussen, P. Potel & P. Südbeck. 2003. High tide roosts in the Wadden Sea: A review of bird distribution, protection regimes and potential sources of anthropogenic disturbance. *Wadden Sea Ecosystem* 16. Wilhelmshaven, Common Wadden Sea Secretariat.
- Lambeck, R.H.D., J.D. Goss-Custard & P. Triplet. 1996. Oystercatcher and man in the coastal zone. In: J.D. Goss-Custard (ed.), *The Oystercatcher: From individuals to populations*, pp. 289–326. Oxford University Press, Oxford.
- Meltofte, H. 1993. Vadefugletrækket gennem Danmark. De involverede bestande, deres træktider og trækstrategier. Dansk Ornithologisk Forening. *Tidsskrift* 87: 1–180.
- Meltofte, H., J. Durinck, C. Nordstrøm & F.F. Rigét. 2006. Trends in wader populations in the East Atlantic flyway as shown by numbers of autumn migrants in W Denmark, 1964–2003. *Wader Study Group Bulletin* 109: 111–119.
- Munster, V.J., C. Baas, P. Lexmond, J. Waldenström, J.M.A. Wallensten, T. Fransson, G.F. Rimmelzwaan, W.E.P. Beyer, M. Schutten, B. Olsen, A.D.M.E. Osterhaus & R.A.M. Fouchier. 2007. Spatial, temporal & species variation in prevalence of influenza A viruses in wild migratory birds. *PLoS Pathogens* 3: e61.
- Nève, G. & A.J. van Noordwijk. 1997. De overleving van scholeksters in de Waddenzee 1980–1994. NIOO report, Heteren.
- Norris, K. 1999. A trade-off between energy intake and exposure to parasites in oystercatchers feeding on a bivalve mollusc. *Proceedings of the Royal Society of London Series B Biological Sciences* 266: 1703–1709.
- Norris, K., R.C.A. Bannister & P.W. Walker. 1998. Changes in the number of oystercatchers *Haematopus ostralegus* wintering in the Burry Inlet in relation to the biomass of cockles *Cerastoderma edule* and its commercial exploitation. *Journal of Applied Ecology* 35: 75–85.
- Norris, K., P.W. Atkinson & J.A. Gill. 2004. Climate change and coastal waterbird populations – past declines and future impacts. *Ibis* 146: 82–89.
- Oosterbeek, K., M. van de Pol, M.L. de Jong, C.J. Smit & B.J. Ens. 2006. Scholekster populatie studies: een bijdrage aan de zoektocht naar de oorzaken van de sterke achteruitgang van scholeksters in de Waddenzee. Alterra Research report. 1344, Alterra, Wageningen.
- Phillipart, C.J.M., J.J. Beukema, G.C. Cadée, R. Dekker, P.W. Goedhart, P.J. van Iperen, M.F. Leopold & P.M.J. Herman. 2007. Impact of nutrient reduction on coastal communities. *Ecosystems* 10: 96–119.
- Piersma, T., A. Koolhaas, A. Dekinga, J.J. Beukema, R. Dekker & K. Essink. 2001. Long-term indirect effects of mechanical cockle-dredging on intertidal bivalve stocks in the Wadden Sea. *Journal of Applied Ecology* 38: 976–990.
- Rappoldt, C. & B.J. Ens. 2006. Scholeksters en kokkels in de Westerschelde; Modelberekening voor de periode 1992–2003 op basis van een verbeterde schatting van de groei en overleving van kokkels in de zomer. SOVON report 2006/06. Beek-Ubergen, SOVON.
- Rappoldt, C., B.J. Ens, M. Kersten & E.M. Dijkman. 2004. Wader Energy Balance and Tidal Cycle Simulator WEBTICS. Alterra report 869, Alterra, Wageningen.
- Rappoldt, C., M. Kersten & B.J. Ens. 2006. Scholeksters en de droogvalduur van kokkels in de Oosterschelde; Modelberekening voor de periode 1990–2045 aan het effect van zandhonger en zeespiegelstijging op het aantal scholeksters. SOVON report 2006/12, SOVON, Beek Ubergen.
- Rehfishch, M.M., G.E. Austin, M.J.S. Armitage, P.W. Atkinson, S.J. Holloway, A.J. Musgrove & M.S. Pollitt. 2003. Numbers of wintering waterbirds in Great Britain and the Isle of Man (1994/1995–1998/1999): II. Coastal waders (Charadrii). *Biological Conservation* 112: 329–341.
- Rose, P.M. & D.A. Scott. 1997. *Waterfowl population estimates*, 2nd edition. Wetlands International report 44, Wetlands International, Wageningen.
- Rusticali, R., F. Scarton & R. Valle. 2002. Taxonomic status of the Oystercatcher *Haematopus ostralegus* breeding in Italy: The eastern limit of *H. o. longipes* has moved 700 km westwards. *Bird Study* 49: 310–313.

- Safriel, U.N., B.J. Ens & A. Kaiser. 1996. Rearing to independence. In: J.D. Goss-Custard (ed.), *The oystercatcher: From individuals to populations*, pp. 219–250. Oxford University Press, Oxford.
- Schnakenwinkel, G. 1970. Studien an der population des Austernfischers auf Mellum. *Vogelwarte* 25: 337–355.
- Sibley, C.G. and B.L. Monroe. 1990. Distribution and taxonomy of the birds of the world. Yale University Press, New Haven.
- Staa, R. & T. Fransson. 2006. EURING list of longevity records for European birds. http://www.euring.org/data_and_codes/longevity.htm
- Stillman, R.A., J.D. Goss-Custard, A.D. West, S.E.A. LeV. dit Durell, S. McGrorty, R.W.G. Caldwell, K.J. Norris, I.G. Johnstone, B.J. Ens, J. van der Meer & P. Triplet. 2001. Predicting shorebird mortality and population size under different regimes of shellfishery management. *Journal of Applied Ecology* 38: 857–868.
- Stroud, D.A., N.C. Davidson, R. West, D.A. Scott, L. Haanstra, O. Thorup, B. Ganter & S. Delaney. 2004. The status of migratory wader populations in Africa and Western Eurasia in the 1990s. *International Wader Studies* 15: 1–259.
- Sutherland, W.J. 1996. Predicting the Consequences of Habitat Loss for Migratory Populations. *Proceedings of the Royal Society of London Series B Biological Sciences* 263: 1325–1327.
- Sutherland, W.J., B.J. Ens, J.D. Goss-Custard & J.B. Hulscher. 1996. Specialization. In: J.D. Goss-Custard (ed.), *The Oystercatcher: from individuals to populations*, pp. 56–76. Oxford University Press, Oxford.
- Thorup, O. 2006. Breeding Waders in Europe: a year 2000 assessment. *International Wader Studies* 14: 1–142.
- Timmermann, G. 1935. Über dem sogenannten atlantischen austernfischer (*Haematopus ostralegus malacophaga* Salomonsen). *Greinar Visindafélags Íslendinga* 1.1: 21–36.
- Triplet, P. 2000. Huitrier-pie. In: G. Rocamora & D. Yeatman-Berthelot (eds), *Oiseaux menacés et à surveiller en France*, pp. 232–233. SEOF, LPO.
- Triplet, P. & R. Maheo. 2000. L'huitrier pie *Haematopus ostralegus* hivernant en France: Evolution des effectifs et modalités d'occupation des l'espace. *Alauda* 68: 109–122.
- Trolliet, B. 2000. Le Vanneau huppé, le Pluvier doré & autres limicoles. In: Enquête nationale sur les tableaux de chasse à tir. Saison 1998–1999, pp. 118–123. Bulletin Technique et Juridique de l'Office National de la Chasse et de la Faune Sauvage.
- van de Pol, M. 2006. State-dependent life-history strategies: a long-term studies on Oystercatchers. PhD thesis, University of Groningen, Groningen.
- van de Pol, M., L.W. Bruinzeel, D. Heg, H.P. van der Jeugd & S. Verhulst. 2006a. A silver spoon for a golden future: long-term effects of natal origin on fitness prospects of Oystercatchers. *Journal of Animal Ecology* 75: 616–626.
- van de Pol, M., B.J. Ens, L.W. Bruinzeel, C. Rappoldt, K. Oosterbeek, D. Heg, M. van der Velde & S. Verhulst. 2006b. What causes the rapid decline in numbers of breeding oystercatchers? In: *State-dependent life history strategies*, pp. 13–39. University of Groningen, Groningen.
- van de Pol, M., I. Pen, D. Heg & F.J. Weissing. 2007. Variation in habitat choice and delayed reproduction: adaptive queuing strategies or individual quality differences? *American Naturalist* 170: 530–541.
- van de Pol, M., K. Oosterbeek, A.L. Rutten, B.J. Ens, J.M. Tinbergen & S. Verhulst. 2009. Biometric sex discrimination is unreliable when sexual dimorphism varies within and between years: an example in Eurasian oystercatchers *Haematopus ostralegus*. *Ibis* 151: 171–180.
- van de Pol, M., Y. Vindenes, B.E. Sæther, S. Engen, B.J. Ens, K. Oosterbeek & J.M. Tinbergen. 2010a. Effects of climate change and variability on population dynamics in a long-lived shorebird. *Ecology* 91: 1192–1204.
- van de Pol, M., L. Brouwer, B.J. Ens, K. Oosterbeek & J.M. Tinbergen. 2010b. Fluctuating selection and the maintenance of individual and sex-specific diet specialization in free-living oystercatchers. *Evolution* 64: 836–851.
- van de Pol, M., B.J. Ens, D.H. Heg, L. Brouwer, J. Krol, M. Maier, K.-M. Exo, K. Oosterbeek, T. Lok, C. Eising & K. Koffijberg. 2010c. Do changes in the frequency, magnitude and timing of extreme climatic events threaten the population viability of coastal birds? *Journal of Applied Ecology* 47: 720–730.
- van de Pol, M., Y. Vindenes, B.E. Sæther, S. Engen, B.J. Ens, K. Oosterbeek & J.M. Tinbergen. 2011. Poor environmental tracking can make extinction risk insensitive to the colour of environmental noise. *Proceedings of the Royal Society: Biological Sciences* 278: 3713–3722.
- van Oers, K., D. Heg & S. Le Drean Quenec'hdu. 2002. Anthelmintic treatment negatively affects chick survival in the Eurasian oystercatcher *Haematopus ostralegus*. *Ibis* 144: 509–517.
- van Treuren, R., R. Bijlsma, J. M. Tinbergen, D. Heg & L. van de Zande. 1999. Genetic analysis of the population structure of socially organized oystercatchers (*Haematopus ostralegus*) using microsatellites. *Molecular Ecology* 8: 181–187.
- Verhulst, S., K. Oosterbeek, A.J. Rutten & B.J. Ens. 2004. Shellfish fishery severely reduces condition and survival of oystercatchers despite creation of large marine protected areas. *Ecology and Society* 9: 17–24.
- Wernham, C.V., M.P. Toms, J.H. Marchant, J.A. Clark, G.M. Siriwardena & S.R. Baillie. 2002. *The Migration Atlas: movements of the birds of Britain and Ireland*. T. & A.D. Poyser, London.
- Wetlands International. 2000. Report on the Conservation Status of Migratory Waterbirds in the Agreement Area. 1–147. Wetlands International, Wageningen.
- Willems, F., R. Oosterhuis, L.J. Dijkzen, R. Kats & B.J. Ens. 2005. Broedsucces van kustbroedvogels in de Waddenzee. SOVON report 2005/07, SOVON, Beek-Ubergen.
- Wolters, M., J.P. Bakker, M.D. Bertness, R.L. Jefferies & I. Moller. 2005. Saltmarsh erosion and restoration in south-east England: squeezing the evidence requires realignment. *Journal of Applied Ecology* 42: 844–851.
- Yésou, P., F. Bernard, J. Marquis, J. Nisser & P. Triplet. 2001. Reproduction de l'Huitrier pie *Haematopus ostralegus* sur l'île de Béniguet, Finistère. *Alauda* 69: 503–512.

APPENDIX 1. OVERVIEW OF RECENT STUDIES AND RESEARCH

H. o. ostralegus is one of the best studied waders in the world. Therefore, this overview is by no means inclusive and only highlights larger projects. Intensive long-term studies on breeding biology have been (or are still being) conducted on islands in Germany (Mellum), the United Kingdom (Skokholm) and the Netherlands (Schiermonnikoog and Texel). Many smaller breeding populations around Europe have been followed less intensively and for shorter periods. There is also a long tradition of long-term research on winter (feeding) ecology in estuaries in especially the United Kingdom (e.g. Exe

and Wash estuary), as well as in France and in the Dutch delta and Wadden Sea. There is a vast scientific literature of the subspecies that covers hundreds of scientific papers. A good collection of references can be found in two publications about *H. o. ostralegus*: Goss-Custard, J.D. 1996. *The Oystercatcher: from individuals to populations*. Oxford University Press, Oxford; and Blomert, A.-M., Ens, B.J., Goss-Custard, J.D., Hulscher, J.B. & Zwarts, L. 1996. Oystercatchers and their estuarine food supplies. *Ardea* 84A: 1–538.

APPENDIX 2. LEGAL STATEMENT

The protection status of *H. o. ostralegus* for each country is given in Table 1 in the main text. In most countries the birds

and their nests are also legally protected, except for France where hunting is allowed. The species is not listed by CITES.

APPENDIX 3. KEY CONSERVATION SITES

Specific areas of international interest in winter (>1% of flyway in winter as defined by the Ramsar Convention) are the Wadden Sea (Netherlands-Germany-Denmark), Delta Estuary (Netherlands), Morecambe Bay, Solway Estuary, Dee Estuary, Thames Estuary, Ribble Estuary, The Wash, Burry Inlet (all United Kingdom), Dundalk Bay (Ireland) and Baie de Mont St. Michel

(France) (Delany *et al.* 1999, www.bto.org). Several of these sites only reach the 1% threshold (10,200 individuals) in occasional years, for example when winters are severe (see also Fig. 2 in the main text). Specific areas of international interest in summer are hard to define as birds are more spread out in space during the breeding season.

