Responses of Great Skuas to climate

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The candidate confirms that the work submitted is his own and that appropriate credit has been given where reference has been made to the work of others.

This work is dedicated to the memory of Andrew Peter Auckland (1976-2000),

whose enthusiasm for seabirds was second-to-none.

He is missed as a friend and colleague.

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Abstract

Forecast climate scenarios indicate global surface temperature to rise by up to 5.8 Celsius degrees (C°) by 2100, although considerably more at high-latitudes. Possible responses of long-lived species, such as seabirds, to climate change are less easy to predict. The Great Skua *Catharacta skua,* adapted for breeding at high-latitudes, may be restricted by heat stress at southern range margins and is an ideal species for which to determine responses to climatic change. A biophysical model constructed for the Great Skua, indicated that the upper limit of the thermoneutral zone was ~10 ˚C and the critical limit, above which evaporative heat loss was no longer sufficient for thermoregulation, was ~20˚C. Within the next 80 years, critical levels will only be exceeded regularly at colonies in arctic Russia or south of current range margins. Field data from Foula, Shetland, in 2002 and 2003, indicated that breeding Great Skuas were currently responding to heat stress by increasing the time spent bathing at the expense of other activities. When foraging conditions were poor, however, bathing was traded-off for extra foraging time and heat was lost by panting. Within Foula, mean operative temperature (a measure of heat stress) at low altitude breeding sites was consistently greater than at higher altitudes, and adult bathing activity was correspondingly more frequent at lower altitudes. Even so, breeding performance (laying date, hatching success and productivity) was not influenced by differences in heat stress exposure, even when adult energy expenditure was high. The flexibility of adult behaviour therefore accommodated current levels of heat stress. Dispersal models indicated that Great Skua breeding populations were still expanding from artificially low levels and, if not restricted by changes in food availability, would spread throughout the coasts of western Scotland and Northern Ireland by 2100. The European Great Skua distribution is probably in equilibrium with climate and future distributions are expected to track changes in food availability. In arctic areas, the timing of spring snow melt constrains the length of the breeding season and was the most probable climatic mechanism restricting seabird breeding distributions. The Great Skua, being primarily limited by pelagic food availability, illustrated the likely impacts of climate change on predominantly sub-arctic seabirds. Uncertainty concerning climatic impacts on marine productivity, combined with interspecific variation in foraging ecology, however, will cause species to respond in individualistic ways to climate change.

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Chapter 1.

General Introduction

1.1 Evidence for recent rapid climatic change

Dramatic changes in global climate over the past century are evident from a variety of sources. For temperature, times-series are reconstructed using tree-ring, coral, ice-core and historical records (Mann, Bradley & Hughes, 1999), for atmospheric composition, long-term records are available from polar and glacial ice-cores (e.g. Etheridge *et al.* (1996)) and direct atmospheric measurements (Keeling *et al.*, 1995). Historical data sets exist for precipitation records (Hulme, Osborn & Johns, 1998) and satellite-borne sensors allow determination of sea- and glacial-ice extent (Houghton *et al.*, 2001). Such sources reveal that mean global surface temperature has increased by 0.6 Celsius degrees (C°) over the past 100 years (Figure 1.1), the extent of snow and ice cover in the Northern Hemisphere has contracted by 10-15 % since the late 1960s and, on average, sea level has risen by 0.2 m worldwide (Houghton *et al.*, 2001). There has also been a concurrent 0.5-1 % per decade increase in overall precipitation for the continents in the Northern Hemisphere, with more than twice that for the tropics, but a corresponding 0.2 – 0.3 % decline per decade for sub-tropical zones (Houghton *et al.*, 2001). Many of these changes are beyond the bounds of natural climate variability (Houghton *et al.*, 2001). Since the end of the last ice, ~10,000 years b.p., global temperatures have risen gradually, although with a rapid increase over the last century (Figure 1.1). Changes in atmospheric carbon dioxide concentrations over the last century have also been rapid, comparable in magnitude to those during the last deglaciation (Sundquist, 1993).

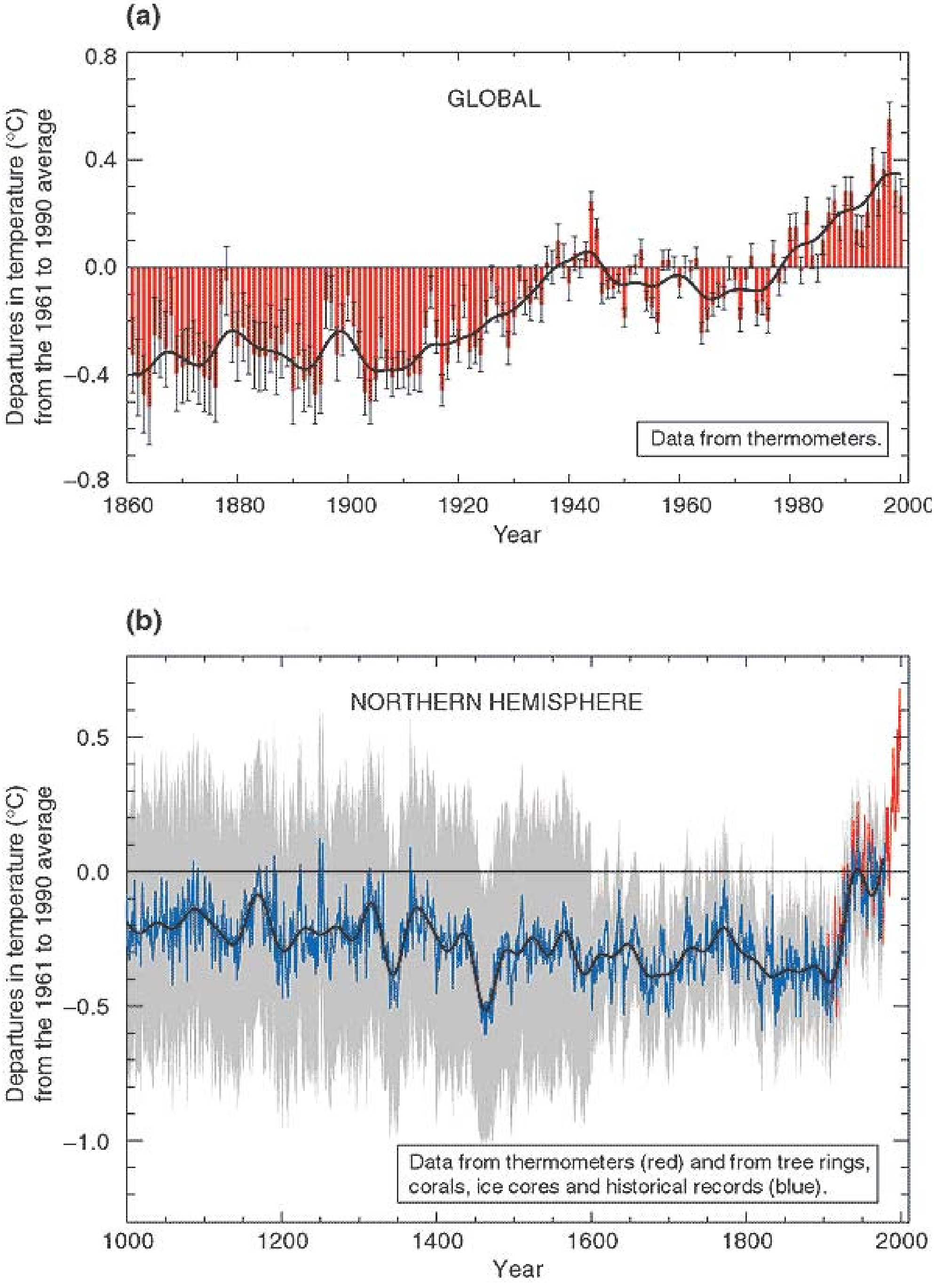

Figure 1.1 (a) Global surface temperature change 1860-2000 and (b) mean annual surface temperature for the Northern Hemisphere over the last 1,000 years. Both figures taken from Houghton *et al.* (2001). 95% confidence limits are given by (a) grey error bars and (b) grey regions.

This is most obvious in the annual concentration of CO_2 in the atmosphere measured at Mauna Loa, Hawaii, that increased from 316.1 ppmv (parts per million by volume) in 1959 to 358 ppmv in 1994 (Figure 1.2) (IPCC, 1996). Greenhouse gases, such as CO_2, all produce considerable positive radiative forcing which tends to warm the Earth's surface (Houghton *et al.*, 2001). Possible climatic changes resulting from such forcing, when compared to those actually observed over the past 50 years, indicate that temperature changes over this period cannot be attributed solely to natural variability or the forcing of stratospheric volcanic aerosols (Tett *et al.*, 1999). However, they can be explained by climatic responses to anthropogenic changes in greenhouse-gas concentrations (Mann, Bradley & Hughes, 1998; Tett *et al.*, 1999).

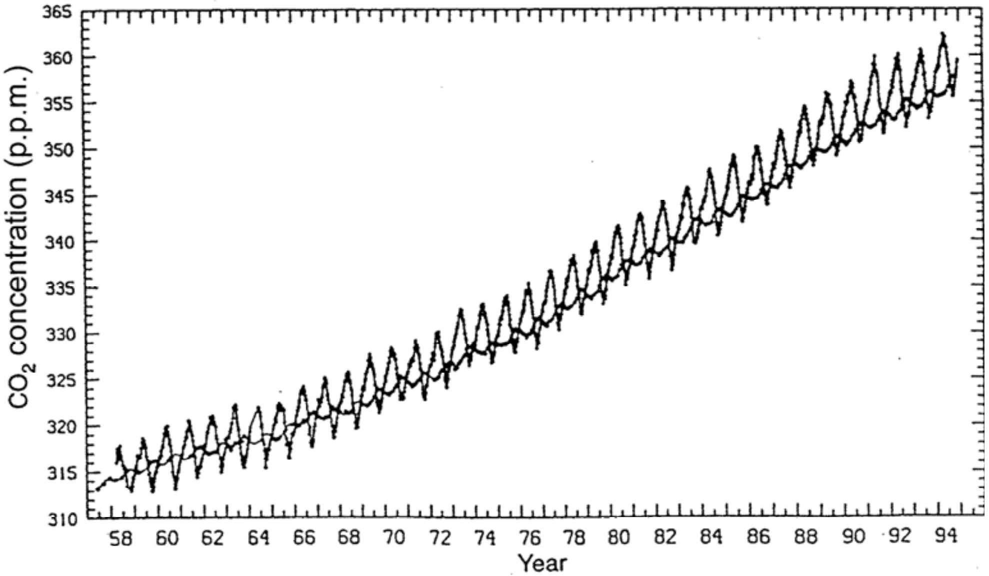

Figure 1.2 Atmospheric carbon dioxide concentrations measured at Mauna Loa, Hawaii (line of high amplitude) and the South Pole (line of low amplitude) from 1958–1996. Data from Keeling(1986), Keeling & Worf (2000).

Regional deviations from global trends, however, can be substantial: climate modeling has indicated that warming at high latitudes is substantially reduced in areas of the North Atlantic and Southern Oceans where deep-ocean mixing occurs (Houghton *et al.*, 2001). At regional scales, indices of large-scale climatic variability have been derived from anomalies in either sea-level temperatures or pressures for different regions, e.g. the Pacific Decadal Oscillation (PDO) for the Pacific Ocean and the Arctic Oscillation (AO) for northern polar regions (Ambaum, Hoskins & Stephenson, 2001; Newman, Compo & Alexander, 2003). In the Pacific Ocean, variability in the PDO is related to frequency and intensity of El Nino Southern Oscillation (ENSO) events (Newman *et al.*, 2003) that strongly influence weather and marine productivity (Barber & Chavez, 1983; Ramusson & Wallace, 1983). In the temperate north Atlantic, climatic variability can be described by anomalies in the North Atlantic Oscillation index (NAOI), calculated from sea level pressure gradients (Hurrell, 1995). Long-term analyses indicate a strongly positive NAOI anomaly since 1980, signifying drier, milder winters in central and southern Europe coupled with lower temperatures and higher precipitation over the north-west Europe (Hurrell, 1995; Wilby, O'Hare & Barnsley, 1997).

1.2 Forecasting future climatic trends

General Circulation Models (GCMs) have been developed to explore how atmospheric circulation may be altered under different climatic regimes (Houghton *et al.*, 2001). These models usually comprise a multi-layered atmosphere overlaid on a spatial grid and incorporate climatic variables such as sea surface temperature (SST), wind speed, water vapour pressure and mean cloud volumes but may also include explicitly modeled variables, such as soil moisture and seasonal solar angle variations (Houghton *et al.*, 2001). Original models provided no information on rates of climate change and were often run until atmospheric carbon dioxide reached equilibrium, commonly at twice the current concentrations (Houghton *et al.*, 2001). Since 1992, GCMs have included components describing rates of change in carbon dioxide concentrations, usually 1 % yr^{-1}, with consequent positive radiative forcing and also negative forcing from other atmospheric components (Houghton *et al.*, 2001). Recent models, such as the UK Meteorological Office's HadCM3 (Wood *et al.*, 1999; Gordon *et al.*, 2000), have also dispensed with 'flux adjustments' (used to restrict models from entering unrealistic states) but still simulate observed atmospheric circulation quite closely (Houghton *et al.*, 2001).

Climatic predictions have been made using GCMs for a range of scenarios over the next 100 years (Houghton *et al.*, 2001). Based on a doubling of global atmospheric CO_2 concentrations by 2100, extrapolated from observed rates of change in atmospheric CO_2, these models indicate an increase in global averaged surface temperature of 1.4-5.8 C° and increases in the frequency and intensity of precipitation (Houghton *et al.*, 2001). Nearly all terrestrial areas are predicted to warm more rapidly than this global average, particularly at high northern latitudes or in the winter months. An increase in the frequency of tropical storms and extreme precipitation events is also predicted (Houghton *et al.*, 2001). Northern Hemisphere snow cover and sea-ice are simulated to decline further over the next 100 years and the Greenland Ice Sheet is predicted to loose mass and contribute to a rise in mean global sea-level of 0.09 -0.88 m by 2100 (Houghton *et al.*, 2001). These predicted rates of climate change are more rapid than any reconstructed for any period within the Holocene, the last ~10,000 years (Huntley, 1995).

1.3 Biological responses to climate change

Responses to recent climate change have been recorded for a wide range of taxonomic groups with diverse geographical distributions (Walther *et al.*, 2002; Moore, 2003; Parmesan & Yohe, 2003; Root *et al.*, 2003). For short-lived or poikilothermic organisms, there is a strong indication of shifts in distribution and abundance (Parmesan *et al.*, 1999; Pounds, Fogden & Campbell, 1999). In contrast, for longer-lived homeothermic taxa current data primarily concern changes in phenology (reviewed in Root et al. (2003)) and breeding success, e.g. Winkel & Hudde (1997). Animals capable of rapid dispersal, such as birds and butterflies, have been able to shift their distributions in response to climatic change (Parmesan *et al.*, 1999; Thomas & Lennon, 1999; Thomas *et al.*, 2001) but other species, particularly long-lived plants, have lower rates of dispersal and may be threatened by extinction as a result of rapidly changing climates (Huntley, 1991; Thomas *et al.*, 2004). Species respond in individualistic ways to climate change (Huntley, 1991) and responses may differ considerably even for closely related species (Warren *et al.*, 2001; Hill *et al.*, 2002) and can be constrained by habitat availability (Hill, Thomas & Huntley, 1999; Hill *et al.*, 2001). Differences in rates of response will lead to changes in the composition of ecological communities and varying susceptibilities of species to extinction (Davis *et al.*, 1998; McCarty, 2001; Walther *et al.*, 2002).

1.4 Susceptibility and responses of high-latitude seabirds to changing climate

Animals living at high-latitudes are adapted to survive and reproduce in cold environments by virtue of their morphology, physiology and ecology (Phillips, Butler & Sharp, 1985; McNab, 2002). Such is the case for resident and migrant seabirds breeding in arctic and sub-arctic regions, that characteristically have high metabolic rates (McNab, 1966; Gabrielsen, Mehlum & Karlsen, 1988; Bryant & Furness, 1995), thick insulative plumage (Furness, 1988) and additional insulative adaptations on their un-feathered extremities (Lustick, 1984; Furness, 1987). Given that climatic warming is expected to be more rapid at high latitudes (Houghton *et al.*, 2001)(section 1.2), such adaptations may cause foraging adults to experience problems of heat-dissipation under forecast climatic regimes (Furness, 1988). To date, no empirical data are available to support this, although the temperate breeding range margins of Great Skuas (*Catharacta skua*) and Arctic Skuas (*Stercorarius parasiticus*) are strongly associated with particular thermal conditions (Furness, 1988).

The sizes and distributions of bird populations are directly influenced by resource availability, particularly food supply, breeding habitat, predation and severe episodic weather events (Newton, 1998). Climatic change can alter the availability of breeding, over-wintering or staging habitats, the size and distribution of prey populations and prevailing weather conditions at all these sites (Huntley, 1995). Seabirds are generally long-lived species with low fecundity and changes in population sizes and distribution will usually lag several years behind changes in resource availability, predation or direct climatic effects (Weimerskirch *et al.*, 2003). Even so, climate has been implicated in many recent changes in the demography of Antarctic and temperate seabird populations (Veit & Hyrenbach, 2001; Croxall, Trathan & Murphy, 2002; Hyrenbach & Veit, 2003; Weimerskirch *et al.*, 2003). In Antarctic areas, changes in the annual retreat of sea-ice have led to a reduction in the survival of wintering Adelie Penguins (*Pygoscelis adeliae*), Emperor Penguins (*Aptenodytes forsteri*) and Snow Petrels (*Pagodroma nivea*) (Croxall *et al.*, 2002), although the proximate causes of increased mortality differ among species. The survival of juvenile Adelie Penguins is reduced during winters with lower extents of sea-ice because of greater distances from roosts to foraging grounds and an increase in susceptibility to predation (Wilson *et al.*, 2001; Ainley, 2002). Reduced krill abundance in warmer waters was the proximate cause of reduced survival of adult Emperor Penguins at Terre Adelie in the late 1970s (Barbraud & Weimerskirch, 2001b). Conversely, survival of adult Snow Petrels was reduced when winter sea-ice was more extensive, probably as a result of concurrent reduction in polynyas, areas of water kept ice-free by currents, that are used by this species (Barbraud & Weimerskirch, 2001b, a). Breeding success of all three species was highest during years of less extensive sea-ice, however, because shorter distances between breeding grounds and foraging areas led to higher provisioning rates of chicks (Croxall *et al.*, 2002), whereas breeding is often deferred during years of extensive summer sea-ice (Barbraud & Weimerskirch, 2001a). Similar impacts of fluctuating sea-ice on seabird species have been observed in Arctic regions (Agler *et al.*, 1999; Gaston, Woo & Hipfner, 2003; Divoky, 2005).

In temperate areas, not dominated by ice dynamics, changes in sea-surface temperatures have been implicated in altered productivity regimes (Reid, 2003) leading to changes in prey abundance at low trophic levels (Reid *et al.*, 1998) and changes in population dynamics (breeding success, survival and incidence of breeding) of seabirds (Montevecchi & Myers, 1997; Thompson & Ollason, 2001; Jones & Hunter, 2002; Durant, Anker-Nilssen & Stenseth, 2003; Harding, Piatt & Hamer, 2003; Inchausti *et al.*, 2003; Grosbois & Thompson, 2005). Changes in food availability are thought to be the major factors affecting numbers of breeding seabirds (Cairns, 1989) and there is some evidence that competition for food resources has shaped the distribution of seabird colonies within the UK (Furness & Birkhead, 1984; Lewis *et al.*, 2001).

The availability of appropriate nesting habitat can also be affected by sea-level or floral change associated with climatic warming (Micol & Jouventin, 2001; Croxall *et al.*, 2002). Changes in vegetation patterns are liable to be most extreme in tundra areas (Huntley & Cramer, 1991), which are important breeding grounds for some seabird species, particularly small skuas (Maher, 1974). Under forecast rates of climatic warming in the Northern Hemisphere, boreal forest regions will probably encroach upon areas of tundra, reducing the extent of breeding habitat available (Zockler & Lysenko, 2001).

Increased competition and predation, resulting from differential rates of spread of individual species, may result from climatic warming (Davis *et al.*, 1998) and changes in the intensity of predation on different seabird species as a direct consequence of climate change is evident in polar regions. For Adelie Penguins, juvenile mortality rates are thought to increase as a result of predation by Leopard Seals (*Hydrurga leptonyx*) when sea-ice extent is relatively sparse (Ainley, 2002). At a breeding colony in arctic Alaska, predation by Tufted Puffins (*Fratercula cirrhata*) on Black Guillemot (*Cepphus grille*) chicks has increased dramatically in recent years ever since adult puffins began to breed at the same colony, most probably because new foraging areas have became available for puffins as a result of progressively earlier seasonal retreat of sea-ice (Divoky, 2005).

Episodic severe weather, such as storms, heavy rain, tornados and heat-waves, can cause up to 90% mortality in some bird populations (Newton, 1998) and 'wrecks' of seabirds can be dramatic during such episodes (e.g. Harris & Wanless (1996)). These weather events can influence survival of seabirds in breeding and wintering areas and can severely reduce breeding success (Schreiber, 2001). Some studies have also linked wind and seasonal storm events to foraging and breeding dynamics of temperate seabirds (Aebischer & Coulson, 1990; Aebischer & Wanless, 1992; Finney, Wanless & Harris, 1999).

1.5 The morphology, taxonomy and ecology of skuas

Skuas are large seabirds of the family Stercorariidae, close relatives of gulls (family Laridae), from which they differ mainly in possessing strong hooked claws, hard scales (skutes) on their legs and a prominent distal nail on the upper mandible (Furness, 1987). All skuas exhibit reversed sexual size dimorphism, with females weighing 11-17 % more than males and often possessing longer wings (Furness, 1987). Skuas are commonly separated into two genera; the smaller *Stercorarius* species with wedge-shaped tails and narrower wings, and the substantially larger *Catharacta* skuas (Furness, 1987). Recent evidence from nuclear DNA supports the placing of all species in a monophyletic group chiefly because of the small genetic distance between Pomarine and Great Skuas (Andersson, 1999; Sangster *et al.*, 2004). It is probable, however, that *pomarinus*

Table 1.1 Classification of the skuas (family Stercorariidae), adapted from Cohen *et al.*(1997) with the modifications of Hamer (2001).

Family	Genus	Species	Sub-species	**Common name (English)**
STERCORARIIDAE	*Stercorarius*	*longicaudus*	*longicaudus*	Long-tailed Skua (western)
			pallescens	Long-tailed Skua (eastern)
		parasiticus		Arctic Skua
	Catharacta	*pomarinus*		Pomarine Skua
		skua		Great Skua
		maccormicki		South Polar Skua
		iönnbergi		Brown Skua
		hamiltoni		Tristan Skua
		chilensis		Chilean Skua
		antarctica		Falkland Skua

originally arose through geographic speciation followed by hybridization with ancestors of *C. skua* (Hamer, 2001). The classification proposed by Hamer (2001) provides the discrimination used throughout this thesis (Table 1.1) because inclusion of all skuas within a single genus *Stercorarius*, as endorsed by Sangster *et al.* (2004), obscures the fact that data on behaviour, feather-lice and mitochondrial DNA all indicate that large skuas and *pomarinus* form one clade and the two smaller skuas another.

Skuas most probably originated in the northern hemisphere where they diverged from the same ancestors as the gulls and are thought to have subsequently colonized the southern hemisphere, eventually to return to the North in the form of the Great Skua (*Catharacta skua*), within the last 500 years (Furness, 1987). All skuas breed at high-latitudes, exceeding 37º (Furness, 1987). *Stercorarius* skuas are mostly restricted in their breeding grounds to the Arctic Circle but both Arctic (*S. parasiticus*) and Long-tailed Skuas (*S. longicaudus*) have a circumpolar distribution (Furness, 1987). Pomarine Skuas (*C. pomarinus*) breed from the Kanin Peninsula in East Russia eastwards through Siberia, Alaska and the Canadian Arctic but are absent from Greenland and across most of Europe (Furness, 1996). All large skuas, with the exception of the Great Skua, breed exclusively in the southern hemisphere, although only the Brown (*C. lönnbergi*) and South Polar Skua (*C. maccormicki*) maintain a circumpolar distribution, the latter breeding at considerably higher latitudes (Furness, 1987). Tristan (*C. hamiltoni*), Falkland (*C. antarctica*) and Chilean Skuas (*C. chilensis*) have a more restricted distribution (Furness, 1987). Breeding Great Skuas are confined to the Western Palearctic either on small islands or remote areas of larger ones, such as Iceland and Svalbard (Snow & Perrins, 1998) (Figure 1.3).

The majority of skua species breed colonially but, although colonies can be extremely dense (up to 200 nests per km^2 for Arctic Skuas on Foula, Shetland (Furness, 1987)), this depends on their diet (Furness, 1987), since those that feed within their nesting territory actively defend larger areas (0.02-0.15 nests per km^2 for Arctic Skuas on the North Slope, Alaska (Maher, 1974)). Incubation for the Great Skua lasts between 26-32 days (Hamer, 2001) but the smaller species have shorter incubation periods, 23-28 days (Snow & Perrins, 1998). The pre-fledging period, from hatching to fledging, is between 40 and 59 days for large skuas (Furness 1987) but only 24-31 for the smaller species (Snow & Perrins, 1998).

Modal clutch size in skuas is two eggs (Furness, 1987), although often a small proportion of pairs in a colony will lay only a single egg (Hamer, 2001). Hatching success is generally 60-70% for all skua eggs, often even higher in Great and Brown Skuas (70-80%) that nest on maritime islands with no nest predators (Furness, 1987; Reindhart, 1997). Skua chicks are semi-altricial and semi-nidifugous (Furness, 1987). Skua chicks are fed by complete regurgitation, the provisioning adult depositing the food on the ground and the chicks consuming it *in situ*, often with the help of the brooding adult if the chicks are very young (Furness, 1987). In colonies with access to abundant food supplies, survival to fledging is very high, but brood reduction may occur when food is limiting (Young, 1963; Lamey, 1995) and overall breeding success may be as low as 8 % in some years (Hamer, Furness & Caldow, 1991). Breeding success is often more variable for South Polar Skuas, because of severe weather (Young, 1963), and Pomarine Skuas, because of variable prey abundance (Maher, 1974). For small skuas nesting in the tundra, eggs and chicks are commonly lost to predatory mammals and birds (Maher, 1974) but predation by conspecifics is very important in large species (Young, 1963; Hamer *et al.*, 1991; Lamey, 1995; Catry & Furness, 1999). For Great Skuas in years of poor availability, adults spend more time foraging and this can lead to territories being left unguarded (Caldow & Furness, 2000) and high chick mortality from conspecific predation (Hamer *et al.*, 1991). Yearly survival of adults is very high and from analyses of ringing recovery data, *Catharacta* skuas appear to have a slightly higher rate of adult survival than the *Stercorarius* skuas (91-4% versus 80-90%) (Furness, 1978; Andersson, 1981; Furness, 1987; Ratcliffe *et al.*, 2002).

Diet and feeding techniques of skuas are extremely variable between individuals, colonies, species and the time of year (Furness, 1987). Pomarine Skuas are lemming specialists during the breeding season (Maher, 1974) but resort to scavenging, kleptoparasitism and predation of small seabirds during the winter months (Furness, 1987). Long-tailed and Arctic Skuas can breed in tundra areas where there are no lemmings at all, exploiting passerines, juvenile shorebirds and even insects during the breeding season (Maher, 1974). Arctic Skuas feed solely by kleptoparasitism of other seabirds during their migration and wintering periods and also when they breed in coastal regions (Furness, 1987). Of the large skua species, only Great and South Polar Skuas catch pelagic prey, sandeels and krill respectively, although the relative importance of these items in the diet varies greatly between colonies (Young, 1963; Phillips *et al.*, 1997). Great Skuas also scavenge behind fishing trawlers (Hudson & Furness, 1988), and this appears to provide a valuable secondary food source for Shetland birds during years of poor sandeel abundance (Furness & Hislop, 1981; Votier *et al.*, 2004). Another common prey item for Great Skuas and other large skuas during the breeding season is other seabirds, taken either by direct predation or scavenging (Furness, 1987). Skuas feeding on burrow-nesting birds or mammals or by scavenging from penguin rookeries commonly hold a breeding territory that overlaps their feeding grounds (Young, 1963; Mougeout, Genevois & Bretagnolle, 1998).

1.6 Examining responses of high-latitude seabirds to changing climates: Great Skuas as a model species

This thesis aims to determine the most probable responses of Great Skuas (*Catharacta skua*) to forecast climatic change and the consequent implications for other seabirds breeding at high-latitudes. Great Skuas have one of the highest conservation values of any breeding British species, with the UK hosting 60% of the world population (Hamer, 2001).

Research over the last 35 years has provided a good understanding of the breeding dynamics of Great Skuas (Hamer, 2001) and detailed records exist concerning the distribution of this species at its southern range margin over the last century (Furness, 1987). Nearly all the Great Skua breeding colonies are currently found within Europe (Figure 1.3) (Furness, 1996; Hamer, 2001) where some of the most detailed climatic records exist (e.g. New *et al.* (1999)). There is also a strong correlation between this distribution and prevailing thermal

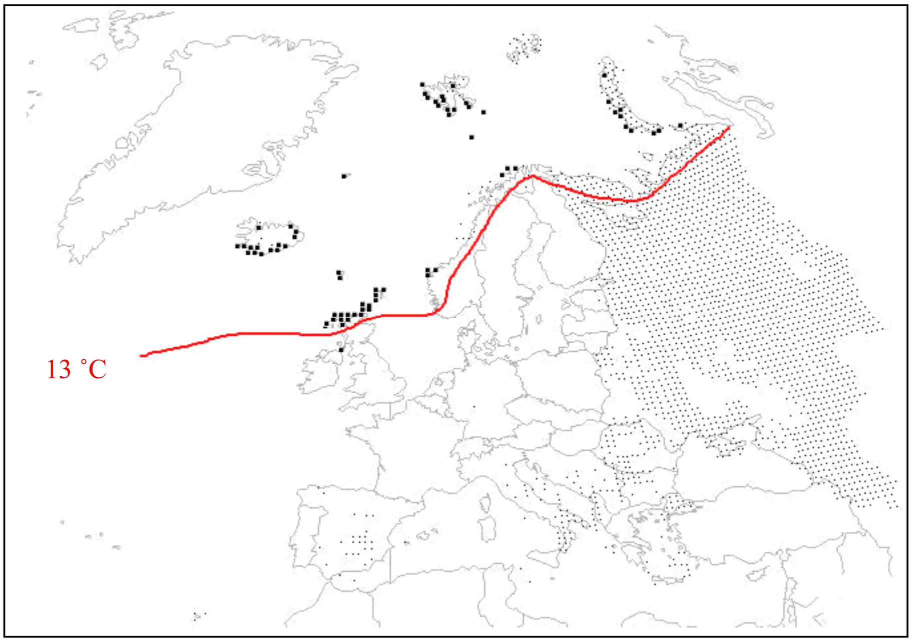

Figure 1.3 The current breeding distribution of the Great Skua (black squares) (Hagemeijer & Blair, 1997) and its association with the 13 ˚C isotherm from 1900 (Bartholomew & Herbertson, 1899), proposed as a possible thermal limit for breeding of this species (Furness, 1988). Small black dots indicate no breeding data.

conditions during the breeding season suggesting a possible climatic limitation in this species (Figure 1.3) (Furness, 1988) and recent range expansion has taken place away from the most southerly boundaries, in arctic Norway, Finland and Russia (Hamer, 2001). By virtue of their morphological and physiological adaptations for breeding in cold environments, Great Skuas breeding at southern range margins in the UK could experience thermal stress during breeding that could act to constrain breeding activities (Furness, 1988). UK breeding populations have expanded rapidly from a bottleneck population (~40 breeding pairs) in the early 1900s, resulting from persecution, (Furness, 1987) to over 6,000 pairs, more than 2,000 of which nest at Foula, Shetland (Furness & Ratcliffe, 2004). However, there are still many areas south of their current distribution where appropriate food resources and suitable breeding habitat exist and this also implies a climatic limitation of breeding latitude (Furness, 1988). During migration, though, Great Skuas encounter a wide range of climatic conditions and therefore should be less likely to be directly affected by climate.

To date, the most regularly observed impacts of climate warming on high-latitude seabirds have been through changes in food availability in response to shifts in the timing and extent of sea-ice (section 1.4). Great Skuas commonly breed in areas where the influence of sea-ice is negligible, as do many European seabird species. Over-winter survival of adult Great Skuas is high (between 89 and 96 % for birds aged 7-22 yr) but influenced by conditions at breeding sites, being reduced during and after seasons characterized by poor food availability (Ratcliffe *et al.*, 2002). Reductions in reproductive success during years of poor food availability are even clearer (Hamer *et al.*, 1991). Being a top predator, however, any climatic effects on food availability that filter up from low trophic levels will be also be harder to detect, especially since adult diet appears very flexible (Votier *et al.*, 2004). Additionally, breeding distributions may be slow to respond to climate because of high philopatry and low fecundity. These aspects of their ecology that may complicate the detection of climate-induced responses also make the Great Skua an ideal model species for which to determine responses to climatic change of general applicability for a wide range of marine predators.

To understand the probable responses of Great Skuas to changing climates, the following questions need to be addressed. Firstly, prevailing heat stress conditions throughout the breeding range of Great Skuas need to be quantified to determine whether or not this species regularly experiences thermal stresses during breeding. Chapter 2 develops a biophysical model, parameterized from results of field studies and available literature, to explore the temporal and spatial variation in heat stress experienced by breeding adults over the past decade.

Secondly, the influence of thermal conditions on adult behaviour, activity budgets, nest site selection, and breeding success needs to be investigated. Chapter 3 examines the behavioural responses of Great Skuas to prevailing heat stress conditions at a colony in the south of their breeding range, employing both proven and novel field techniques, and focusing on freshwater bathing as a response to heat stress. Chapter 4 links behavioural responses to reproductive success, examining the influence of microclimate and breeding site in years of contrasting food availability and experimentally manipulated reproductive cost.

Thirdly, it is important to examine responses to climate at larger scales. In Chapter 5, detailed models of the dispersal and spread of breeding colonies are constructed with data from fieldwork, long-term studies and the published literature, to assess the degree to which climate limits breeding distributions and the likely future spread of breeding colonies within the UK. This chapter aims to determine whether correlations between breeding distribution and air temperature result from mechanistic climatic limitations or from a lag in the spread of Great Skuas from small breeding populations in the early twentieth century.

Fourthly, the extent to which current distributions of northern hemisphere skua species can be attributed to mechanistic limitations associated with climate requires investigation, as do the most probable mechanisms limiting distributions.

In addition, probable changes in species distributions and the potential for bioclimatic models developed for skuas to simulate the likely responses of other seabird species require further study. Chapter 6 employs response surface models to explore the most probable mechanistic relationships between prevailing climatic conditions and current distributions of skua species throughout Europe. These models are then used to simulate future breeding ranges under forecast climatic change.

Finally, chapter 7 provides a general discussion, examining the most likely responses of Great Skuas to forecast climatic change and the possible consequences for other high-latitude seabirds and cold-adapted species.

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Chapter 2.

Spatial and temporal variation in exposure to heat stress for Great Skuas throughout their breeding range

Summary

Great Skuas (*Catharacta skua*) are adapted to breed at low ambient temperatures and reproductive success may be directly constrained by overheating at breeding colonies. A biophysical model was developed using heat transfer equations to quantify positive energy balance (heat stress) at current and potential breeding colonies, and explore temporal variation in heat stress. The model predicted the upper threshold of the thermoneutral zone for adult Great Skuas to be reached at air temperatures of 10.6 °C and the critical limit, at which heat dissipation by maximal evaporative cooling is exceeded, to be 20.6 °C. Critical heat stress decreased with increasing colony latitude, although at all colonies this thermal limit was exceeded on only a few days each year. Heat stress was highest during the more energetically-costly incubation and mid-to-late chick-rearing stages, because metabolic heat production was the most important process contributing to heat stress. The southern limit of the breeding distribution of Great Skuas is associated with mean July temperatures of 13 °C, rather than the critical limit of 20 °C, suggesting that trade-offs between breeding and thermoregulatory behaviour may occur if temperatures regularly exceed 13 °C. Under forecast climatic warming, most current Great Skua breeding colonies are unlikely to experience critical heat stress on a daily basis, even by 2080. Great Skuas breeding in arctic Russia or at any new colonies founded south of the current range margin, however, will probably need to employ thermoregulatory behaviours other than panting on a regular basis.

2.1 Introduction

Climatic warming is predicted to be most extreme in arctic regions and mean air temperatures in some areas may increase by as much as 8 Celcius degrees (C°) by 2100 (Houghton *et al.*, 2001). Many species will be affected directly by changes in temperature regimes (McCarty, 2001; Bale *et al.*, 2002) and there is growing evidence of changes in phenology (Root *et al.*, 2003), distribution (Croxall, Trathan & Murphy, 2002) and size of breeding populations (Smith *et al.*, 1999) for a diverse array of taxa. Ectothermic animals are often directly influenced in their activities by ambient temperatures (Cloudsley-Thompson, 1991) and may be expected to exhibit behavioural and/or physiological adjustments if they are to ameliorate the impacts of climatic warming. However, many long-lived homeotherms breeding at high latitudes are constrained in their ability to loose heat, because they possess adaptations for increased endogenous heat production and conservation (Gabrielsen, Mehlum & Karlsen, 1988). Skuas (Family Stercorariidae) are high-latitude seabirds capable of high levels of activity at low temperatures because of their high basal metabolic rate and body temperature (Bryant & Furness, 1995), thick skutes on their legs, and heavy insulative plumage (Furness, 1987, 1988). Effective temperatures can often exceed 30 ºC in the Arctic summer (Klaassen, 1994) and this could lead to difficulties in heat dissipation for adults at breeding colonies during periods of warm weather, with negative consequences for feeding and guarding of chicks, and hence for chick growth and survival (Furness, 1988). The rapid temperature rise predicted in arctic regions over the next 100 years (Houghton *et al.*, 2001) may therefore require skuas and other high-latitude species to make behavioural and physiological adjustments if they are to maintain their current breeding distributions.

For homeothermic animals, external thermal exchange (via convection, conduction, radiation and evaporation) is balanced against metabolic heat production to maintain more-or-less constant body temperature (McNab, 2002). The range of temperatures under which this balance is maintained without active thermoregulation is known as the thermoneutral zone (Monteith & Unsworth, 1990). As ambient temperature rises above this threshold, further heat loss occurs via evaporative cooling or behavioural responses such as ptiloerection that reduce radiative heat gain within thick plumages or alter convective heat loss (McNab, 2002). Conduction from the feet is also thought to be of considerable importance for heat-loss in marine birds (Lustick, 1984) and, because Great Skuas possess insulative scales, or skutes, on their legs in addition to a dense plumage (Furness, 1987), the webs of the feet should be important sites for heat exchange. At extreme temperatures or high vapour pressures, evaporative cooling cannot be increased further and birds undergo hyperthermia, increasing their body temperature (Monteith & Unsworth, 1990), although larger birds can maintain low levels of heat storage temporarily (Lustick, 1984). For Great Skuas, high levels of territorial attendance are necessary to guard chicks against predation by conspecifics (Catry & Furness, 1999). Adults breed on low-lying moorland or tundra vegetation (Furness, 1987) and incubation and chick-rearing restricts their ability to thermoregulate by seeking shade or selecting different microhabitats.

The breeding range of Great Skuas is expanding rapidly at its eastern margin in arctic Russia, but not at its southern margin in the UK (Hamer, 2001). To examine whether or not this difference is related to differential exposure to heat stress across the breeding range, a biophysical model (O'Conner & Spotila, 1992) was developed to quantify the upper limits of the thermoneutral zone and the threshold temperature at which the capacity for evaporative cooling was exceeded. Biophysical models relate thermal inputs, such as metabolic heat production, to heat transfer mechanisms such as convection and conduction (O'Conner & Spotila, 1992) and reveal the conditions under which animals may be constrained by their thermal environment. Similar models have been used for exploring the ecology of poikilothermic animals (Spotila, 1972; Tracy, 1982; Casey, 1992) but only rarely for homeotherms (e.g. McCafferty *et al*. (2001)). This is the first time that such a model has been constructed for a high-latitude seabird. Using outputs from the model, this chapter examines seasonal, yearly and latitudinal variation in heat stress exposure, the relative importance of environment and morphology in determining heat stress intensity and the possible link between heat stress and the reproductive success of Great Skuas.

2.2 Methods

2.2.1 Data retrieval and formatting

Environmental data (maximum global radiation, maximum air temperature and grass temperatures, mean wet and dry bulb temperatures, mean proportional cloud cover and base-height and mean wind speed) were retrieved for 15 potential or actual Great Skua breeding sites from the British Atmospheric Data Centre's Meteorological Office Station (MET) and European Synoptic (ES) databases for years of near-complete data coverage. Potential breeding sites at latitudes outside the current breeding range were chosen to explore whether heat stress conditions outside the current Great Skua breeding range were very different from those in areas in which this species breeds. Sites were chosen that had adequate data coverage and were either large colonies for other seabird species (Isles of Scilly, Azores), or areas for which there were occasional breeding records for Great Skuas (Northern Ireland). Table 2.1 details the locations, years of coverage and datasets used in all modeling, while their geographical locations are shown in Figure 2.1. Data for Spitsbergen, Svalbard, were retrieved from the Stiftung Alfred-Wegener-Institut für Polar und Meeresforschung in der Helmholtz-Gemeinshaft (AWI). If a variable was unavailable at a specific colony, data from the nearest station were used, except in the following cases: global radiation was unavailable for ES data and was calculated from latitude and date (see Appendix A1.1); grass temperature (T_{grs})

Table 2.1 Latitude, longitude, breeding incidence, data span and data source for locations modeled. Breeding incidence: ✓= confirmed breeding, **?** = possible breeding (known colony within 100 km), ✕ = confirmed non-breeding (source Snow and Perrins (1998)). **?**✕= recent breeding record within 50 km (R. W. Furness, pers. com.). Data sources: see text.

Location	Latitude	Longitude	Recorded Breeding	Data span (years)	Source
Spitsbergen (Svalbard)	78.900 N	11.900 E	✓	1993 – 2002	AWI
Bjornoya (Bear Island)	74.310 N	19.010 E	✓	1990 – 1996	ES
Jan Mayen (Norway)	70.560 N	8.400 W	✓	1990 – 1996	ES
Murmansk (Russia)	68.590 N	33.070 E	**?**	1990 – 1996	ES
Sojna (Russia)	67.530 N	44.080 E	**?**	1990 – 1996	ES
Bodo-vi (Norway)	67.160 N	14.220 E	**?**	1990 – 1996	ES
Keflavikurflugvollur (Iceland)	63.580 N	22.360 W	✓	1990 – 1996	ES
Thorshaven (Faeroe Islands)	62.010 N	6.460 W	✓	1990 – 1996	ES
Foula (Shetland, UK)	60.154 N	2.072 W	✓	1989 – 2002	MET
Fair Isle (Shetland, UK)	59.526 N	1.626 W	✓	1989 – 2002	MET
Hoy (Orkney, UK)	58.289 N	2.898 W	✓	1989 – 1999	MET
Handa (Sutherland, UK)	58.289 N	5.070 W	✓	1989 – 1999	MET
St. Kilda (Western Isles, UK)	57.811 N	8.563 W	✓	1989 – 1999	MET
County Fermanagh (N. Ireland, UK)	54.400 N	7.650 W	**?**✕	1989 – 1999	MET
Isles of Scilly (UK)	49.913 N	6.295 W	✕	1989 – 1999	MET
Azores (Portugal)	38.460 N	27.060 W	✕	1990 – 1996	ES

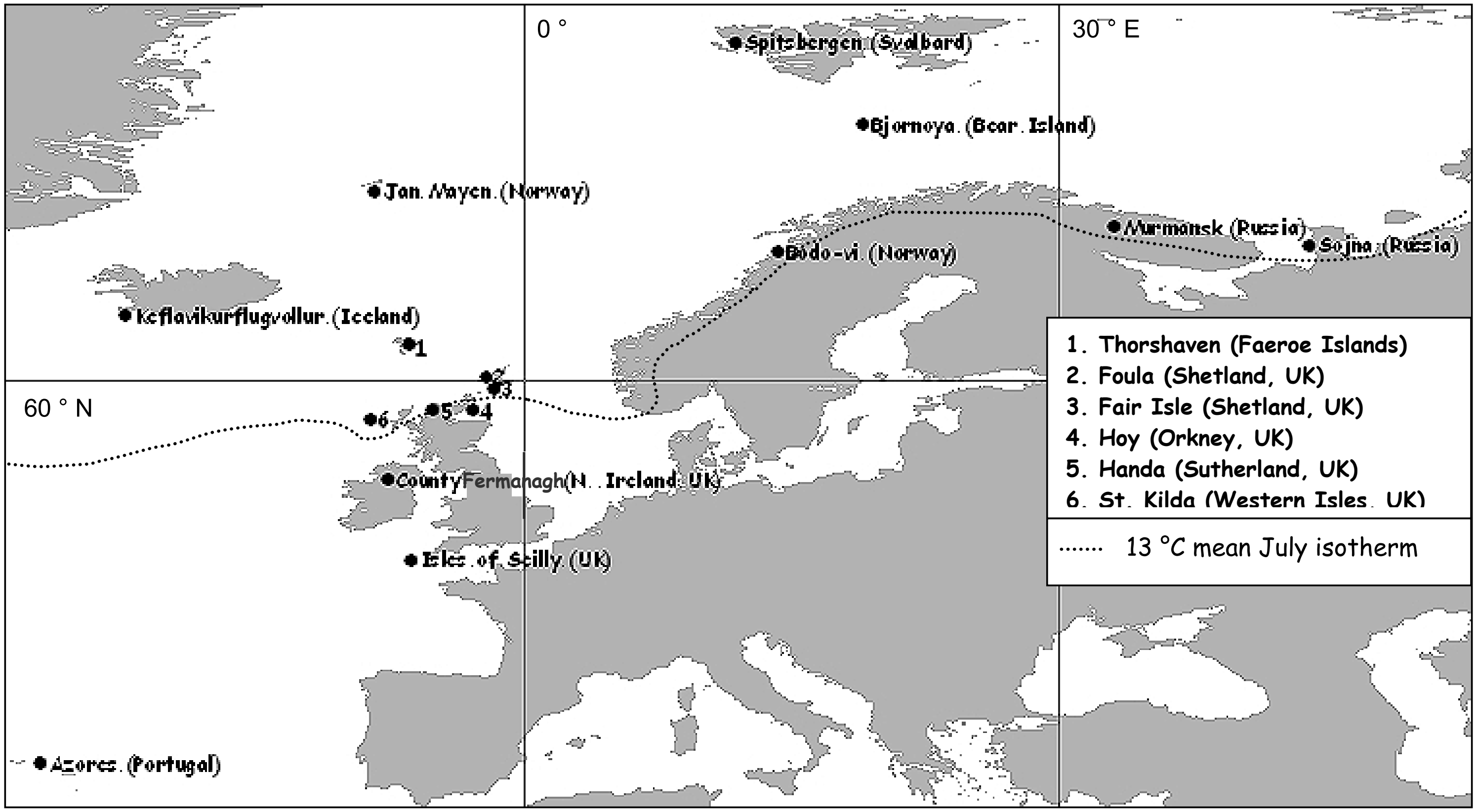

Figure 2.1 Geographical locations of the 16 sites for which seasonal heat stress of breeding adult Great Skuas was modeled. Only the Isles of Scilly and Azores do not support skua breeding colonies (Snow & Perrins, 1998). The 13 °C mean July isotherm (1900) is shown to illustrate the close correspondence with the realised breeding range (meteorological data are from Bartholomew & Herbertson (1899)).

was unavailable for ES and AWI data, and was approximated by regression with air temperature (T_a) ($F_{1,3428} = 858.3$, $R^2 = 0.2$, $P < 0.001$). This regression equation, derived from 14 years of data at Fair Isle (the location with the longest grass temperature time series), was:

$$T_{grs} = 2.00\ (SE \pm 0.18) + 0.29\ (SE \pm 0.01)\ T_a \qquad \text{Eqn 2.1}$$

Wet and Dry Bulb temperatures were converted into vapour pressure (e), using the following equation, from Monteith and Unsworth (1990):

$$e = \gamma(T_D - T_W) \qquad \text{Eqn 2.2}$$

where, $\gamma = 0.67$ (psychometer constant), T_D and T_W are dry and wet-bulb temperatures, respectively. Air temperature, vapour pressure, wind speed were converted from hourly measurements into daily (09:00-21:00 BST) means. Global radiation was converted into a single daily maximum.

2.2.2 Biophysical model

The model is a thermal energy balance equation for heat-exchange between an animal and its environment (O'Conner & Spotila, 1992) (Figure 2.2, eqn 2.3). The seven components sum to give an energy surplus or deficit. When energy balance was positive (surplus), animals were considered to be heat stressed.

The model was run to provide a single daily value for maximum potential heat stress, calculated as energy balance per second (W $bird^{-1}$; watts per bird). Two versions of the model were used, differing only in the equations used to

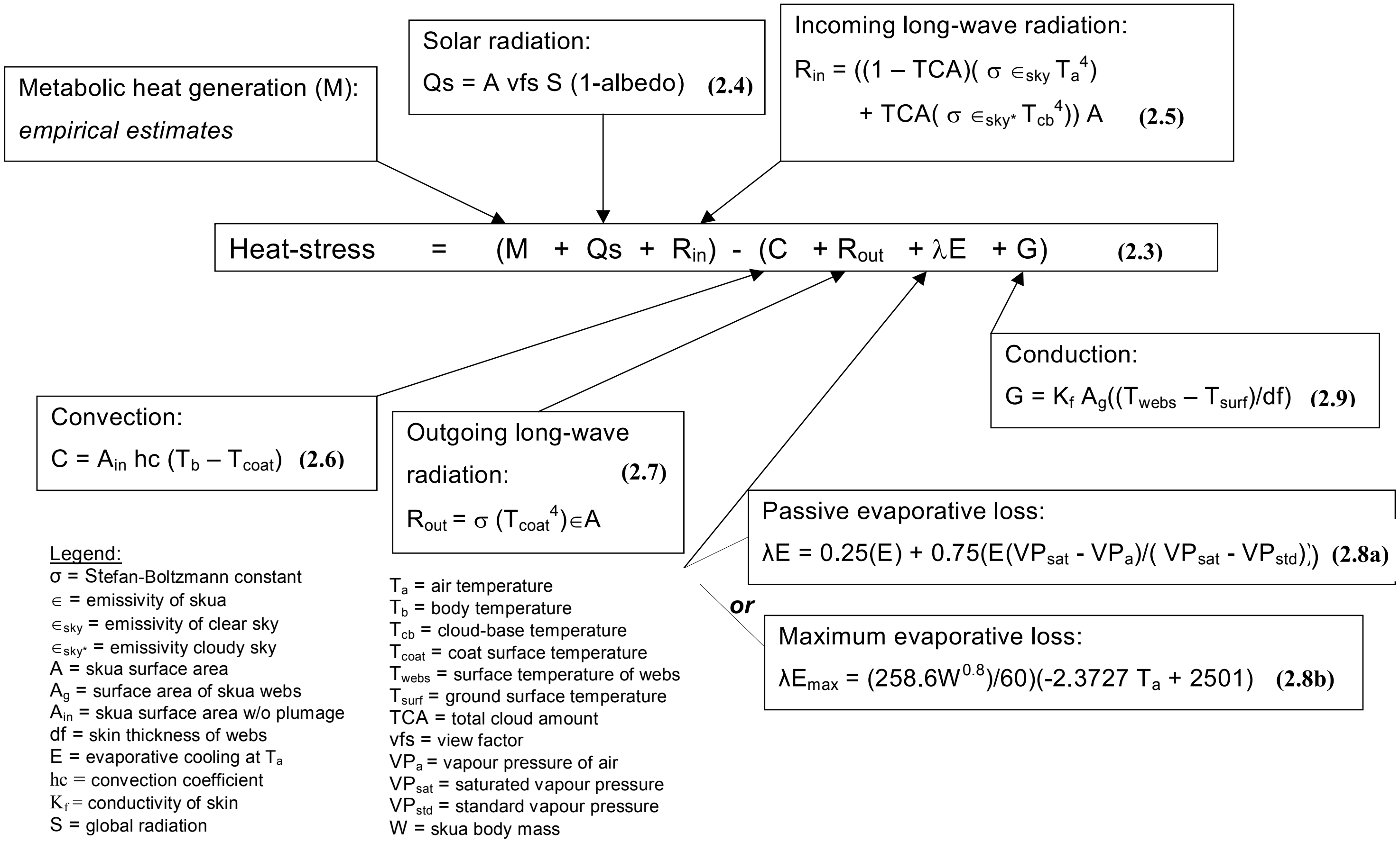

Figure 2.2 Structure of the biophysical model. The balance equation (2.3) comprises seven separate equations representing processes of heat transfer between a skua and its environment. The two models use different evaporative cooling scenarios: either passive (PM) (2.8a) or maximal (MM) heat loss (2.8b) (panting). Values for metabolic heat generation are taken from the literature (Table 2.3).

Table 2.2 Species-specific (Great Skua) parameters of the model: values, units and source.

Parameter	Value	Units	Source
mass (W)	1600	g	Furness (1987)
radius with plumage	0.1987	m	empirical
surface area	0.125	m^2	empirical
Body temperature (T_b)	42.0	°C	Furness (1988)
Plumage depth	0.026	m	empirical
Plumage density	15327.3	gm^{-3}	Furness (1988) and empirical
Albedo	0.34 (estimated)	none	Monteith & Unsworth (1990)
Thermal conductivity~wind exponent (c)	0.45 (estimated)	none	Bakken (1990)
Thermal conductivity of webbing between toes (webs)	0.14 (for leather)	$Wm^{-1}°C^{-1}$	www.hukseflux.com/thermal%20conductivity/thermal.htm
Temperature of webs (T_{web})	34.0 (estimated)	°C	Wolf & Walsberg (1996)
Area of web conductive surface (Ag)	0.00296	m	Empirical
Thickness of webs (df)	0.0015	m	Empirical

predict evaporative heat loss. The “passive” model (PM) quantified the upper threshold of the thermoneutral zone (when evaporative cooling was a passive process (Figure 2.2, eqn 2.8a)) and the “maximal” model (MM) determined the critical threshold over which the capacity to loose heat by evaporative cooling at a maximal rate was exceeded (Figure 2.2, eqn 2.8b). For both models, conductive heat loss was assumed to be maximised and radiative and convective heat exchange were passive processes not influenced by adjustments in posture or orientation. Both models were run for dates between March 1st and October 31st in each breeding location (to span the period in which Great Skuas are in the vicinity of their breeding sites) for each year of data (Table 2.1). All species-specific parameter values used in the model are shown in Table 2.2, other non-specific constants and thermal properties are given in Appendix A1.2, Table A.1.

Table 2.3 Estimates of field metabolic rates (FMR) of adult Great Skuas and duration of the six stages in the breeding cycle. 3.5 × BMR is the average FMR estimate of Phillips, Thompson & Hamer, (1999), 4.1 × BMR reflects a 0.6 increase from incubation activities (Grant, 1984), 5.0 × BMR has been recorded for Great Skuas in poor foraging conditions (Hamer, Furness & Caldow, 1991) and 4.0 × BMR is an estimate based on these values.

Breeding stage	Length (days)	FMR (multiple of BMR)	FMR (W bird^{-1})	Components of FMR
Pre-breeding	varies (eqn 2.10)	3.5	21.79	standard, courtship, territoriality
Incubation	29	2.1	25.53	standard, incubation
Early chick-rearing	13	3.5	21.79	standard, provisioning of small chicks
Mid chick-rearing	22	5.0	31.13	standard, provisioning of large chicks
Late-chick-rearing	varies (eqn 2.11)	5.0	31.13	standard, provisioning of large chicks
Post-breeding	14	4.0	24.90	standard, defending non-independent fledglings

Values for metabolic heat generation (M) were field metabolic rates (FMR) estimated for adult Great Skuas breeding at Foula, Shetland (Table 2.3). Durations of the six breeding stages were taken from Hamer (2001) or calculated from predicted modal laying Julian dates (L_d) and length of chick development (L_{growth}), both of which increase with latitude (ϕ) (Young, 1977; Hamer, 2001):

$$L_d = 1.8954\ \phi + 24.52 \qquad \text{Eqn 2.10}$$

$$L_{growth} = 0.5556\ \phi - 18.33 \qquad \text{Eqn 2.11}$$

where, L_{growth} is the length of the late chick-growth period in days. Equations 2.10 and 2.11 are derived from regressions with latitude using Great and Arctic Skua data from Hamer (2001) and Furness (1987).

Energy input from short-wave solar radiation (Qs), incorporating both direct and diffuse radiation (Figure 2.2, eqn. 2.4), depended on global radiation (S), Great Skua surface area, plumage albedo, depth and density and the proportion of the bird directly exposed to the sun (vfs) (O'Conner & Spotila, 1992). To simplify calculations, the animal was modeled as a sphere of surface area equal to that of an adult Great Skua, following O'Conner & Spotila (1992). Despite this false assumption, modeling the effect of shape and air flow on heat loss would unnecessarily complicate a model developed to examine seasonal and regional variation in relative heat stress, that could not include small scale phenomena such as wind direction and posture because of data limitations.

Incoming long-wave radiation (R_{in}) (Figure 2.2, eqn. 2.5) was calculated from air temperature (T_a), cloud-base temperature (T_{cb}), emissivity of the sky in clear ($\in_{sky}$) and cloudy ($\in_{sky*}$) conditions, and the proportion of cloud cover (TCA) (Monteith & Unsworth, 1990). For simplification, three levels of cloud were identified: high-level cloud (cirrus) had cloud base height (CBH) > 7009 m and $\in_{sky*} = 0.7$, medium-level cloud (stratus) had CBH = 1980-7009 m and $\in_{sky*} = 1.0$, and low-level cloud (cumulus) had CBH ≤ 1980 m and $\in_{sky*} = 1.0$ (Ruffner & Bair, 1984). Where fog was recorded, or if T_a was below dew point temperature, $\in_{sky*} = 1.0$ and $T_{cb} = T_a$, otherwise the dry adiabatic lapse rate was used to determine cloud-base temperature:

$$T_{cb} = -0.00984 \text{ CBH} + T_a$$ Eqn 2.12 (Monteith & Unsworth, 1990)

Convective energy transfer (C) (Figure 2.2, eqn. 2.6) was derived from the temperature gradient between the skin surface (T_b) and plumage surface (T_{coat}), the skin surface area (A_{in}) and the convection coefficient (hc):

$$hc = 6.77 \times V^{c}$$ Eqn 2.13 (adapted from O'Conner and Spotila (1992))

where, V is wind speed and c is the exponent describing the dependence of thermal conductivity upon wind speed (e.g. Bakken (1990)).

Outgoing long-wave radiation (R_{out}) (Figure 2.2, Eqn 2.7) was calculated as a function of plumage surface temperature (T_{coat}) and several constants (Monteith & Unsworth, 1990). T_{coat} was estimated as air temperature (T_a) plus heat input from solar radiation (Qs) :

$$T_{coat} = T_a + (Qs / (mc \times Cp))$$ Eqn 2.14

where, mc is the mass of the plumage surface that absorbs solar radiation and Cp is the specific heat capacity of feathers.

Passive evaporative heat loss (λE) (Figure 2.2, eqn. 2.8a) was calculated as a linear decrease in energy transfer via evaporation (E) with decreasing difference in vapour pressure between the respiratory surface (VP_{sat}) and the air (VP_a) (respiratory loss) but maintaining a constant 25 : 75 % ratio of cutaneous to respiratory evaporative loss (Monteith & Unsworth, 1990). E was derived from an exponential relationship with air temperature (T_a) using data from Calder and King (1974) and Dawson & Hudson (1970):

$$E = 6.0\times10^{-7} (T_a^{\ 2.4155}) \times (-2.3727\ T_a + 2501) \qquad \text{Eqn 2.15}$$

where $E = 0$ at $T_a = 0$ °C, as water freezes at this temperature. This equation incorporated the elevated capacity for heat loss allowed Great Skuas by gular fluttering (rapid fluttering of the gular area of the throat)since the equations of Calder and King (1974) were derived from birds that gular flutter (frogmouth, roadrunner, pigeon & ostrich).

Maximal evaporative heat loss (λE_{max}) (Figure 2.2, eqn. 2.8b) was calculated from an allometric relationship with water-loss (Calder & King, 1974) combined with changes in the latent heat of evaporation at different air temperatures (Monteith & Unsworth, 1990).

Conductive heat loss to the ground (G) (Figure 2.2, eqn. 2.9), thought to be of considerable importance in marine birds (Lustick, 1984), was a function of the conductivity (K_f), area (A_g) and thickness of the webs on the feet (df), and the temperature difference with the ground (O'Conner & Spotila, 1992). In the absence of an empirical value (for incomplete time-series), ground surface temperature ($T_{surf)}$ was estimated from eqn. 2.14, substituting the appropriate values for soil (Appendix A1.2). Conduction was assumed to occur only through the skin of the webs because skuas have skutes on their legs to minimise heat loss (Furness, 1987), and to be maximized by maintaining the webs at a high temperature (T_{web}), estimated as 34 °C (Wolf & Walsberg, 1996).

2.2.3 Model sensitivity, analysis and accuracy

Sensitivity analysis of the maximal version of the biophysical model (MM) was carried out for environmental variables and fixed parameters (Table 2.4), recording the change in the output resulting from independently raising each variable or parameter by 1 % of its median value (following Phillips *et al.*, 1999). To quantify changes in model output for more extreme environments, environmental variables were independently adjusted to their upper and lower quartile values and parameters were either increased by 5 %, or to extreme values taken from the literature.

The accuracy of the model was assessed by linear regression of predicted energy balance (for model runs without metabolic heat production (Table 2.3) or evaporative cooling (eqns 2.8a & b)) with operative temperatures calculated from data for Foula, Shetland, between May and August of 2002 and 2003. Operative temperature is the temperature achieved by a blackbody object under prevailing environmental conditions and does not incorporate metabolic heat production or evaporative heat loss (Bakken, 1992). Operative temperatures were calculated from empirical measurements at the colony using a 75 mm diameter water-filled copper sphere covered with a feathered Great Skua pelage. Internal temperatures approximated operative temperature (Bakken, 1992), providing an approximation of thermal loading but not accounting for metabolic heat production or evaporative cooling (Walsberg & Weathers, 1986). Regression analysis was used to develop an equation to predict operative temperature from air temperature recorded simultaneously (full details in Chapter 3, section 3.2.1).

2.2.4 Thermal thresholds for the Great Skua

The operative temperatures at which Great Skuas were predicted to exhibit heat stress for both passive and maximal evaporative cooling models were calculated from linear regression of operative temperatures measured empirically at Foula in 2002 and 2003 with output from both models (see section 2.2.3). Operative temperature thresholds, above which birds were predicted to experience heat stress (positive energy balance), occurred where regression lines intercepted the x-axis at 0.0 W bird^{-1} energy balance. Since operative temperature spheres have higher specific heat capacity (Cp) than air (most of the sphere volume was water: Cp = 4.184 Jg^{-1}K^{-1}, whereas Cp for air ~ 1.0 Jg^{-1}K^{-1}), these threshold values were converted into air temperature equivalents using the regression equation determined in Chapter 3 (section 3.2.1).

2.2.5 Temporal variation in heat stress and its relation to the North Atlantic Oscillation and reproductive success of Great Skuas

Generalized linear models (GLMs) with normal errors and identity link functions, appropriate for normally-distributed response data (Nelder & Wedderburn, 1972), were fitted for passive and maximal models to examine differences in energy balance between breeding stages (Table 2.3), years and locations (including these as covariate factors in the model). Variation in climatic indices in north-west Europe, such as air and sea temperatures, is know to correlate with changes in the North Atlantic Oscillation (Ottersen *et al.*, 2001), calculated as the difference in atmospheric pressure between Azores and Iceland in the North Atlantic Oscillation Index (NAOI) (Hurrell, 1995). GLMs with normal errors and identity link functions were also fitted to determine if mean energy balance within each breeding stage for each year from 1990 to 1996 was related to corresponding yearly NAOI values (retrieved from http://www.cgd.ucar.edu/~jhurrell /nao.stat.winter.html), controlling for variation attributable to location by including this as a covariate factor. Both of these GLMs were repeated replacing mean energy balance with the proportion of days in which energy balance was positive during a stage as the dependent variable, and using binomial errors and logit-link functions accordingly.

A GLM was also fitted to determine if the mean productivity of Great Skuas at Foula, Fair Isle and Hoy (mean number of chicks fledged per nest) was related to either mean energy balance throughout incubation, mid and late chick-rearing stages or annual NAOI values (location and Shetland sandeel abundance included as covariate factors). Sandeel abundance data from Shetland was used to account for the strong relationship between sandeel availability and Great Skua productivity (Hamer *et al.* 1991) because it was the most available archive in the region, even though birds from Hoy probably commonly exploit more local sandeel stocks. This analysis was restricted to Hoy, Foula and Fair Isle because productivity data were only available from these sites (annual data collected from >100 nests in each location between 1989 and 2002, (R.W.Furness unpublished data)) and Shetland sandeel abundance was more likely to be related to food availability at these colonies. Also, this GLM was restricted to incubation, mid and late chick-rearing stages since results of prior analyses (section 2.3.3) indicated that heat stress was most probable within these stages. Sandeel abundance was the total number of 0-group sandeels in the previous year (since Great Skuas feed mainly on 1+ year groups (Hamer *et al*. 1991)) estimated for the whole of Shetland, taken from ICES (2002) and Oro & Furness (2002). This GLM was repeated replacing mean energy balance with proportion of days of positive energy balance during incubation and mid and late chick-rearing.

2.2.6 Latitudinal trends in heat stress

Seven-year means (± SD) for annual energy balance and for the proportion of days in a year when energy balance was positive were calculated for each colony, using data for years 1990 to 1996, available at all locations except Spitsbergen (data from 1993 to 1999 were used for this colony). Latitudinal trends in these values were examined by linear regression with colony latitude.

All statistical analyses were undertaken using Genstat (Genstat, 1993) and SPSS (Norusis, 2000) statistical software.

2.3 Results

2.3.1 Model performance and sensitivity

The model was most sensitive to changes in bird mass, radius, plumage density, web skin temperature and thickness, and specific heat capacity of feathers (Table 2.4). Different components of size had contrasting effects on modeled heat stress: a larger radius increased the surface area available for absorption of solar radiation and raised heat stress (positive energy balance) whereas a greater mass increased maximal evaporation, reducing heat stress. Elevated body temperature (T_b) and temperature of webs (T_{webs}) raised the temperature difference between the animal and its environment, increasing convective and conductive heat loss, respectively. Increased thickness of the webs inhibited conductive exchange with the ground leading to increased heat stress. Increasing plumage density and specific heat capacity of feathers (Cp) caused reductions in the heat lost by long-wave radiation, increasing heat stress.

The model was less sensitive to percentile changes in environmental variables than to changes in the fixed parameters (Table 2.4). Given the wide range of input values for environmental variables at all colonies, however, their overall effect on energy balance was considerable. Running the model using upper and lower quartile values for each variable separately resulted in a change of 1.4 - 7.4 % in estimated energy balance (except for vapour pressure, that had a negligible effect on heat-balance) (Table 2.4). Increasing wind speed increased convective heat loss and reduced heat stress. Increasing air and ground

Table 2.4 Sensitivity of biophysical model to changes in environmental variables and parameter values: % change in output of maximal model when variables or parameters are increased by 1 or 5 % above median or fixed values and when changed to upper or lower quartile values or extremes reported in the literature (mass, Dunning (1993); T_b, Furness (1988); c, Bakken (1990); T_{web}, empirical field data (unpublished)).

		Sensitivity to moderate values (% change in output for given change in value)		Sensitivity to quartile values (% change in output for given change in value)		Sensitivity to extreme values	
Variable / Parameter	Median or fixed value	1 %	5 %	lower quartile	upper quartile	Extreme value	% change
Mass (g)	1600.0	-1.22	.	.	.	1300.0	+23.40
Radius (m)	0.1258	+0.97	+4.94	.	.		.
T_b (°C)	42.0	-0.79	.	.	.	41.5 40.0	+0.94 +3.78
Plumage density (gm^{-3})	16093.7	+0.59	+2.84	.	.	.	.
Plumage depth (m)	0.0273	<0.01	<0.01	.	.	.	.
albedo	0.357	+0.06	+0.30	.	.	.	.
c (conductivity)	0.450	-0.22	.	.	.	0.540	-4.58
foot length (m)	0.0588	<0.00	<0.00	.	.		.
foot height (m)	0.0609	<0.00	<0.00	.	.		.
T_{web} (°C)	34.0	-1.01	.	.	.	15.6 23.6 42.0	+54.76 +30.95 - 23.81
web thickness (m)	0.0016	+0.87	+4.19	.	.	.	.
Cp ($Jg^{-1}K^{-1}$)	1.785	+0.59	+2.84	.	.	.	.
Qs (Wm^{-2})	102.4	-0.06	.	2.20	-3.57	.	.
T_a (°C)	8.19	+0.11	.	-2.86	3.45	.	.
VP_a (kPa)	1.03	<0.01	.	<0.01	<0.01	.	.
DewPT (°C)	4.92	<0.01	.	<0.01	1.45	.	.
T_{grass} (°C)	4.46	+0.11	.	-4.38	4.20	.	.
Wind speed (ms^{-1})	5.06	-0.21	.	7.10	-7.42	.	.
TCA (proportion)	0.72	-0.01	.	0.42	-0.15	.	.
CBH (m)	196.9	-0.01	.	0.60	-1.48		

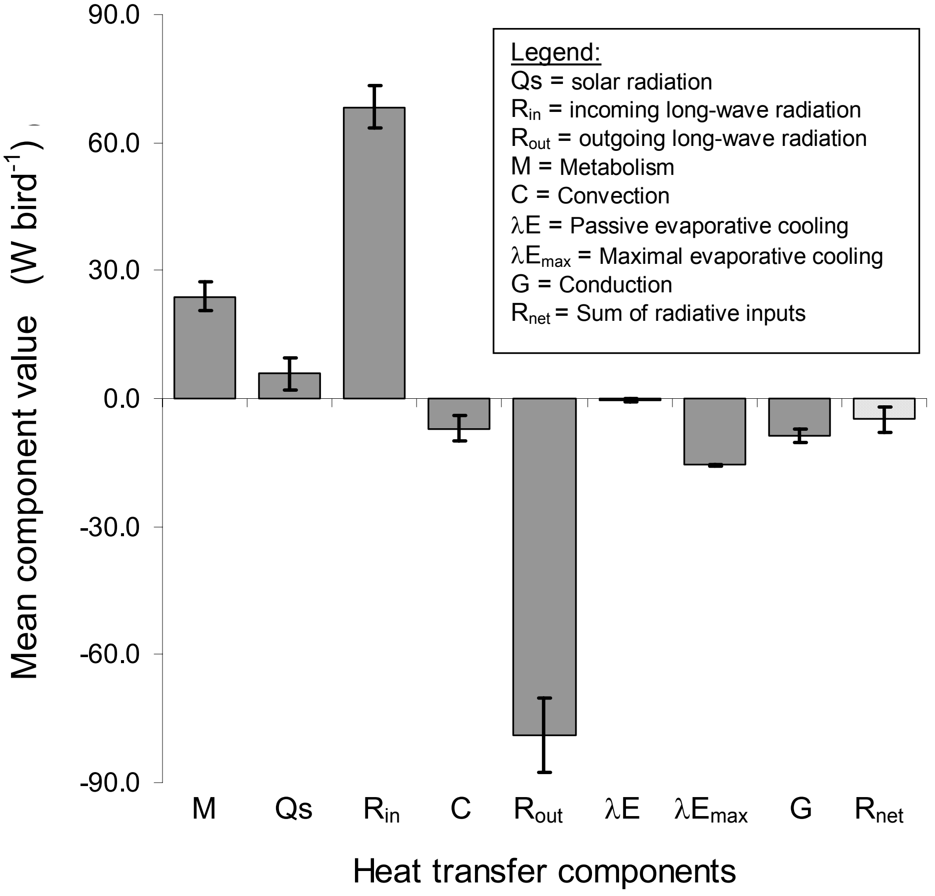

Figure 2.3 Mean values (± 1 SD) for main components of heat balance (parameters of the balance equation, eqn. 2.3), calculated using all output from every run of the biophysical model. Negative values indicate a mean cooling effect. R_{net} is the sum of Qs, R_{in} and R_{out}.

temperatures reduced the temperature difference between the animal and its environment, restricting convective and conductive heat loss, respectively. Elevating solar radiation raised plumage temperatures, increasing the temperature difference with the air, and so increasing convective and radiative heat loss. Increasing dew point temperature (DewPT) increased estimated cloud temperature and the tendency for low-level condensation, leading to elevated heat stress via increased incoming radiation. Altering vapour pressure of the air (VP_a) and cloud cover (TCA), however had little effect on heat stress.

The contribution of seven main components of the energy balance equation (Figure 2.2, eqn 2.3) to overall energy balance varied considerably (Figure 2.3). Although values for incoming and outgoing long-wave radiation were large, when combined their overall contribution to energy balance (R_{net}) was less than that of metabolic heat production, conduction and convection. Evaporative cooling was only important in the biophysical model when modeled at a maximal rate (Figure 2.3).

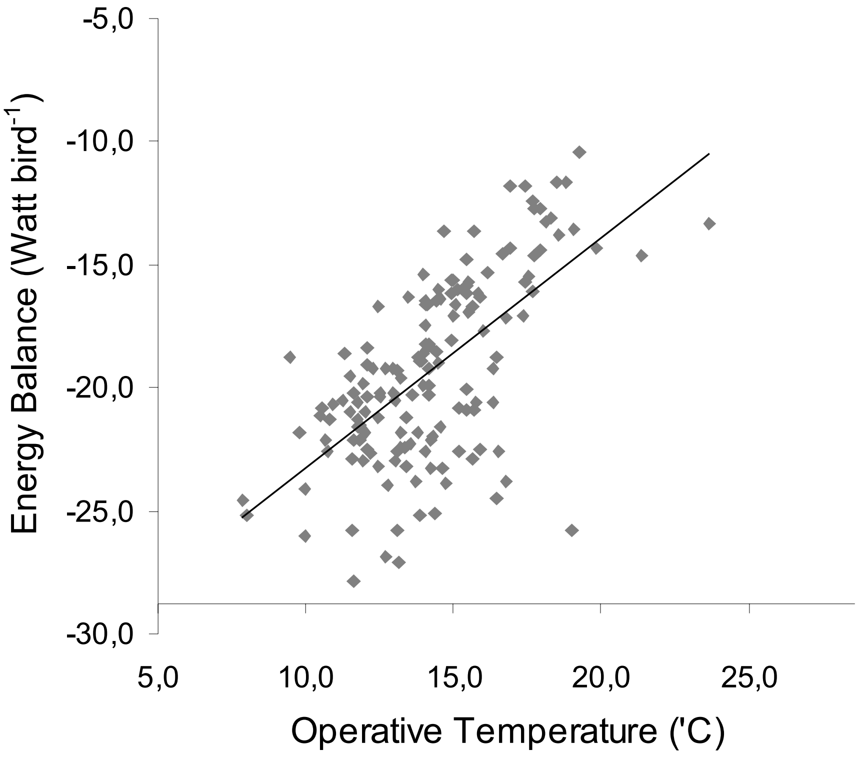

Figure 2.4 Accuracy of the biophysical model: energy balance predicted by the model (without metabolic heat production or evaporative cooling) on days of different maximum daily operative temperature (determined from empirical data). The regression equation shown (y = 0.93x - 32.6) explained 40 % of the variance in modeled energy balance ($F_{1,152} = 100.5$, $R^2 = 0.40$, $P < 0.001$).

Modeled output, without metabolic heat production or evaporative cooling, for Foula in 2002 and 2003 was strongly correlated with operative temperature predicted from measured environmental data at this site in these years (Linear Regression: $F_{1,152} = 100.5$, $R^2 = 0.40$, $P < 0.001$, Figure 2.4). This linear relationship indicates that even though energy balance was the estimated maximum *rate* of energy transfer and did not contain the information about duration of exposure that was inherent in maximum *temperatures* measured empirically by operative temperature spheres, temporal variation in both measures was determined by the same heat-transfer mechanisms. This illustrates that output from the biophysical model faithfully replicated variation in potential heat stress conditions measured in the field.

2.3.2 Thermal thresholds of the Great Skua

The operative temperature thresholds above which energy balance was positive were 12.1 °C for the passive model (PM) (upper limit of the thermoneutral zone) and 24.0 °C for the maximal model (MM) (temperature at which capacity for heat loss by evaporative cooling is exceeded). The equivalent air temperatures at which these thresholds were reached were 10.6 and 20.6 °C, respectively, derived using an equation from the regression of simultaneous operative and air temperatures measurements made at Foula.

2.3.3 Temporal variation in heat stress and its relation to the North Atlantic Oscillation and reproductive success of Great Skuas

Modeled energy balance for Great Skuas differed significantly between stages of the breeding season for both passive (PM) (GLM: $F_{5,\ 37205} = 12399.3$, $P < 0.001$)

and maximal models (MM) (GLM: $F_{5,\,37205} = 12608.4$, $P < 0.001$). In both cases, energy balance was higher during incubation, and in mid- and late-chick rearing than at other stages (Figure 2.5a). The proportion of days on which energy balance was positive was also significantly higher in mid- and late-chick rearing and incubation stages (PM, GLM: $F_{5,888} = 1941.5$, $P < 0.001$; Figure 2.5b). There was significant annual variation in energy balance, with low levels of heat stress in 1989 and 2000-2002, and greater heat stress in the early and late 1990s, although the pattern of annual variation differed for the different breeding stages (Figure 2.6a). The proportion of days on which energy balance was positive was highest in the late 1990s for all breeding stages except incubation (GLMs,

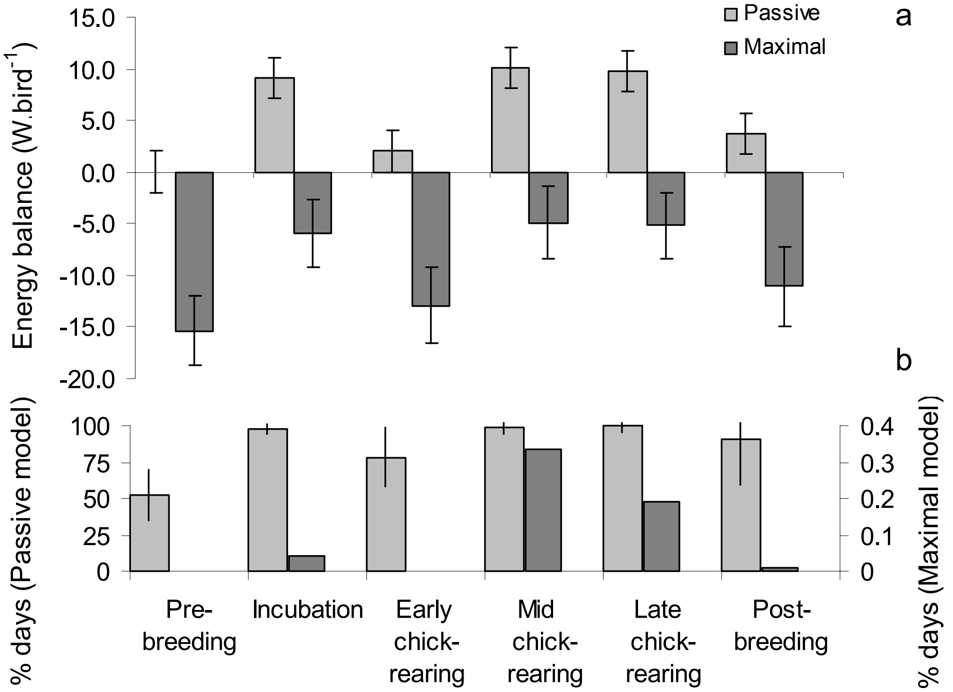

Figure 2.5 (a) Mean (± 1 SD) energy balance and (b) percentage of days on which energy balance was positive in the six breeding stages for both models over all locations and years combined. Standard deviations for % days of the maximal model were 0.0, 2.3, 0.0, 9.2, 7.9 and 0.5 % for the breeding stages in order shown, but omitted for clarity. Formal statistics were not available for MM because the predominance of zero values prevented convergence of maximum-likelihood estimates during GLM parameterisation.

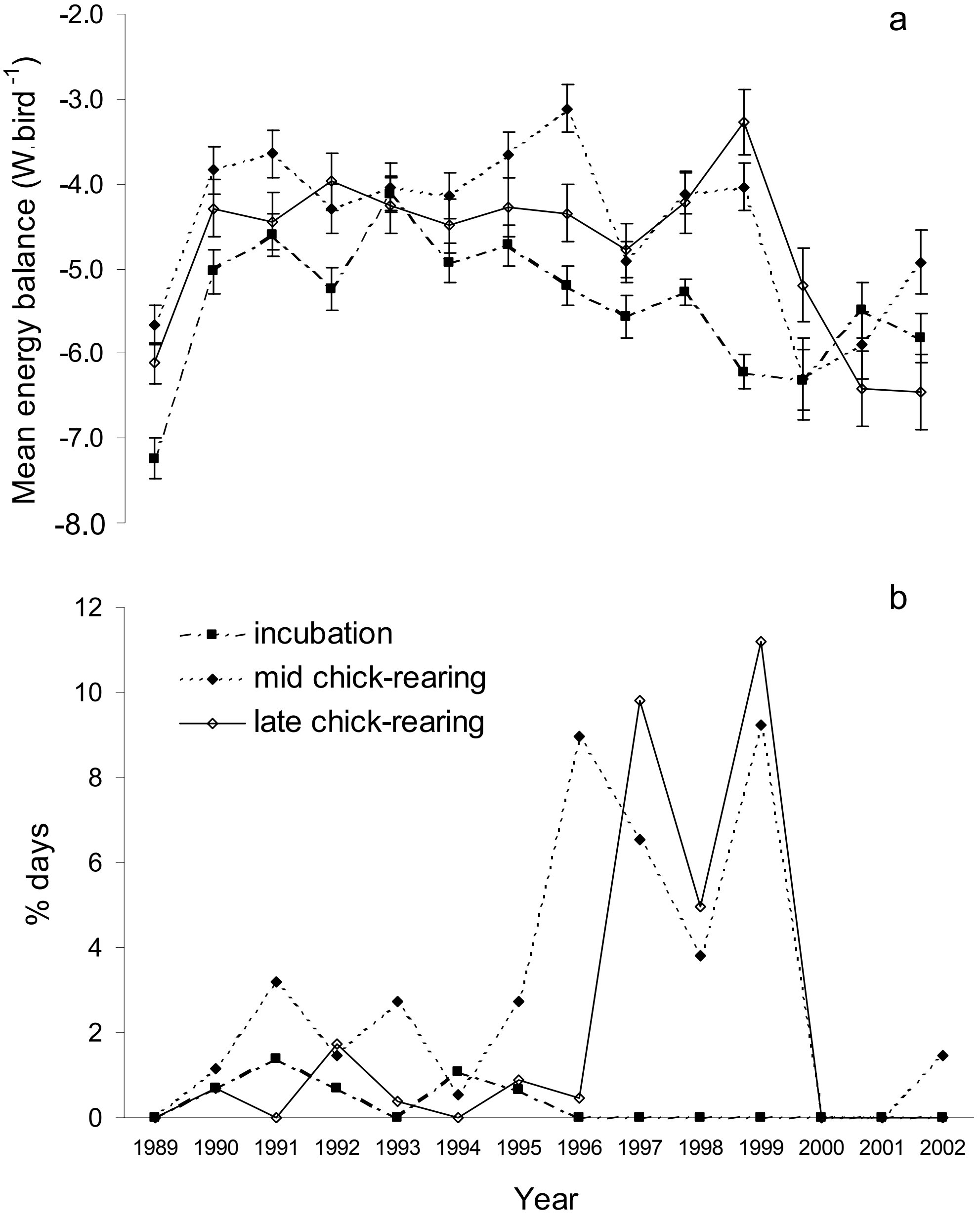

Figure 2.6 (a) Mean (± 1 SD) energy balance and (b) % days of positive energy balance for the maximal model (MM) within incubation, mid and late chick-rearing stages for all years. Differences in mean energy balance were significant in GLMs between years (MM: $F_{13, 37197}$ = 32.7, P < 0.001; PM: $F_{13,31797}$ = 36.3, P < 0.001) and stages. Formal statistics were not available for % days from the MM (see Figure 2.5).

stage*year interaction, PM: $F_{65,37145}$ = 5.2, P < 0.001; MM: $F_{65,37145}$ = 4.4, P < 0.001; Figure 2.6b). Mean energy balance from both models was negatively correlated with the North Atlantic Oscillation Index (NAOI) (GLMs, PM: $F_{1, 892}$

= 6.96, $P < 0.01$; MM: $F_{1, 892} = 5.47$, $P < 0.05$). The proportion of days on which energy balance was positive also showed a negative correlation with NAOI (GLMs, PM: $F_{1, 892} = 59.6$, $P < 0.001$). Mean productivity of Great Skuas (chicks fledged per nest) at Hoy, Fair Isle and Foula, however, was not related to mean energy balance (GLMs, PM: $F_{1, 37} = 0.02$, $P = 0.89$; MM: $F_{1, 37} = 0.00$, $P = 0.95$), the proportion of days on which balance was positive (GLMs, PM: $F_{1, 37} = 0.10$, $P = 0.75$; MM: $F_{1, 37} = 0.27$, $P = 0.60$), or NAOI (GLMs, PM: $F_{1, 37} = 0.04$, $P = 0.85$; MM: $F_{1, 37} = 0.03$, $P = 0.87$).

2.3.4 Latitudinal trends in heat stress

Table 2.5 Mean energy values (± SD) for main parameters of heat transfer at sites of extreme latitude and absolute and percentage difference between these latitudes. For each parameter, means across all 16 study sites are for comparison.

Parameter	Mean from all 16 sites (Wm^{-2})	Azores (38.5 ˚N) Mean (Wm^{-2})	Spitsbergen (78.9˚N) Mean (Wm^{-2})	Parameter change from 38.5 to 78.9° latitude (Wm^{-2})	%
Metabolic heat production (M)	23.9 (± 3.3)	24.2 (± 2.8)	23.4 (± 3.1)	-0.8	-3.3
Convection (C)	-7.0 (± 2.9)	-1.9 (±2.5)	-8.3 (± 3.3)	-6.4	-92.0
Passive evaporative loss (λE)	-0.4 (± 0.2)	-1.8 (± 0.6)	0.0 (± 0.0)	1.8	468.8
Maximal evaporative loss (λE_{max})	-15.6 (± 0.1)	-15.4 (± 0.1)	-15.7 (± 0.1)	-0.3	-2.0
Conduction (G)	-8.6 (± 1.6)	-7.7 (± 1.2)	-9.6 (± 1.8)	-1.9	-21.8
Solar radiation (Q_s)	5.8 (± 39)	11.2 (± 6.4)	3.6 (± 3.2)	-7.6	-132.0
Incoming long-wave radiation (R_{IN})	68.4 (± 4.8)	80.8 (± 3.7)	60.4 (± 5.4)	-20.4	-29.8
Outgoing long-wave radiation (R_{OUT})	-79.0 (± 8.7)	-101.5 (± 14.1)	-65.4 (± 7.8)	36.1	45.6
NET radiative flux (R_{net})	-4.9 (± 2.9)	-9.5 (± 5.9)	-1.4 (± 1.3)	8.1	165.5

Mean seven-year energy balance declined significantly with increasing latitude when evaporative cooling was modeled at a maximum rate but did not show any latitudinal trend when evaporative cooling was passive (Figure 2.7a). The small but significant decline in energy balance with latitude was due mainly to higher

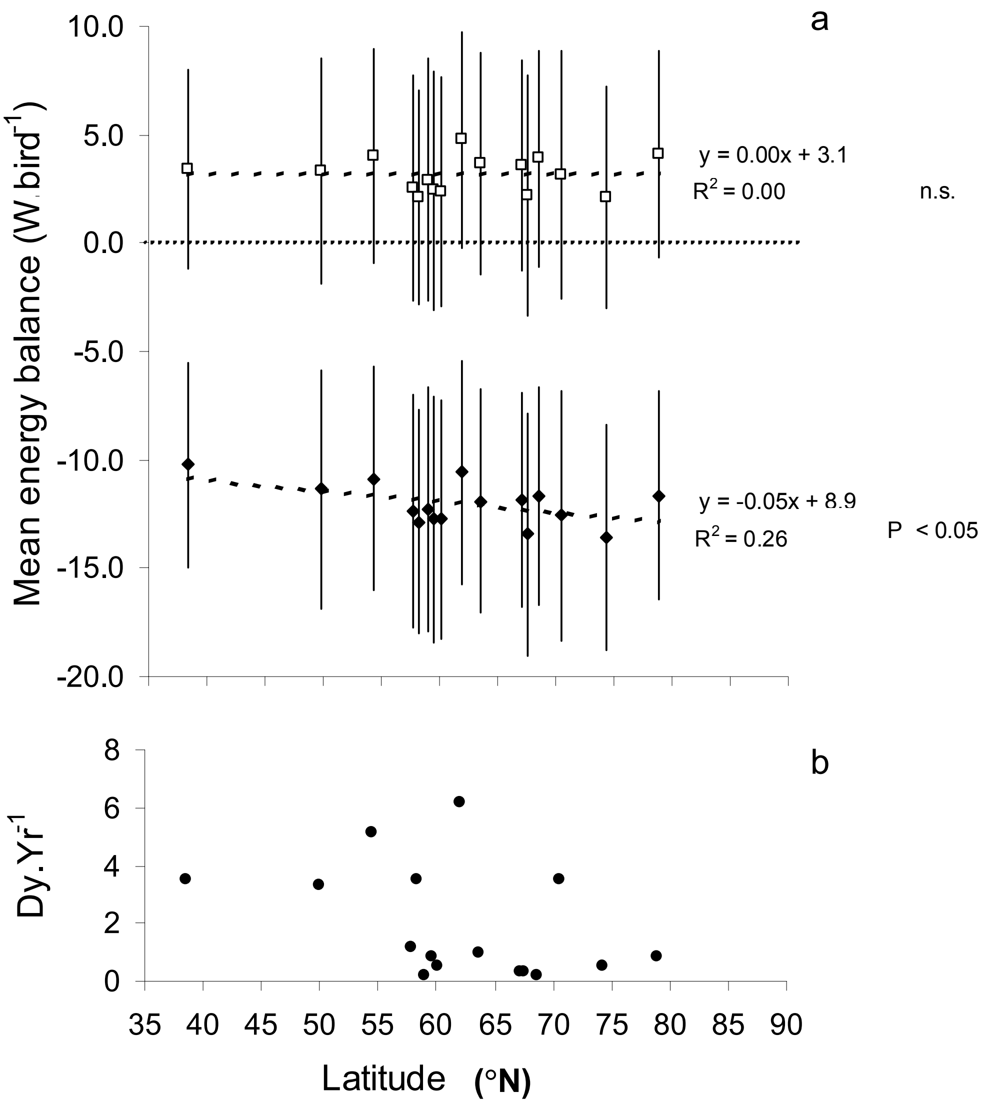

Figure 2.7 Seven year (a) mean (± SD) energy balance for passive evaporative model (open squares) and maximal model (black diamonds), and (b) number of days in which energy balance was positive per year (maximal model). Equations, R^2 and significance of linear regressions are given.

conductive and convective energy losses at high latitudes (Table 2.5), since these contribute the most to mean energy balance (section 2.3.1). Energy lost by passive evaporative cooling also declined significantly with latitude (Linear Regression: $y = 0.044x$, $R^2 = 0.86$, $P < 0.001$) reducing overall energy balance at lower latitudes in the passive model and removing the latitudinal trend observed in output from the maximal model. The number of days in which energy was positive also showed no significant latitudinal variation (Linear Regression: $F_{1,14} = 3.2$, $P = 0.09$; Figure 2.7b).

2.4 Discussion

2.4.1 Temporal variation in exposure of breeding Great Skuas to heat stress

The biophysical model constructed produced daily estimates of positive energy balance (heat stress) for individual adult Great Skuas at actual and potential colonies both within and outside the current breeding range. Similar models have been used successfully for exploring the ecology of poikilotherms (Spotila, 1972; Tracy, 1982; Casey, 1992) but only rarely for homeotherms (e.g. McCafferty *et al*. (2001)). The model indicated that, for Great Skuas, the most influential processes determining heat stress were metabolic heat production, maximal evaporative heat loss (panting/gullar fluttering), conduction and convection. These in turn were influenced by environmental variables, particularly convective heat loss that was higher at high wind speeds and under intense solar radiation (due to increased temperature of the insulating plumage surface) but inhibited at high air temperatures. Conductive heat loss was reduced when ground temperatures increased, although the ability of birds to alter the temperature of their feet was not included in the model and may be very important for marine birds (Lustick, 1984), especially given the sensitivity of the model to changes in this parameter (Table 2.4)

Heat stress (positive energy balance) was highest during mid-to-late chick rearing (>12 day old chicks) and incubation. This resulted from a combination of increased metabolic rate from elevated adult activity during these stages (maintaining eggs at incubation temperature (Grant, 1984) or provisioning large chicks (Furness, 1988)) and the high mid-summer temperatures that occurred concurrently. The proportion of days on which energy balance was positive was also higher during these stages, indicating that adult Great Skuas were more likely to actively thermoregulate at these times. Indeed, these were the only stages in which energy balance was ever predicted to be positive by the maximal model and therefore the only periods in which adults would be predicted to require behavioural and physiological responses other than panting/gullar fluttering in order to alleviate heat stress.

Heat stress intensity at Great Skua breeding colonies was negatively correlated with variation in the North Atlantic Oscillation Index, a good indicator of broad-scale climatic variability (Hurrell, 1995). A positive phase of the NAOI indicates cooler conditions in the north-west Europe (Hurrell, 1995) explaining this negative relationship with modeled heat stress. Yearly variation in both heat stress intensity and the proportion of days of predicted heat stress was evident during all breeding stages and the model predicted that adults were most likely to have been heat stressed during the late 1990s. There was no correlation between mean annual heat stress and breeding success within the last 14 years for Great Skuas breeding at Hoy, Fair Isle and Foula. It is known that poor food availability leads to breeding failure in this species (Hamer *et al*. 1991) and, even though data on sandeel availability were included in this analysis, variations in the diet of Great Skuas breeding in this area and uncertainty in the suitability of fisheries estimates (Votier *et al.* 2004), especially for these fairly widespread colonies, probably masked any influence of heat stress conditions. Consequently, impacts of heat stress are probably small, presumably because at these sub-arctic colonies the majority of skuas are able to avoid overheating by behavioural mechanisms (altering their orientation to the sun or wing drooping) (Lustick, 1984), use of water on territory (Hand, Hunt & Warner, 1981), bathing (Chapter 3), or other physiological methods when energy balance exceeds that effectively dissipated by maximal evaporative cooling. Since metabolic heat production appears to be the main factor contributing to heat stress, skuas may also be able to avoid overheating by restricting activity during periods of critical heat stress, as observed bird species breeding in desert areas (Dawson & Bartholomew, 1968; Tieleman & Williams, 2002).

2.4.2 Latitudinal variation in heat stress and consequences of forecast climatic change

Heat stress declined with latitude when evaporative heat loss was modeled at a maximal rate, but not when birds were modeled to employ only passive evaporative cooling. This was because lower temperatures at higher latitudes resulted in lower rates of passive evaporative loss despite lower humidity, counteracting increased conductive and convective heat losses at these locations. Modeled maximal evaporative heat loss, however, was not affected by vapour pressure because this rate was determined more by physiology of the bird. Consequently, the probability of Great Skuas requiring to thermoregulate by panting in order to supplement passive heat losses was the same at all colonies, regardless of latitude, whereas the probability of birds exceeding the threshold at which panting was no longer sufficient to dissipate thermal loads decreased with latitude. There was no significant effect of latitude on the proportion of days during which birds were critically heat stressed because this threshold was reached only on a maximum of eight days in any one year, although the trend was similar to that described above for heat stress intensity (Figure 2.7c).

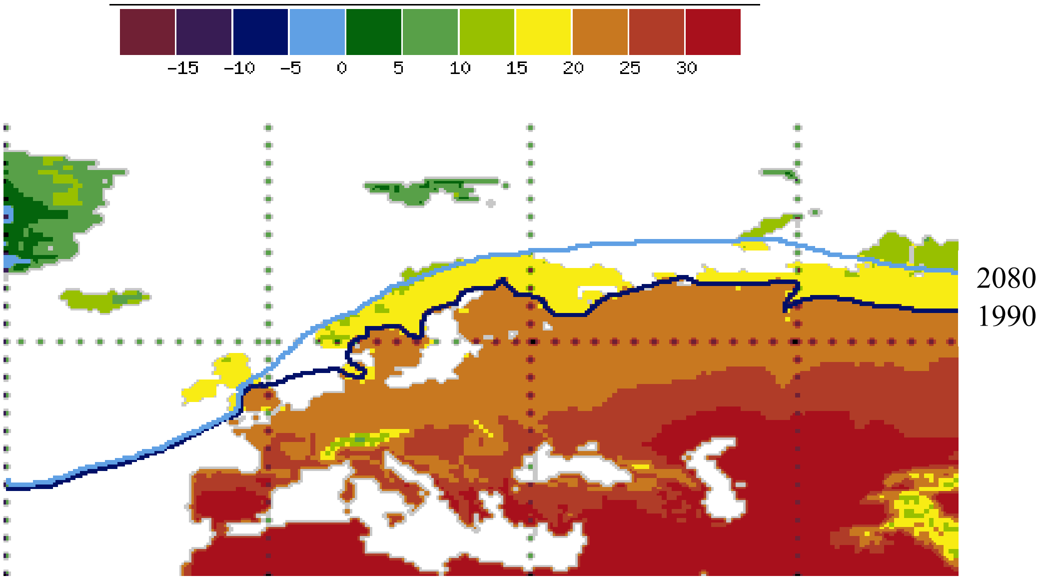

Figure 2.8 Mean maximum July air temperature (°C) for observed 1961-1990 climatology. The lower (black) line is the 20 °C mean July isotherm for 1969-1990 and the upper (blue) line is the 20 °C mean July isotherm predicted for 2080 from HadCM2 general circulation model scenario IS92a. These isotherms are the predicted limits of thermal stress at which heat loss mechanisms other than evaporative cooling are required. Data from the IPCC (http://ipcc-dcc.cru.uea.ac.uk). Temperatures (°C) are given in the legend.

The upper air temperature threshold of the thermoneutral zone for Great Skuas was predicted to be 10.6 °C whilst 20.6 °C was the threshold for effective thermoregulation by employing evaporative cooling (panting) at a maximal rate.

While this threshold was estimated by comparison of predicted positive energy balance with operative and air temperature measurements made over two years at one site (Foula, Shetland), within-year variation in heat stress conditions was far greater than that observed between sites or years (compare Figure 2.5 with Figures 2.6 & 2.7) indicating that these thresholds are likely to hold throughout the entire breeding range of the Great Skua. Within the temperature range between these two thresholds, birds can thermoregulate by panting/gullar fluttering alone but over ~20 ºC other heat loss behaviours become necessary. Figure 2.8 shows the current distribution of this upper thermal limit and that forecast for 2080, throughout the regions where Great Skuas breed (see Figure 2.1). The breeding distribution of Great Skuas in the late 1980s showed marked association with the 13 °C mean July isotherm at the end of the nineteenth century (Figure 2.1) (Furness, 1988) rather than current estimated 20 °C thermal limit (Figure 2.8). This suggests that although Great Skuas are able to cope physiologically in air temperatures above 13 °C, regular daily exposure to these temperatures may require time-consuming thermoregulatory activities, such as bathing, to be traded-off against essential breeding activities. Alternatively, Great Skuas may not be restricted to breeding in regions where July air temperatures remain below 13° C but, as a result of their high philopatry (Hamer 2001), may have yet to spread to suitable locations beyond the southern range margins (this is explored in Chapter 5).

Within the next 80 years, a large proportion of possible breeding locations for the Great Skua will regularly exceed the thermal limit at which adults are required to thermoregulate by panting at a maximal rate (Figure 2.8). However, because the current distribution is restricted close to the 13 °C isotherm only very few current colonies, such as those on Nova Zemlya, will experience regular critical heat stress as a consequence of this change. Even so, it should be anticipated, given the forecast rates of climatic warming at high-latitudes (Houghton *et al.* 2001), that thermoregulatory demands will increasingly influence the foundation of future breeding colonies.

2.4.3 The biophysical model

Energy contribution from all heat transfer processes approximated the ranges quoted in the literature for studies of birds and mammals (Table 2.6), with the main differences arising from use of different species and environmental conditions. The heat transfer processes that were most important in determining modeled heat stress for Great Skuas were metabolic heat generation, maximal evaporative cooling, conductive and convective heat loss. The model was correspondingly most sensitive to the parameters that influenced these processes: wind speed, ground and air temperatures and short-wave solar radiation, the size of the bird and characteristics of its plumage and feet (the route for conductive heat loss). Changes in heat stress with latitude and year primarily resulted from changes in conductive and convective heat loss, whereas seasonal variation was driven by breeding activity and corresponding changes in metabolic heat production. Great Skuas are known to have both high basal (Bryant & Furness, 1995) and field metabolic rates (Hamer *et al.*, 1991; Phillips *et al.*, 1999) so it is unsurprising that metabolic activity contributes primarily to heat stress. Basal metabolic rate (BMR) is known to vary between species breeding at different latitudes (Ellis, 1984), and low BMR is often cited as an adaptation for avoiding heat stress at low latitudes (Klaassen, 1994). Thus, the high metabolic rates of Great Skuas may become disadvantageous at lower latitudes.

Table 2.6 Mean energy values for modeled heat transfer processes and those available in the literature. Study conditions for published data are given. Metabolic heat generation and evaporative cooling were derived from the literature (see methods, section 2.2.2)

	Mean energy contribution (Wm^{-2})			
Heat transfer component	This study	Published values	Study conditions	Source
Convection	55.8	20.9, 41.8	hypothetical bird at 20 °C, different wind speeds	Calder & King (1974)
Conduction	68.4	28.0, 40.0	pig at 20 °C, different substrate	Mount (1967)
Net Radiation	39.3	5.0, 31.3	sheep at 15 and 36 °C	Monteith & Unsworth (1990)
		20.0, 70.0	rabbits, different seasons	Althoff *et al.* (1997)

Conductive heat loss via the feet is suspected to be important for marine birds (Lustick, 1984) and, in the absence of active panting, is predicted to be the primary method of heat loss for Great Skuas. Convective heat loss is of slightly lesser importance than conductive heat loss because of the high plumage mass and hard scales on the legs of skuas (Furness, 1988) restricting heat loss to the webbing of the feet. In the maximal model, evaporative loss was the primary form of heat loss, which is the case for birds at high air temperatures (Dawson & Hudson, 1994), but the capacity for energy loss by this process did not vary greatly with time or location (Table 2.5).

The model accurately predicted heat stress at Foula in 2002 and 2003, daily predicted energy balance explaining 40 % of the variability in operative temperatures. The relative temporal and spatial predictions of the model were realistic despite the following assumptions. Energy balance was modeled as a daily snapshot at the time when positive energy balance was most probable and so did not account for the duration of the exposure. Chronic exposure may be important in determining how heat stress impacts on breeding because many birds are able to store excess heat over small time scales (Phillips *et al.*, 1985). The shape of an animal, here simplified to a sphere, may greatly influence convective heat loss (Calder & King, 1974) because shape affects the friction, and consequently the width of the boundary layer, between the animal's surface and the air (Porter *et al.*, 2000). Bakken (1990) found that the exponent describing the dependence of convection on windspeed (see Eqn. 2.13) varied between 0.5-1.0 for taxanomic mounts of six bird species. The assumption of a spherical shape therefore, probably leads to substantial errors in estimation of absolute, although not relative, convective heat loss at high wind speeds but, because of the model sensitivity to wind speed (Table 2.3), positive heat stress was already very unlikely under these conditions. Although extremes in evaporative cooling were modeled, changes in behaviour (e.g. orientation, posturing, flying, utilizing water) and physiology (e.g. changes in blood circulation and therefore temperature of the legs and feet) (Lustick, 1984) were not accounted for and these may allow birds to reduce positive energy balance below critical thresholds. Orientation with respect to the sun (reducing exposed surface area, increasing insulation of exposed surface and exposing the white surfaces) can alter net radiative transfer by as much as 130 Wm^{-2} for Herring Gulls (*Larus argentatus*) (Lustick, Battersby & Kelty, 1978) but this is probably less effective for Great Skuas, that have a more uniformly dark plumage. Even so, further heat loss can be achieved by immersing feet in water (Lustick *et al.* 1978), and presumably even more from bathing. Consequently, output from the model reflected critical thresholds at which such adjustments would be required, not lethal limits.

Results from these modeling activities suggest that breeding Great Skuas only rarely experience the critical heat stress conditions under which thermoregulatory behaviours other than panting become necessary. Great Skaus are transequatorial migrants (Furness, 1987) and presumably utilize such behaviours as bathing, soaring at high altitudes and resting on water (increasing conductive heat loss) (Lustick, 1984) to cope with higher heat stress at low latitudes. Similar methods are probably used at breeding colonies in Shetland and Orkney, near the lower latitude margin of their breeding range, since current heat stress conditions do not appear to significantly impair breeding. Given forecast climatic warming, however, several colonies in arctic Russia and any new colonies founded to the south of the current range will be subject to conditions that necessitate regular use of thermoregulatory behaviours other than panting, such as bathing, that may be traded-off against breeding activities.

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Chapter 3.

Bathing behaviour of a high-latitude seabird: relationships with ambient temperature and foraging activity

Summary

Climate warming at high latitudes has the potential to impair breeding in cold-adapted homeotherms by increasing heat stress during daily activities. Bathing has previously been suggested as being important for thermoregulation mainly in hot desert areas, but it is also a way in which high-latitude species such as Great Skuas *Catharacta skua* (Brünnich) may reduce heat stress at breeding sites. At a colony in the south of their breeding range, Great Skuas bathed more during periods of greater heat stress, both within each day and comparing between days. Time spent bathing was inversely related to time spent foraging, and pairs given supplementary food not only reduced their foraging activity but also increased their time spent bathing in addition to increasing their territorial attendance. Thus, in addition to a trade-off between foraging and territorial attendance, there was also a trade-off between foraging and bathing. This trend is exemplified by large and consistent reductions in the size of bathing flocks in years when food availability was low. The ability of high-latitude homeotherms to alter their daily activity budgets in response to heat stress has implications for models predicting changes in the distributions of species in response to climate change. Currently, however, climate change is more likely to affect Great Skuas and other high-latitude seabirds by altering food availability than through direct physiological effects (see Chapter 6).

3.1 Introduction

There is growing evidence that climate change over the past 30 years has had profound impacts on a wide range of species (Moore 2003; Parmesan & Yohe 2003; Root *et al*. 2003). However, the nature of this evidence varies greatly between taxa. For short-lived or poikilothermic organisms, there is a strong indication of shifts in distribution and abundance (Parmesan *et al*. 1999; Pounds, Fogden & Campbell 1999). In contrast, for longer-lived homeothermic taxa such as birds, current data primarily concern changes in phenology (reviewed in Root et al. 2003) and breeding success (e.g. Winkel & Hudde (1997)). Climate envelope models of the relationship between climate and distribution have predicted range retractions and population declines leading to large-scale extinctions of birds, based on forecast changes in distributions of suitable climate space (Thomas *et al*. 2004). However, current evidence of climate-induced range shifts and population changes is limited (Smith *et al*. 1999; Thomas & Lennon 1999; Croxall, Trathan & Murphy 2002) and some studies have concluded that bird distributions have not yet been affected by climate (Archaux 2004). Those climatic influences that are evident for long-lived marine predators have been found to act indirectly, altering food and habitat availability (Micol & Jouventin, 2001; Croxall, Trathan & Murphy, 2002), rather than by directly changing species' thermoregulatory requirements, and consequent shifts in species distribution have lagged behind climatic change (Weimerskirch *et al.*, 2003). Recent climate change has been at a rate unprecedented within the last 10,000 years (Huntley 1995) but, even so, homeotherms may have been able to make physiological or behavioural adjustments to reduce the possible direct impacts (Pearson & Dawson 2003) and limit range shifts over the short-term. For instance, individuals may reduce heat stress by altering posture (Lustick 1984; Lustick, Adam & Hinko 1980) or orientation with respect to the sun (Lustick, Battersby & Kelty 1978), by soaring at high altitudes (Piersma 2002) or by active panting and gular fluttering (Dawson & Hudson 1994). Orientation in Herring Gulls (*Larus* argentatus) can reduce heat stress temporarily by as much as 130 Wm^{-2} (Lustick, Battersby & Kelty, 1978) and because air temperature drops by 5-10 Celsius degrees (C°) per km altitude, depending on saturation (Monteith & Unsworth, 1990), high-altitude flight can also quickly reduce heat stress. Individuals may also reduce heat stress by drinking or bathing in cool water: this not only lowers core body temperature but also replaces water lost during panting, and probably requires less energy than prolonged panting (Dawson & Hudson 1970; Hand, Hunt & Warner 1981). Bathing is presumably a more effective heat-loss method than standing in water, which in turn is thought to allow greater heat loss than changes in orientation (Lustick *et al.*, 1978). However, no studies to date have examined the importance of bathing as a response to thermoregulatory conditions.

Seabirds breeding at high latitudes display morphological and physiological adaptations to low ambient temperatures, including heavy insulative plumage and high basal metabolic rates (Gabrielsen, Mehlum & Karlsen 1988; Bryant & Furness 1995), and so might be expected to experience problems of heat dissipation at higher temperatures. Climate warming is predicted to be greatest at high latitudes (Houghton *et al*. 2001) but there are currently few data addressing the capacity of individuals to employ behavioural means to reduce the direct physiological impacts of climate warming in these areas. Great Skuas *Catharacta skua* (Brünnich) have a breeding distribution confined to colonies where mean temperature is < 13 °C during July, the month of most intense breeding activity (Furness 1988). It has been suggested that problems of heat dissipation may inhibit foraging activity and be a critical factor in determining this species' southern range margin (Furness 1988). Both Great Skuas and Tristan Skuas *Catharacta hamiltoni* (Hagen) have been observed to bathe communally at freshwater lakes near their breeding territories, although whether the main function of this activity is thermoregulation, feather maintenance or social interaction is currently unclear (Furness 1987).

In this study, the bathing activity of Great Skuas was examined at a colony in the south of their breeding range to determine its importance in thermoregulation. Possible trade-offs with foraging and chick-guarding activities were examined and the influence of food availability on bathing activity was explored by experimentally supplementing adult diets.

3.2 Methods

Fieldwork was carried out at the Great Skua colony (approx. 2400 breeding pairs) at Foula, Shetland (60°08’N, 2°05’W), in the southern part of this species’ breeding distribution (Mitchell *et al.* 2004), during the breeding seasons (5 May - 6 August) of 1994, 2002 and 2003.

3.2.1 Developing an index for heat stress conditions

Relative humidity, air and soil temperature, solar radiation and wind speed were logged as 10 min means using Data Hog II™ loggers (Skye Instruments Limited, Wales, UK) on breeding territories. At the same time, the internal temperature of a water-filled copper sphere of radius 75 mm, covered with a feathered Great Skua pelage and placed at the colony was logged. This approximated the operative temperature of an unheated taxidermic mount with surface area equal to that of an adult Great Skua. Such models provide acceptable approximations of thermal loading by measuring the temperature that the body would attain in the absence of metabolic heat production or evaporative cooling (Walsberg & Weathers 1986).

The range of values for the most complete time-series of climate variables and operative temperatures measured simultaneously at Great Skua territories during the warmest part of the day are given in Table 3.1. Recorded operative temperatures and climatic variables were normalised by square-root or arc-sine transformation (Table 3.1); normality assessed by probability plots (Zar, 1999).

The transformed data series was reordered randomly to remove autocorrelation, reducing the dependence of values at time *t* on those at time *t*-1 (Shumway & Stoffer 2000).

Table 3.1 Descriptive statistics (untransformed) and transformations for all logged variables used in regression analysis of predicted operative temperature. This series was logged at Ristie (60°09'16.1 N, 2°04"58.1 W, Altitude 60m) from 13:00 to 16:00 BST between 15 May and 5 August 2003 (n = 1577).

Logged Variable	Mean	Minimum	Maximum	Transformation
Relative Humidity (%)	83.4	62.9	100.0	Arcsin
Air Temperature (°C)	15.1	6.9	24.8	Square-root
Soil Temperature at 30 mm depth (° C)	17.3	8.1	26.1	Square-root
Direct Solar Radiation (Wm^{-2})	414.5	25.1	884.7	Square-root
Wind Speed (m sec^{-1})	2.48	0.00	9.95	Square-root
Operative Temperature (°C)	17.6	8.0	30.0	Square-root

The model that best predicted operative temperature from normalised climatic variables was determined by best subset regression (Draper & Smith 1998). This indicated the best regression model from a set of models with different numbers of predictor variables (in this case limited to between 1 and 4), to retain variable *combinations* that may be important rather than discarding variables according to their *individual* contributions (stepwise regression). Since there were strong correlations between the logged environmental variables, such as air temperature and solar radiation (Spearman rank: $r_{s\ 11832} = 0.61$, $P < 0.001$), many regression models with multiple predictors suffered from multicollinearity and were discarded (Draper & Smith, 1998). Transformed air temperature ($\sqrt{T_a}$) explained the most variation in transformed operative temperature ($\sqrt{T_e}$) ($F_{1,1576} = 7037.1$, $P < 0.001$, $R^2 = 0.81$), according to the following equation:

$$\sqrt{T_e} = \{-0.1465 + (1.114\sqrt{T_a})\} \qquad \text{Eqn. 3.1}$$

By squaring the right hand-side of this equation, operative temperatures (an index of heat stress that breeding adults experienced) were estimated in all three years because empirical measurements were not available for 1994.

To verify that operative temperature estimates derived in this way were a good index of heat stress conditions, heat stress behaviours (panting, gullar fluttering and wing drooping) were observed for Great Skuas at their breeding territories in 2002 and 2003. The presence or absence of these behaviours and whether a bird was incubating/brooding or not was recorded between 13:00-16:00 BST at 10 minute intervals, for over 72 breeding individuals in each year. These behavioural watches were repeated at least five times during each breeding season, giving up to 12 hours of continuous observation for some individuals in a year.

3.2.2 Bathing activity

Birds at the main freshwater bathing site on Foula (Mill Loch) were observed through a 20 × telescope from a distance of < 60 m for periods of 3-12 hours on a minimum of 17 occasions spanning the breeding season each year. On each occasion, the number of birds bathing every 10 mins and the number of birds joining the bathing flock during each 10-min interval was recorded. These data were then used to calculate the average flock size (mean of counts at start and end of 10-min interval) and the flock turnover rate (number of arrivals divided by average flock size). The mean duration of bathing bouts was then calculated as recording interval divided by turnover rate. Comparison of the number of birds bathing (flock size multiplied by turnover rate) on different days was restricted to observations between 14:00h and 16:00h because all daily observations included this period. The length of individual bathing bouts was also sampled for a subset of individuals in 2002 and 2003 (n =179): each bout, from arrival at the loch until the end of bathing, was timed by direct observation.

Several hundred Great Skuas breeding at Foula have been colour-ringed since 1988 (Hamer *et al*. 1991; Ratcliffe *et al*. 2002). Colour-ring combinations of individuals roosting and preening beside the bathing site were recorded in 2002 and 2003. The breeding status of these birds was then determined from observations at breeding territories.

3.2.3 Relationship between bathing and foraging

In order to determine how bathing activity was related to day-to-day variation in foraging conditions around the colony, the mean number of birds attending breeding territories was determined from spot counts of at least 70 territories on the same days that bathing activity was recorded. Since breeding Great Skuas only leave their territories to forage or bathe (Furness 1987), and time spent bathing is thought to represent only 1 % of the time activity budget of breeders

(Ratcliffe & Furness, 1999), daily attendance measured in this way is a reliable index of foraging effort (Hamer *et al*. 1991; Caldow & Furness 2000).

To provide an experimental assessment of the influence of foraging on bathing activity, 32 breeding pairs were selected in 2003 from an area of colony about 200 m north of Mill Loch. Sixteen of these pairs were given 600 g of cat-food, placed on their territory between 10:00 and 12:00 BST on nine days between late incubation and the middle of chick-rearing. This represented about 45 % of the daily food requirements of birds (adults plus chicks) in each territory (Ratcliffe 1993). Birds at all territories readily consumed supplements by the third occasion that they were provided. There was no difference between supplemented and control pairs in brood size or hatching date of first chick (brood size: $\chi^2_2 = 1.06$, P = 0.6; hatching date: $t_{32} = 0.34$, P = 0.7). Unfortunately, only a few of these birds were colour-ringed and so age and sex of individual adults was not possible to determine accurately. The time that adults spent away from territory foraging and bathing plus the number and duration of each type of trip were recorded from 13:00-16:00 BST on the final six days of supplementary feeding, when all supplements were consumed. Bathing and foraging are the two main activities performed off-territory (Furness 1987), and occasions when adults flew towards Mill Loch or returned to the territory with saturated plumage, not attempting to feed their chicks and eliciting no begging responses from their partners were assumed to be bathing trips.

3.2.4 Analyses

A generalized linear mixed effect model (GLMM) (Schall, 1991) with binomial error distribution and logit link was fitted, using Genstat software (Payne 1997), to determine the relationship between the probability of breeding skuas exhibiting heat stress behaviours and estimated operative temperature. This model accounted for variation resulting from incubating/brooding activity, breeding site, stage of breeding cycle and year by including these as covariate fixed factors and used the identity of individuals and breeding pairs as random factors to avoid pseudoreplication and non-independence. Wald statistics are reported for components from GLMM analyses and their significance determined by comparison with percentiles of the χ^2-distribution (Elston, Horgan & Hunter, 2001).

A generalized linear model (GLM) with Poisson error distribution and logarithmic link function was fitted to determine the effect of the factors, operative temperature, adult territorial attendance, date and year, on the number of Great Skuas bathing between 14:00 and 16:00 each day. A separate GLM, with Poisson errors and logarithmic link, and including the same factors, examined yearly differences in only the number of colour-ringed breeders bathing within this time period, for 2002 and 2003. A GLM with normal errors and identity link function, appropriate for normally-distributed response data (Nelder & Wedderburn, 1972), was used to examine the relationship between the length of individually observed bathing bouts and operative temperature, with mean flock-size (at the beginning of a bout), daily adult attendance and year as covariate factors, to control for their effects on bathing length.

A series of generalized linear mixed models (GLMM) (Schall 1991) were fitted to determine the effect of supplementary feeding on bathing and foraging activity of breeding pairs (see Table 3.2 for response variables), accounting for variation resulting from breeding stage (egg or chick), brood size, hatching date, operative temperature, adult territorial attendance and date by including these as covariate fixed factors. The identity of each pair was included as a random factor in these models to account for pseudoreplication. Errors had Poisson distributions with logarithm-link functions in models 1 and 2, and binomial distributions with logit-link functions in models 3-6 (Table 3.2).

3.3 Results

3.3.1 Measuring heat stress

The probability of breeding Great Skuas exhibiting heat stress behaviour was positively correlated with operative temperature estimated from the regression with air temperature (Figure 3.1). Of all significant covariates, operative temperature was the second strongest predictor of heat stress behaviour, after whether a bird was incubating/brooding or not (mean (± SE) probability of

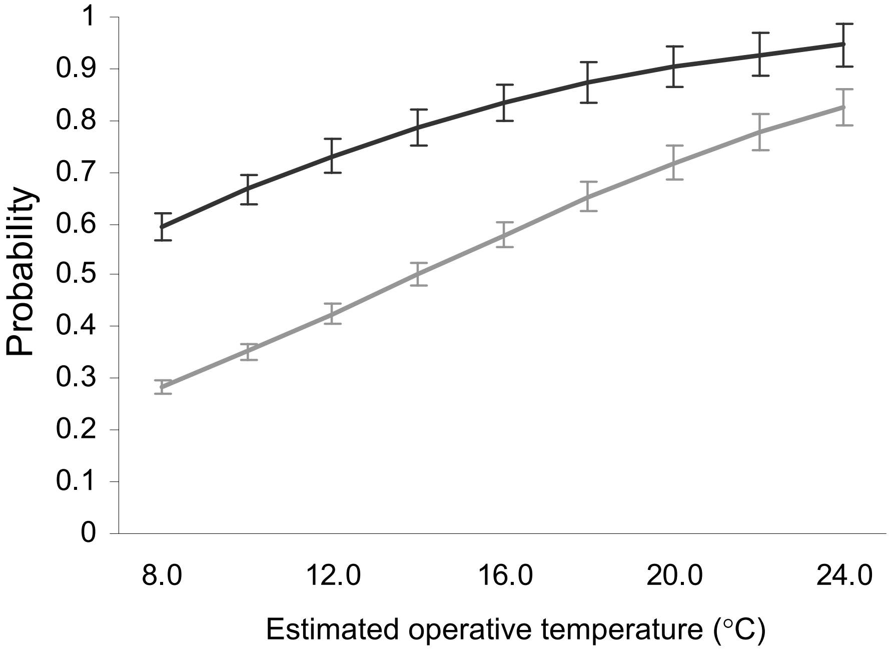

Figure 3.1 Mean probability of adult Great Skuas exhibiting heat stress behaviour at different operative temperatures in 2002 (black) and 2003 (grey). Probabilities are estimated from components of the most parsimonious GLMMs, error bars are standard errors of the estimates. Data shown are for actively incubating skuas breeding at Fleck. The effect of operative temperature was highly significant (GLMM: $\chi^2_{1,10619} = 44.74$, $P < 0.001$, $n = 10750$). Yearly differences were also significant (GLMM: $\chi^2_{1,10619} = 9.72$, $P < 0.01$, $n = 10750$).

exhibiting heat stress behaviour: when incubating/brooding, 0.23 (± 0.001) , otherwise, 0.02 (± 0.001) ; GLMM: $\chi^2_{1,10619} = 524.8$, $P < 0.01$, $n = 10750$).

3.3.2 Bathing activity

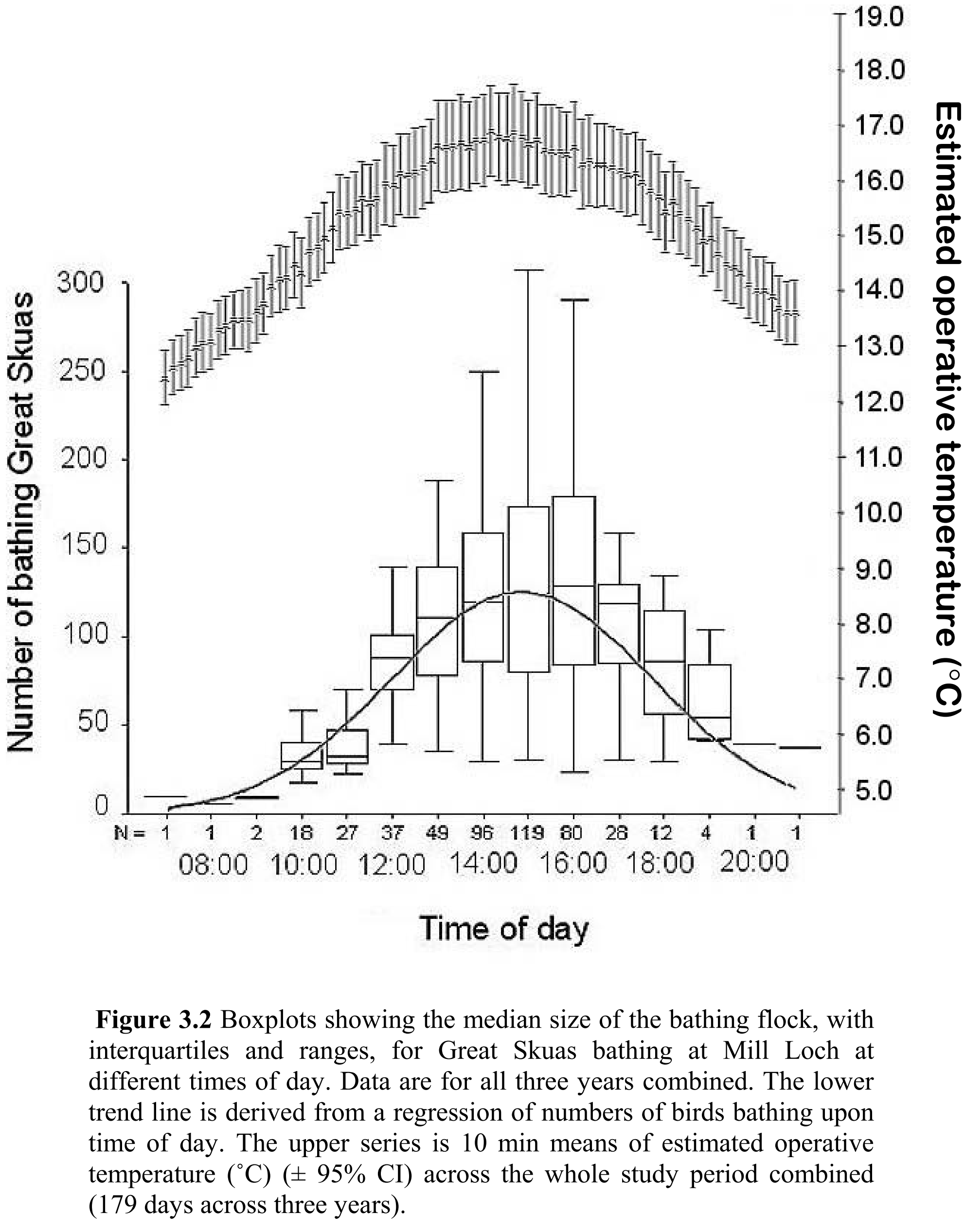

Figure 3.2 Boxplots showing the median size of the bathing flock, with interquartiles and ranges, for Great Skuas bathing at Mill Loch at different times of day. Data are for all three years combined. The lower trend line is derived from a regression of numbers of birds bathing upon time of day. The upper series is 10 min means of estimated operative temperature (˚C) (± 95% CI) across the whole study period combined (179 days across three years).

On average, 2.3% (SD ± 1.7) of birds bathing at Mill Loch were colour-ringed individuals known to be breeding in 2002 and 2003, with no difference in this proportion between years (GLM: t27 = 1.25, P = 0.2). Fewer than 10 % of Great Skuas breeding at Foula are colour-ringed (Catry *et al.* 1998; Ratcliffe *et al.* 2002) suggesting that at any one time more than 20% of the bathing flock (including unmarked birds) at Mill Loch were breeders. The average size of bathing flocks during each hour showed a daily cycle, with time of day explaining 44% of the total variation in numbers ($F_{2, 473} = 188.8$, $P < 0.001$, $R^2 = 0.44$; Figure 3.2). There was a peak between 14:00h and 16:00h in both operative temperature and size of bathing flocks (Figure 3.2), indicating that more birds bathed under warmer conditions. More importantly, within each year, the overall number of birds bathing within this peak period each day was significantly greater on days of higher mean operative temperature (GLM: $t_{29} = 12.54$, df = 1, $P < 0.001$; Figure 3.3). This value incorporated not only flock size but flock turnover (birds arriving and leaving during this period) and indicated that the overall number of Great Skuas bathing was higher on days of elevated heat stress. Most bathing activities involved drinking and complete immersion, also indicating the likely importance of this activity for heat-loss and thermoregulation.

The number of birds bathing was higher in 1994 than in 2002 (GLM: $t_{29} = 15.46$, df = 1, $P < 0.001$) or 2003 (GLM: $t_{29} = 35.75$, df = 1, $P < 0.001$; Figure 3.3). Again, bathing number was the product of flock size and flock turnover and because flock size and turnover were negatively correlated with one another ($r_s = -0.61$, $n = 280$, $P < 0.001$) more birds bathed on days when midday bathing flocks

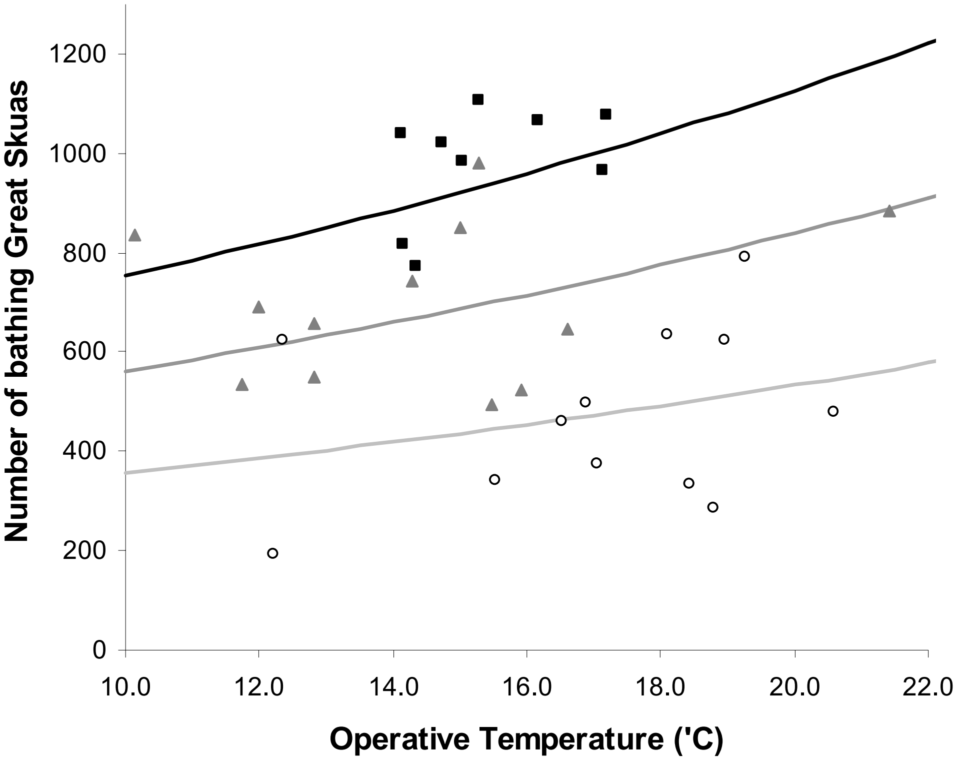

Figure 3.3 Daily total number of Great Skuas bathing at Mill Loch between peak hours (14:00 –16: 00) at different estimated operative temperatures in all years: 1994 (black squares and dark line), 2002 (grey triangles and grey line) and 2003 (open circles and light grey line). Regression lines are derived from GLM analysis ($F_{5,24} = 428.75$, $P < 0.001$).

were small, but had high turnover. Consequently, individual bathing bouts calculated from turnover rate were shorter in small flocks because of high flock turnover. As a result of larger bathing numbers in 1994 (Figure 3.3), and correspondingly smaller bathing flocks with higher flock turnover, bathing bouts were much shorter in 1994 than in 2002 or 2003 (median = 10.0 mins, interquartile range [IQR] = 1.9; median = 19.8 mins, IQR = 13.2 and median = 30.5 mins, IQR = 24.8 respectively;

Kruskall-Wallis test; $H_{2,35} = 25.7$, $P < 0.001$). Direct observations of lengths of individual bathing bouts confirmed this year effect (GLM: $F_{1,178} = 95.17$, n= 179, $P > 0.001$) and revealed a positive relationship between operative temperature and bathing length, independent of flock size (Figure 3.4). More birds also bathed later in the season in all three years (GLM: $t_{29} = 4.49$, df = 1, $P < 0.001$).

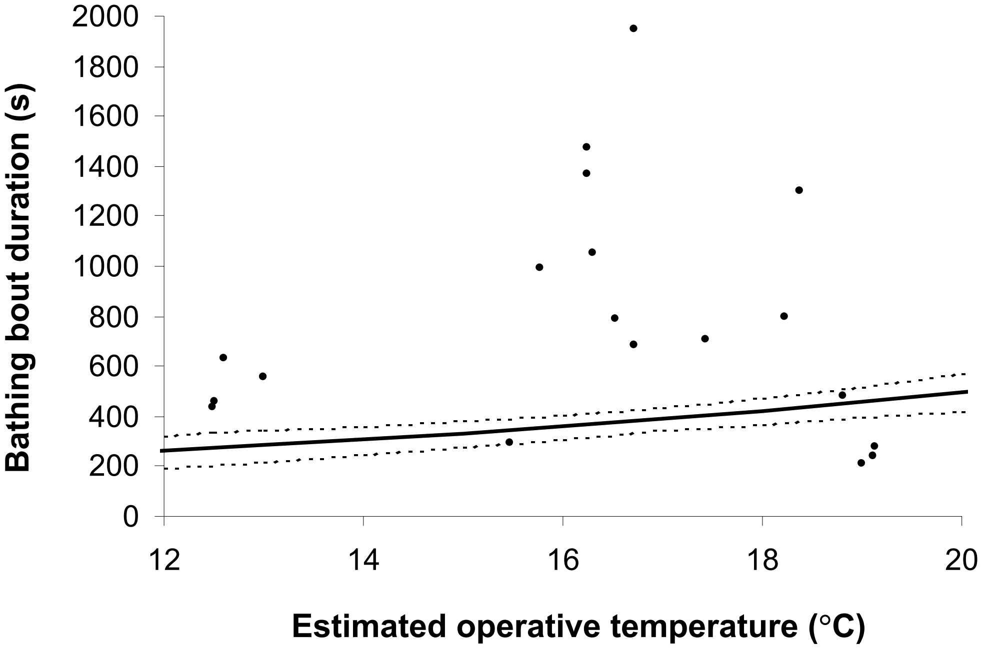

Figure 3.4 Predicted relationship between length of individual bathing bouts and estimated operative temperature from GLM analysis ($F_{1,178} = 4.26$, n= 179, $P > 0.05$). Mean flock-size, food availability (adult attendance) and year (2002 and 2003) were included in the model as as covariates. Dotted lines are ± 1 S.E..

3.3.3 Bathing in relation to foraging

After accounting for the effect of operative temperature on bathing activity, more birds bathed on days when territorial attendance was high and presumably foraging conditions were good (GLM: $t_{29} = 5.62$, df =1, $P < 0.001$). Adult territorial attendance was not, however, related to mean daily operative temperature on days during which bathing was observed (Spearman rank correlation: $r_s = -1.05$, $n = 30$, $P = 0.6$). Pairs given supplementary food spent significantly more time bathing and less time foraging than did control pairs (Table 3.2). Supplemented pairs also made more bathing trips and significantly fewer foraging trips, which were shorter in duration than those of controls (Table 3.2). In addition, supplemented pairs had significantly higher attendance (% time) at their breeding territories than did control pairs (supplemented median = 73.1%, IQR = 26.3; control median = 64.3%, IQR = 27.6; Wilcoxon signed-ranks test; $Z_{61} = 2.92$, $P < 0.005$).

Table 3.2 Results of statistical analysis (GLMM) of the effect of supplementary feeding on Great Skua time budgets between 13:00-16:00 BST. Means and variability of supplemented and non-supplemented pairs, Wald statistics and significance values (df =1, n = 146) are given for each variable.

Model	Response Variable	Mean (± SD)		Wald statistic (χ^2)	P value
		Fed	Unfed		
1	Number of bathing trips (in 3 hr)	1.02 (0.10)	0.58 (0.07)	13.67	< 0.001
2	Number of foraging trips (in 3 hr)	0.32 (0.04)	0.42 (0.04)	5.03	< 0.05
3	Time spent bathing (% of 3 hr watch)	12.2 (1.3)	8.6 (1.2)	4.20	< 0.001
4	Time spent foraging (% of 3 hr watch)	14.7 (2.5)	27.1 (2.5)	10.92	< 0.001
5	Mean bathing trip duration (min)	16.7 (1.6)	14.9 (1.6)	0.43	0.514
6	Mean foraging trip duration (min)	24.4 (4.5)	47.8 (4.8)	11.31	< 0.001

3.4 Discussion

There was a clear diurnal cycle in freshwater bathing activity, with largest bathing flocks occurring during the period of maximum operative temperature (Figure 3.2). Operative temperature was a good predictor of heat stress conditions, indicated by a strong correlation with the observed frequency of heat-loss behaviour in breeding Great Skuas, but this pattern could reflect diurnal variation in foraging activity rather than variation in heat stress. However, the number of birds bathing was also greater on days of overall higher operative temperature within each year (Figure 3.3), suggesting that this variation in time spent bathing was in direct response to heat stress conditions. Bathing appears to be important because, despite cannibalism being the main cause of breeding failure in this species (Hamer, 2001), adults left their territories and chicks in order to bathe and at least 20% of birds bathing at Mill Loch were breeders.

Bathing and drinking have been cited as being of possible importance for thermoregulation and water balance (Dawson & Hudson 1970), but the few previous field studies of this phenomenon were restricted to low-latitude species (Thomas & Robin 1977). For example, in the Morrocon steppe, more sandgrouse were found to utilise freshwater sites for drinking on hotter days (Thomas & Robin 1977). This is the first time that variation in activity budgets in response to heat stress conditions has been documented for a homeotherm breeding at high-latitudes.

Adult attendance at breeding territories was not related to operative temperature but more birds bathed on days when territorial attendance was high and foraging conditions were presumably good, irrespective of heat stress conditions. Increased bathing could have primarily reflected the activity of non-breeders rather than breeding birds. However, breeding birds given supplementary food not only spent less time foraging but also spent more time spent bathing, and made more bathing trips in addition to spending more time on territory. This increase in time spent bathing by fed pairs was only one third of that for territorial attendance, indicating the relative importance of these two activities for breeding Great Skuas. These data show that in addition to a trade-off between foraging and territorial attendance, there was also a trade-off between foraging and bathing.

Breeding success of Great Skuas at Foula was higher in 1994 (0.8 chicks pair^{-1}) than in 2002 (0.6 chicks pair^{-1}) or 2003 (0.1 chicks pair^{-1}), due largely to lower prey availability in the latter years (Walsh, Brindley & Heubeck 1995; Mavor *et al.* 2002, 2003). Breeding success in this species is known to decrease with increasing time spent off-territory (Catry & Furness, 1999; Caldow & Furness, 2000), usually as a result of elevated foraging effort when food is scarce (Hamer, Furness & Caldow, 1991). Bathing numbers were highest in 1994 but reduced in 2002 and even lower in 2003 (Figure 3.3) probably as a result of bathing being traded-off for increased foraging time in the latter two years. The probability of breeding Great Skuas exhibiting heat loss behaviours, such as panting and gullar fluttering, on territory was higher in 2002 than 2003 (Figure 3.1). This probably resulted from very poor food availability in 2003 causing high breeding failure and limiting breeding in that year to the most experienced pairs (Chapter 4). These individuals are known to exhibit enhanced coordination of their breeding activities (Caldow & Furness, 2000) that presumably led to reduced mean individual metabolic expenditure for breeders in 2003 and lower intensities of heat stress experienced (Chapter 2). Durations of bathing bouts showed the opposite pattern to that seen in bathing activity, being longest in 2003 and shortest in 1994 and suggesting a negative relationship between the number of birds bathing and the time spent bathing per individual. Observations at the bathing loch suggested that in large bathing flocks, interruptions to bathing caused by interactions with other conspecifics often led individuals to prolong bathing bouts. Irrespective of flock size, though, individual bathing bouts were longer on days of higher operative temperature, suggesting that thermoregulation, rather than social interaction, is the primary purpose of freshwater bathing. Bathing numbers were also higher later in the season in all three years but this was probably due to the arrival of large numbers of non-breeders at the colony (Klomp & Furness 1992).

Climate change currently appears more likely to affect Great Skuas and other high-latitude seabirds by altering food availability than by direct physiological effects (Durant, Anker-Nilssen & Stenseth 2003; Croxall 2004). However, heat stress for animals breeding at high latitudes is likely to become increasingly important given projected rises of up to 6 C° in air temperatures within the next 100 years (Houghton *et al*. 2001). Great Skuas and probably many other vertebrates adapted for breeding in these regions have the ability to ameliorate the effects of rising temperatures by employing heat-loss behaviours such as bathing, which offer a way to supplement energetically-costly thermoregulatory behaviour such as panting, with fewer problems of water conservation. However, any time spent bathing is traded-off against that available for foraging, and so it could impose an additional constraint on reproductive success, particularly in years of low food availability. All these factors indicate that, even if currently climatic change is impacting species indirectly, rapid temperature rise at high-latitudes may begin to impact directly on the physiology and ecology of species and should be accommodated in models forecasting the consequences of changing climates.

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Chapter 4.

Within-colony variation in the breeding ecology of Great Skuas in relation to heat stress

Summary

Aspects of the breeding ecology of Great Skuas may vary within colonies in relation to nest-site location and microclimate, and studying such local-scale variation could lead to improved predictions of influences of climate change on breeding distributions. The breeding ecology of Great Skuas was examined at sites on Foula, Shetland, that differed in altitude, proximity to coast and thermal exposure, using both natural and experimentally enlarged broods. Sites differed by up to 3 Celsius degrees (C°) in operative temperatures experienced by adults. Foraging time was traded-off for extra bathing time at the warmest site but at higher altitudes foraging effort was higher, bathing was less frequent and birds reduced thermal loading by panting on territory. Despite this, there were no differences in breeding performance at different altitudes, indicating that behavioural responses were sufficient to cope with variation in thermal regimes. Forecast temperature rises in the UK are less extreme than at higher latitudes and food availability currently appears to be more important than heat stress in determining Great Skua breeding performance and distribution.

4.1 Introduction

Climate warming in the late twentieth century was greater than at any previous time over the last 10,000 years (Huntley, 1995). Mean global air temperature is projected to rise by as much as 5.8 Celsius degrees (C°) between 1990-2100 and at high latitudes in America and Asia this change is likely to be 40 % higher than the global mean (Houghton *et al.*, 2001). In northern Europe, conservative estimates for increases in air temperature are around 6.5 C° by 2080 for arctic and subarctic regions (from climate models using A1B SRES scenario (Houghton *et al.*, 2001)). At the margins of their range, populations persist in areas of broadly unsuitable habitat (Thomas *et al.*, 1999; Thomas *et al.*, 2001). By selecting the areas of highest suitability available within these marginal regions, many species maintain viable breeding populations (Thomas *et al.*, 1999; Hill *et al.*, 2002; van der Ree & Bennett, 2003). It is likely that climate warming at low-latitude range margins will quickly enhance the competitiveness of insurgent species from lower latitudes, displacing these marginal populations (Davis *et al.*, 1998; Thomas *et al.*, 2001). Given the scale of range shifts predicted to result from changing climatic conditions (Thomas *et al.*, 2004), even populations in less marginal areas are likely to become restricted to high quality sites as climatic suitability diminishes. In order to predict climate-induced range shifts with any accuracy, heterogeneity in site quality must be determined, especially the availability of sites that may still maintain suitable microclimates following climatic warming.

Many seabirds have wide geographical distributions but are restricted within these areas to particular breeding sites (Buckley & Buckley, 1980) and, within colonies, there is often great variation in nest-site quality (Montevecchi & Wells, 1984; Burger & Gochfeld, 1991; Stokes & Boersma, 1991; Harris *et al.*, 1997). Suitable cover provided by vegetation, rocks or ledges can limit the exposure to thermal extremes experienced by breeding adults and their chicks (Salzman, 1982; Buttemer & Astheimer, 1990; Stokes & Boersma, 1998) and so reduce the requirement for brooding (Klaassen, 1994). Such cover can also increase the breeding success of ground-nesting seabirds by reducing the proportion of eggs lost to predators (Cassady & St. Clair, 1996; Stokes & Boersma, 1998; Mallach & Leberg, 1999; Good, 2002; Velando & Freire, 2003) and limiting intraspecific aggression at high breeding densities (Burger & Gochfeld, 1988; Cassady & St. Clair, 1996). Other important characteristics of nest sites are proximity to water (Burger & Lesser, 1978; Hand, Hunt & Warner, 1981), including freshwater for drinking and bathing (for Great Skuas, Kittiwakes and Fulmars at Foula (Furness, 1987; Furness, pers. comm.), and suitable prey (Young, 1963; Pierotti & Annett, 1991; Votier *et al.*, 2004).

Great Skuas (*Catharacta skua*) have a breeding distribution restricted to northern Europe and arctic Russia (Hamer, 2001). The largest breeding colonies for this species are in the northern British Isles (Mitchell *et al.*, 2004), less than 300 miles from the southern range margin. Adult Great Skuas exhibit high natal philopatry (Klomp & Furness, 1992), with territory size and location varying little between years (Catry, Ratcliffe & Furness, 1997). At Foula, Shetland, the second largest Great Skua colony in the world (Mitchell *et al.*, 2004), breeding pairs nest primarily amongst wet moorland vegetation (Hamer, 2001) but occupy a wide range of sites, varying in exposure, altitude and vegetation. The impacts of this variation in microclimate on breeding ecology have not previously been assessed.

This chapter reports the influences of site (location and vegetation) and microclimate on breeding biology, examined for Great Skuas at Foula in 2002 and 2003. In 2003, some adults were given experimentally enlarged broods to illustrate the importance of any site and microclimate effects observed. In both years, breeding parameters and aspects of time/activity budgets were recorded at different sites with distinct microclimates.

4.2 Methods

Fieldwork was carried out at Foula during the breeding seasons (5 May - 6 August) of 2002 and 2003. Foula is a small island (~ 14 km^2) that supports over 2400 breeding pairs of Great Skua, and has been the site of a long-term study of this species since the mid-1970s (Ratcliffe & Furness, 1999).

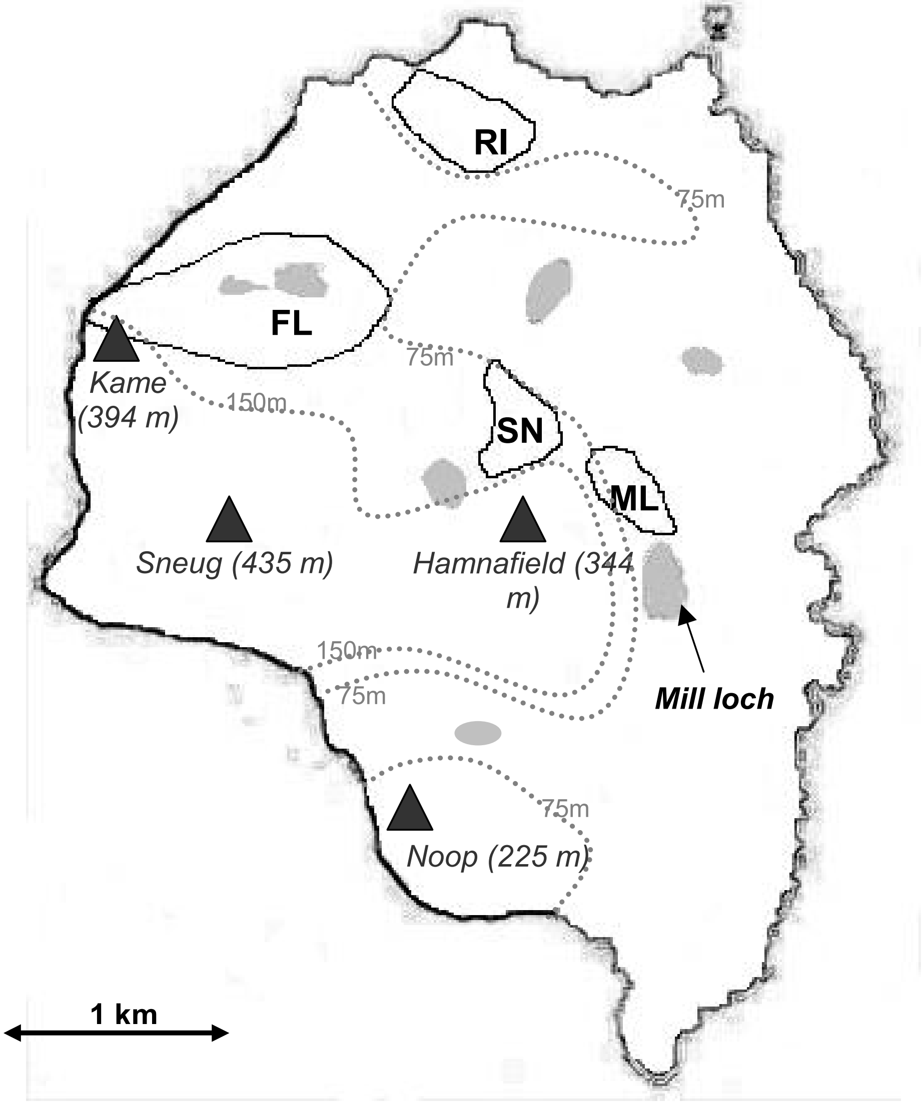

Figure 4.1 Map of Foula showing the four study sites, Fleck (FL), Mill Loch (ML), Ristie Marsh (RI) and South Netherfandal (SN). Bathing lochs are represented by grey shading and Mill Loch, the main bathing site, is labelled. Black triangles indicate the island's four major summits (height in m). Broken lines are 75 m and 150m contours.

Table 4.1 Details of study sites at Foula in 2002 and 2003, including location (point at which environmental measurements were taken), aspect (direction of maximum exposure to the sky), altitude, maximum number of study nests followed, number of behavioural watches and minimum and maximum daily (24hr mean) operative temperatures over days in which behavioural watches took place.

					2002			2003		
	Easting	Northing	Aspect (compass direction)	Altitude (m)	Total no. study nests	No. behavioural watches	Max, min daily operative temperature (º C)	Total no. study nests	No. behavioural watches	Max, min daily operative temperature (º C)
Fleck	-2º05’36.5	60º08’39.7	N	129	22	5	12.1, 14.8	70	5	15.0, 19.6
Mill Loch	-2º03’54.8	60º08’16.6	E	41	21	5	12.3, 16.2	-	-	-
Ristie	-2º04’58.1	60º09’16.1	SSE	60	20	5	13.9, 17.0	53	5	15.4, 19.4
South Netherfandal	-2º04’14.4	60º08’33.8	ESE	82	22	5	11.5, 14.8	-	-	-

4.2.1 Selecting study sites

Four sites of contrasting altitude and exposure (Fleck, Mill Loch, Ristie Marsh and South Netherfandal) were selected to examine how nest site microclimate and location influenced breeding activity and reproductive success (Figure 4.1, Table 4.1). These sites differed in distance from the main freshwater bathing loch, Mill Loch (Figure 4.1). Although some sites had smaller freshwater lochs nearby, these were far less important for bathing, supporting bathing flocks never exceeding ~50 Great Skuas (pers. obs.), compared with flocks sizes of over 100 birds observed daily at Mill Loch (Chapter 3, Figure 3.2). The number of nests followed each year is given in Table 4.1. Different territories were selected at each site each year to avoid non-independence of data. To reduce variation associated with parental quality,pairs laying more than ten days from the modal laying date in each year were not selected for study.

In 2002, egg laying and hatching dates and the growth and survival of chicks were measured at each site, and adult behaviour was observed during incubation and chick-rearing. Since operative temperature was greatest at Ristie Marsh and lowest at The Fleck in 2002 (Figure 4.2), in 2003 the same observations were made only at these two sites. In 2003, the energetic cost of breeding was increased for all study pairs by experimentally increasing each brood to three chicks, under licence from Scottish Natural Heritage (SNH). Chicks were transferred from donor nests (matched by laying date) between 1-3 days after hatching. Only two of these manipulations failed, when the donor chicks were either rejected or left the surrogate nest: these were excluded from subsequent analyses and the two chicks were placed at alternative nests not included in the study.

4.2.2 Measuring microclimate and site-specific differences in vegetation cover

Operative temperature for the whole study period was estimated from measurements of air temperature, at 10 min intervals at each site, using the regression equation (Eqn. 3.1):

$$\sqrt{T_e} = \{-0.1465 + (1.114\sqrt{T_a})\},$$

developed in chapter 3 (regression statistics: $F_{1,1576} = 7037.1$, $P < 0.001$, $R^2 = 0.81$). Since all sites were within two kilometres of each other, between-site heterogeneity in microclimate was limited to differences in sea mist frequency, orographic rainfall (precipitation caused by forced upwards flow of air over hills), both related to altitude and aspect, and the shading of sites by steep hills early and late in the day. Relative humidity (RH) provided a strong measure of mist intensity and rainfall, and solar radiation (Qs) accurately recorded shading at different sites (pers obs). Both of these measures were highly correlated with air temperature (RH: $r_{s\ 19716} = -0.51$, $P < 0.001$; Qs: $r_{s\ 19716} = 0.59$, $P < 0.001$) once autocorrelation was removed by randomizing the time series (Shumway & Stoffer, 2000)(Chapter 3), indicating that trends in operative temperature accounted for the main differences in microclimate between sites.

Percentage cover, sward height and vegetation type contributing most to nest-cover (in all cases grasses) were estimated from a sample of five 1 m^2 quadrats at each breeding site in 2002. Quadrats were placed according to random number cell selection within a grid map of each site. Soil moisture was estimated in each quadrat by measuring water uptake (mm of paper wetted in five seconds) on a strip of blotting paper (10 mm width) inserted 10 mm into the soil.

4.2.3 Timing of breeding, hatching success, chick growth and survival

Ages of study adults were determined from colour-ring combinations (birds had been ringed as chicks with a monel ring and subsequently recaptured and colour-ringed (Hamer, Furness & Caldow, 1991; Ratcliffe *et al.*, 2002). In both 2002 and 2003, the laying date of the first egg of each study pair was determined by visiting nests every second day during the laying period. The volume of the first laid egg was calculated from its length and breadth (Coulson, Potts & Horobin, 1969).

Nest checks were resumed 25 days after laying (modal incubation period at Foula is 28 days (Hamer, 2001)) to determine hatching success, and continued until chicks had fledged. Growth of chicks from study nests was determined by measurement of body mass and wing length (maximum chord excluding down (Redfern & Clark, 2001)) every four to seven days until fledging. Chicks were individually colour-marked under license from SNH using a combination of nail varnish on the claws and sheep-marker spray on the breast. Following Hamer et al. (1991), chicks were recorded as dead if they were not located on three consecutive visits to the territory. .

4.2.4 Adult behaviour and territorial attendance

To examine variation in adult behaviour between sites, five behavioural watches were made at each site in both years (Table 4.1). All watches spanned the period 13:00-16:00 BST, when operative temperature was found to be highest (Chapter 3, Figure 3.2). During watches, the behaviour of both adults of a focal pair (maximum sample size per site: 13 pairs in 2002, 24 pairs in 2003) was recorded from spot-checks at 10 min intervals, providing up to 12 hours of observation for each individual in a year. In 2003, focal adults at both sites were matched by brood size and hatch date (± 1 day), to ensure broadly comparable samples despite small sizes. Adults that were present on territory were recorded as incubating/brooding, bathing (if bathing within their territory) or other (roosting, standing, preening and territorial defense). If adults exhibited heat-loss behaviour (panting, gular-fluttering or drinking) this was also recorded. If absent from the territory an adult was categorized as either bathing or foraging since these are the only two activities commonly performed off-territory (Furness, 1987; Catry & Furness, 1999). Bathing trips were distinguished by adults flying towards freshwater lochs or, when they returned, having saturated plumage or not attempting to feed their chicks and eliciting no begging response from their partner. If neither adult was on territory the nest site was counted as deserted for that spot check.

For each observation, stage in the breeding cycle of focal adult was defined as follows: incubation (between laying and hatching date of first egg), early chick-rearing (up to 12 days after hatching), mid chick-rearing (13-34 days after hatching) and late-chick rearing (35-44 days after hatching).

4.2.5 Foraging conditions, nesting density and diet

Several covariates were measured to reduce variance not resulting from differences in site or heat stress exposure. The proportion of pairs attending breeding territories, determined daily from spot counts of at least 70 territories in both years, was used as a proxy for foraging conditions in the vicinity of the colony (Hamer *et al.*, 1991). In both years, mean distance between a study nest and its two nearest neighbours was used to indicate territory size. Diets of birds at each territory were assessed from regurgitated pellets collected from all territories twice in 2003 (during early-mid laying and late chick-rearing). In each case, these data were used to calculate the proportion of pellets at each territory that comprised seabirds. Diet was included in analyses only for 2003 because data were not available for all sites in 2002.

4.2.6 Analyses

All statistical analyses were performed using Genstat (Genstat, 1993) software unless otherwise specified. All between-site differences in environmental variables recorded in 2002 were compared with ANOVA. Paired *t*-tests contrasted simultaneous operative temperature measurements between The Fleck and Ristie Marsh in 2003. A generalized linear mixed effect model (GLMM) (Schall, 1991) with normal error distribution and identity link function, for the analysis of normally distributed data (Nelder & Wedderburn, 1972), determined yearly differences in paired operative temperature measurements (made simultaneously at different sites), with pairing identity included as a random factor to avoid pseudoreplication. Wald statistics are reported for components from GLMM analyses, their significance determined by comparison with percentiles of the χ^2-distribution (Elston, Horgan & Hunter, 2001).

Variation between sites and years in clutch size, nesting density, egg volume and laying date was compared with separate general linear models (GLMs) to ensure that study pairs at different sites were comparable. The former GLM was fitted with binomial errors and logit link with laying date and first egg volume included as covariates. All other GLMs had normal errors, identity links and included brood size (prior to manipulation), territory size, and (for laying date analysis only) egg volume as covariates. Site-specific and yearly differences in hatching success were examined in a GLM with binomial errors and logit link, incorporating laying date, volume of the first egg and territory size as covariates.

Mass and maximum wing chord growth of chicks were analyzed separately in non-linear mixed effects models (NLMEs) because few complete growth curves were available for individual chicks because of small sample sizes and high chick mortality. In these models wing and mass had a logistic relationship with age:

$$\text{Mass (or wing)} = \varphi / 1 + e^{-\,k\,(\text{age} - t0)} \qquad \text{Eqn. 5.1}$$

where, φ = asymptote, k = scale parameter and t_0 = point of inflection. Models were fitted in S-plus (Insightful Corporation, 2001) and stepwise addition of factors (year and site) and covariates (egg laying date, brood size, hatching order, survival) determined the most parsimonious model in each case (Pinheiro & Bates, 2000).

In 2002, chicks were not recaptured at regular intervals at each site because more sites were studied and so robust mark-recapture analysis was not possible. Instead, individuals not found during a territory check but recaptured later in the season were removed from the analyses (< 3% of chicks). A GLMM, with binomial errors and logit link, was fitted to determine whether survival varied between sites, accounting for variation resulting from hatching order, brood size and hatching date by including these as covariate fixed factors. The random factors in this model were chick and nest identity, to avoid pseudoreplication from repeated measurements of the same individual and non-independence of siblings, In 2003 recapture rate was only 89 % and Cormack-Jolly-Seber (CJS) mark-recapture models (Cormack, 1964; Jolly, 1965; Seber, 1965) were built and tested using the program MARK (White & Burnham, 1999) to avoid unrealistically low estimations of survival. These models compared recapture and survival probabilities in six recapture periods for chicks at different sites, incorporating hatch date, hatching order and brood size as covariates. Akaike's Information Criterion (Akaike, 1973) corrected for small sample size and overdispersion ($QAIC_c$) was used to select the best model (Burnham & Anderson, 1998). For both years, mean productivity (chicks fledged per nest) for each site was hatching success × overall chick survival (estimated without brood size as a covariate: overall survival then included the combined effect of time period and brood size). Four GLMMs with binomial error distribution and logit links (Models 1, 2, 3 & 4) examined differences between years and sites for different independent variables: the probability of adults exhibiting three different behaviours (heat-loss (1), bathing (2), foraging (3)) and the probability of the nest site being deserted (4). Data were all individual spot checks made during every watch at all sites in both years. Individual and nest identity were random factors to account for repeated measures and non-independence of observations of adults from the same pair, respectively. Covariates entered into maximal models to accommodate their effects on adult behaviour were: heat stress conditions (predicted operative temperature), time of day (as a quadratic factor to account for the daily cycle in activity (Chapter 3, Figure 3.1)), stage in the breeding cycle, adult quality (laying date, volume of first egg), overall nest productivity, daily adult attendance (index of foraging conditions) and nest density. Observations of foraging and bathing were excluded from the heat-loss GLMM (model 1 above) because it was not possible to determine heat-loss when adults were absent from territories. Incubating/brooding behaviour was an additional factor in this model because birds often exhibited heat-loss whilst incubating or brooding. Data from only one member of each pair were used in the desertion GLMM (model 4 above) (the individual was chosen randomly, since sex was undetermined for most birds) and nest number was the only random factor. The effect of diet on adult behaviour was explored with additional GLMMs fitted with data from only 2003, the year in which diet samples were available. To determine whether foraging effort outside this midday period varied between years, a GLM was fitted to data from all morning spot-checks of adult territorial attendance, including date as a covariate to account for changing patterns of attendance throughout the season.

4.3 Results

4.3.1 Nest-site microclimate

Measured operative temperatures (heat stress) varied significantly between sites, differences being most extreme between The Fleck and Ristie Marsh (on average Ristie Marsh was 2.75 ºC warmer) (Figure 4.2). Independent of site effects, operative temperatures were significantly lower in 2003 than 2002 (predicted means from GLMM: 2003, 11.76 °C; 2002, 11:04 °C; GLMM: $\chi^2_{1, 4035} = 67.29$, $P < 0.001$, $n = 4040$), although this difference (mean difference 0.72ºC) was smaller than those between sites (Figure 4.2). Of all breeding sites, the Fleck was characterised by the lowest levels of heat stress, highest frequency of mist and greatest degree of shading (least direct solar radiation) (Figure 4.2). Grasses provided the majority of nest cover at all sites, although at Mill Loch, where grass cover was sparse, many territories were dominated by low-lying mosses (Figure 4.2). Grass sward height was similar at all sites but soils were driest at Mill Loch (Figure 4.2).

4.3.2 Timing of breeding, chick growth, survival and productivity

Breeding density was highest at South Netherfandal (Table 4.2). There were no differences in clutch size or laying date between sites, although clutches were generally smaller and laid later in 2003 than in 2002 (Table 4.2). Hatching success and overall productivity were similar at all sites in both years (Table 4.2).

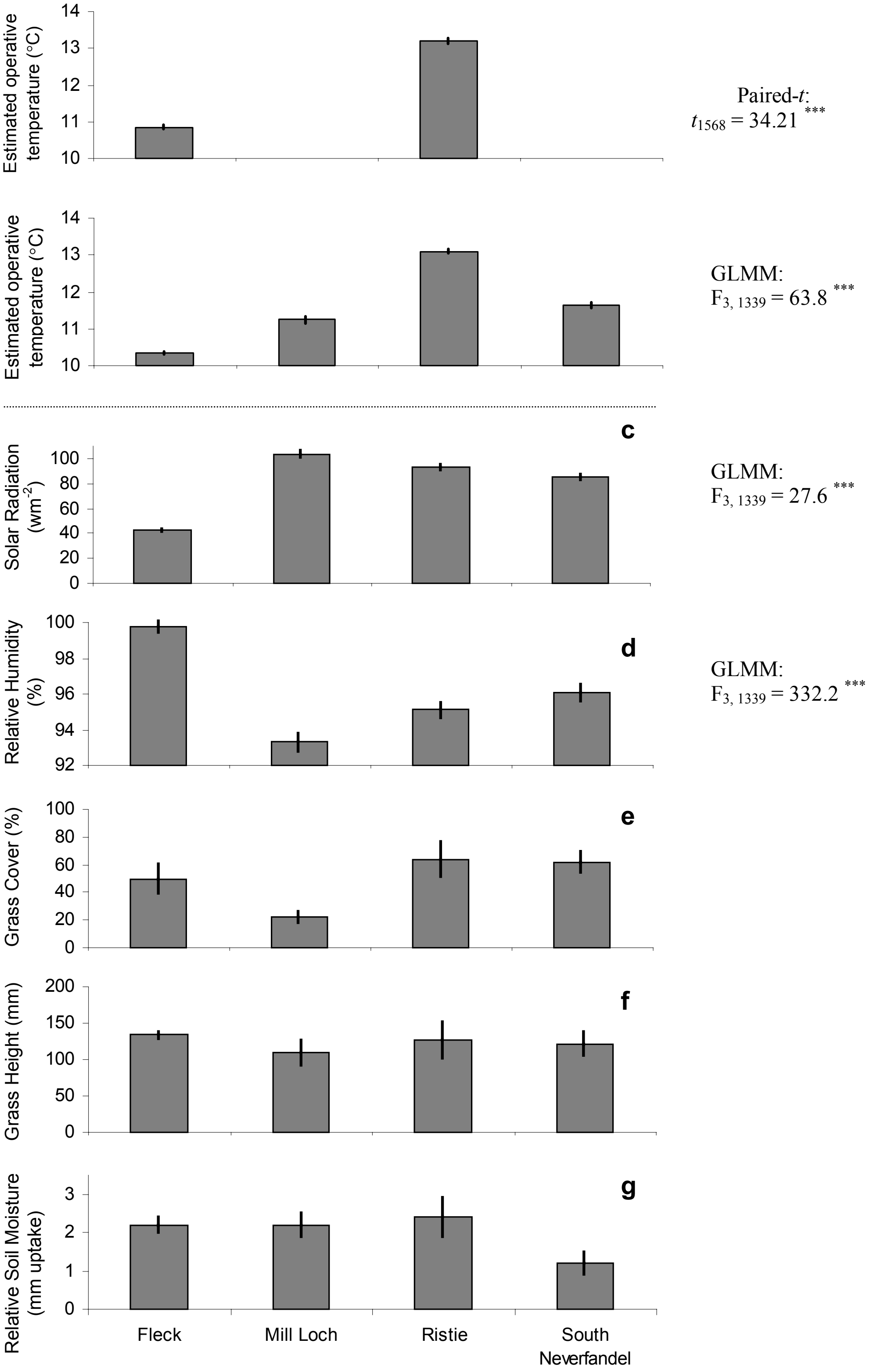

Figure 4.2 Mean (± 1 SE) (a) operative temperature measured at all sites in 2002 and (b) 2003. Mean (± 1 SE) (c) solar radiation, (d) relative humidity, (e) grass cover and (f) height and (g) relative soil moisture at all sites in 2002 are shown for comparison, although some sample sizes were too small for statistical evaluation. Statstics indicated by *** for site-specific differences are highly significant ($P < 0.001$).

Growth in mass of chicks was not significantly different between years (growth asymptote (φ): $t_{611} = 0.78$, df = 428, $P = 0.4$), once variability in growth resulting from eventual fate (whether a chick fledged or died: NLME models projected growth curves for chicks that died during the study), laying date, egg volume, brood size and hatching order had been accounted for (Figure 4.3). However, asymptotic wing length of chicks was significantly lower in 2003 than in 2002 (means from NLME: 2002, 340 mm; 2003, 305 mm; $t_{611} = 5.34$, df = 425, $P < 0.001$). Chicks reared at Mill Loch exhibited small but significant reductions in the rate of growth up to 20 days of age but final asymptotic mass and wing length of chicks was similar at all sites in both years (Mass, Figure 4.3; Wing, logistic parameters: t_0 , $t_{611} = 2.51$, df = 425, $P < 0.05$; k , $t_{611} = 2.62$, df = 425, $P < 0.01$ φ, $t_{611} = 1.17$, df = 425, $P = 0.24$).

Mean chick survival (± SE) was similar in both years, with 64.0 (± 0.1) % of hatching chicks surviving to fledging in 2002 and 72.5 (± 0.1) % in 2003. The significance of these small differences was not possible to determine because of the different methods used in their estimation. Mean chick survival was no different between sites in either year (2002, GLMM, $\chi^2_{1,\,399} = 0.06$, $P = 0.98$, n = 404; 2003, site was excluded from the best fitting CJS model in Table 4.3). In both years, survival was higher in larger broods (2002, GLMM, $\chi^2_{1,\,398} = 64.15$, $P < 0.001$, n = 402; 2003, Table 4.3) but was unaffected by hatching order (2002,GLMM, $\chi^2_{2,\,397} = 2.68$, $P = 0.1$, n = 404, 2003, Table 4.3). Chicks hatched late in the season had a lower survival probability in 2002 (GLMM, $\chi^2_{1,\,401} = 11.49$, $P < 0.001$, n = 404) but hatch date did not significantly influence survival in 2003 (Table 4.3).

Table 4.2 Means (± 1 SE) of various breeding parameters for Great Skuas breeding at different sites and years within the Foula colony. Yearly values (in bold) for combined sites are predicted from GLM (incorporating significant covariates). Significance levels: $^{n.s.}$ P >0.05, ** P < 0.01 and *** P <0.001.

	2002					2003			GLM Test Statistics	
Site	Fleck	Mill Loch	Ristie	South Neverfandel	**All sites**	Fleck	Ristie	**All sites**	Year Comparison	Site Comparison
Sample size (n)	19	18	11	18	**66**	66	51	**117**	-	-
Nearest neighbour distance (m)	52.2 (± 4.2)	53.3 (± 5.5)	61.2 (± 4.6)	41.2 (± 5.2)	**54.1 (± 3.3)**	55.5 (± 2.6)	64.5 (± 3.1)	**57.4 (± 2.4)**	$F_{1,173} = 0.54^{n.s.}$	$F_{3,173} = 5.21^{**.}$
Natural clutch size (eggs)	1.95 (±0.05)	1.83 (± 0.11)	1.83 (± 0.09)	1.94 (± 0.06)	**1.90 (± 0.02)**	1.73 (± 0.05)	1.62 (± 0.07)	**1.68 (± 0.02)**	$F_{1,188} = 10.38^{***}$	$F_{3,185} = 1.13^{n.s.}$
Volume of first egg (mm^3)	84.7 (0.41)	81.6 (±1.4)	81.7 (±1.7)	82.7 (±1.4)	**83.3 (±0.9)**	80.5 (±0.7)	80.9 (±0.8)	**80.5 (±0.6)**	$F_{1,183} = 5.68^{*}$	$F_{3,183} = 0.41^{n.s.}$
Laying date[1] (Julian date)	140.3 (± 1.4)	138.5 (± 1.7)	142.6 (± 1.5)	139.5 (± 1.7)	**139.9 (±0.9)**	143.5 (± 0.9)	145.7 (± 1.1)	**144.4 (± 0.8)**	$F_{1,183} = 17.6^{***}$	$F_{3,178} = 1.69^{n.s.}$
Hatching success (proportion of eggs hatching)	0.75 (± 0.07	0.64 (± 0.10)	0.63 (± 0.09)	0.61 (± 0.10)	**0.66 (± 0.05)**	0.78 (± 0.07)	0.66 (± 0.07)	**0.72 (± 0.06)**	$F_{1,148} = 0.48^{n.s.}$	$F_{3,182} = 0.92^{n.s..}$
Overall productivity (chicks fledged/ nest)[2,3]	0.40 (± 0.15)	0.40 (± 0.20)	0.45 (± 0.20)	0.47 (± 0.20)	**0.42 (± 0.10)**	0.49 (± 0.18)	0.52 (± 0.25)	**0.52 (± 0.18)**	-	n.s. (see text)

[1] means predicted for nests with a natural clutch size of 2, [2] productivity is the sum of hatching success and cumulative chick survival (hatching to fledging), standard errors are cumulative, [3] 2003 data predicted from most parsimonious CJS model (without brood size).

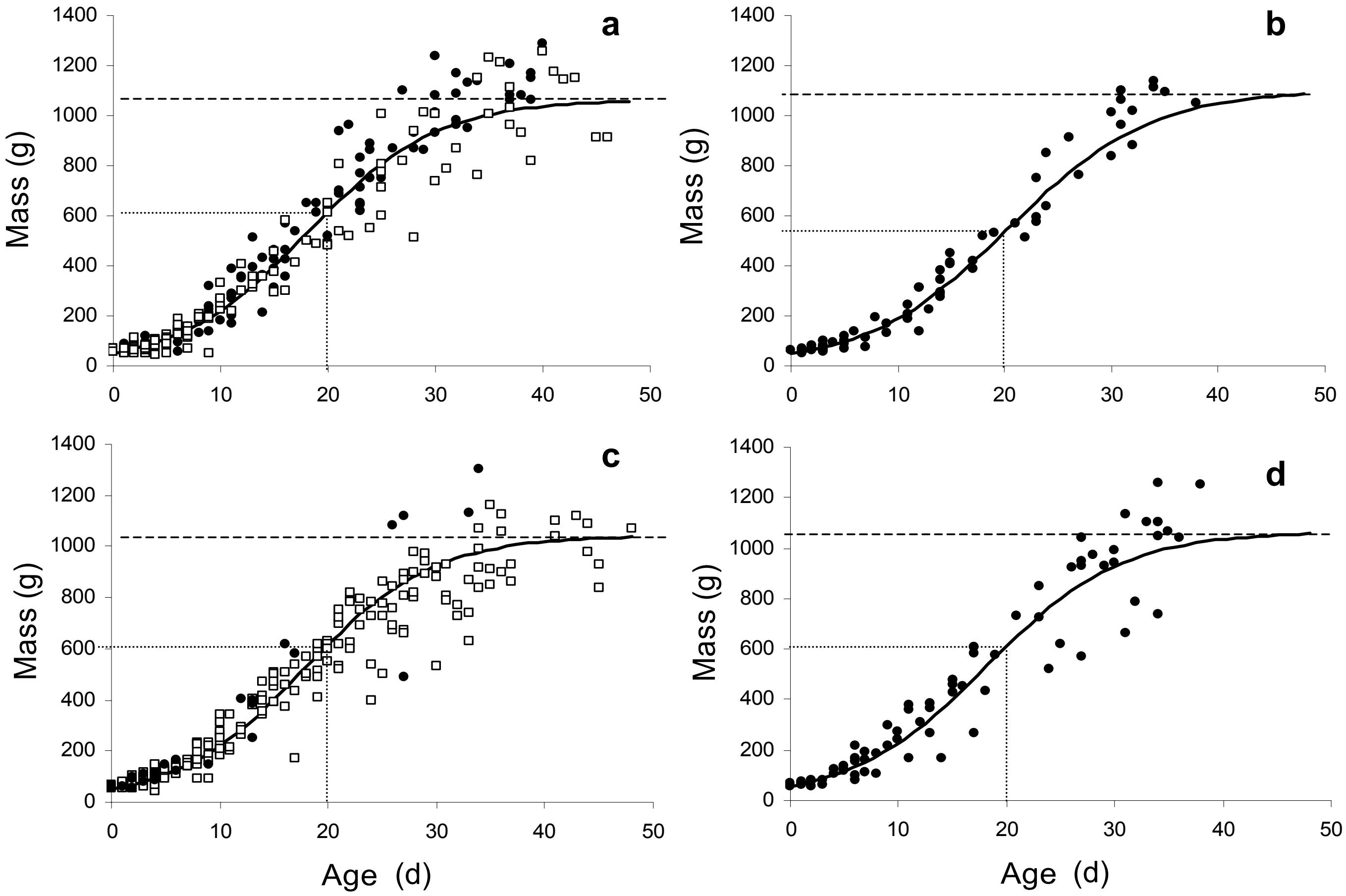

Figure 4.3 Age-specific mass of skua chicks reared at (a) Fleck, (b) Mill Loch, (c) Ristie and (d) South Neverfandel, in 2002 (black circles) and 2003 (open squares). Logistic trend line is from the most parsimonious non-linear mixed effects model, not different between years. Growth asymptote (dashed line) was not significantly different between sites ($t_{611} = 1.29$, df = 445, $P = 0.2$). There was a small but significant reduction in early growth for chicks (dotted line) at Mill-Burns (difference in logistic parameters: t_0, $t_{611} = 2.60$, df = 428, $P < 0.01$; k, $t_{611} = 2.92$, df = 428, $P < 0.01$). Fate of a chick (fledged or dead) ($t_{611} = 4.78$, df = 428, $P < 0.0001$), brood size ($t_{611} = 2.56$, df = 428, $P < 0.05$), egg volume ($t_{611} = 2.67$, df = 428, $P < 0.01$) and hatching order ($t_{611} = 2.94$, df = 428, $P < 0.005$), also significantly influenced growth.

Table 4.3 Most parsimonius CJS model for Great Skua chick survival in 2003 (n = 89) and best model incorporating site differences in survival. Different survival (Φ) and recapture (p) parameters are represented by each term within (): $t_{[x,y]}$ indicate different parameters for recapture periods x and y; period-specific brood-size is included as a covariate. Lowest $QAIC_c$ = 85.16, $\hat{c}$ = 3.56.

No.	Model	No. of parameters	$\Delta QAIC_c$	$QAIC_c$ weight
1	$\Phi(t_{[2\text{-}4,5\text{-}7]}$ +brood size$)/p(t_{[2,3\text{-}7]})$	4	0.00	0.146
2	$\Phi($site + $t_{[2\text{-}4,5\text{-}7]}$ +brood size$)/p(t_{[2,3\text{-}7]})$	5	1.75	0.061

4.3.3 Adult behaviour and territorial attendance

In 2002, the probability of breeding adults exhibiting heat-loss, bathing and foraging behaviour or simultaneously deserting breeding territories between 13:00 and 16:00 BST all differed significantly between sites. The probability of bathing off-territory was highest for adults breeding at Ristie, but heat–loss behaviour was more commonly observed at Fleck and Mill Loch (Figure 4.4). Half of the difference in heat-loss probability between sites was attributable to site-specific differences in operative temperature, although less than 30 % of the difference in bathing probability between sites resulted from differences in microclimate (Table 4.4). Overall site-specific differences, although significant, were small: mean differences in these two behaviours were at most 2 % of the three hour watch period (or 3.6 min) (Figure 4.4). For many birds, however, up to 74 % of watch periods were spent panting and up to 68 % bathing, but individuals varied because of differences in the heat stress exposure within their territories (shading, nest cover and standing water) and their activities prior to the

Table 4.4 Statistics for the effect of site from the most parsimoniuos GLMMs using data from both years but with and without operative temperature included as a factor. When operative temperature is not included in the model, site effects incorporate the effects of operative temperature (microclimate). Changes in the Wald statistic indicate the magnitude of importance of site in the GLMM.

		Without operative temperature			With operative temperature		
	N	Wald χ^2	df	P	Wald χ^2	df	P
Heat-loss	10750	84.74	3,10621	< 0.001	42.85	3,10619	< 0.001
Bathing	14076	14.18	3,12945	0.003	10.77	3,12944	0.013

watch. Differences between sites in the mean probability of bathing were also much higher on days when mean daily operative temperature exceeded 13 °C: at most 9% of the watch (or 16.2 min) was spent bathing off-territory. In 2002, simultaneous desertion of territories by both members of a breeding pair was significantly more frequent at the Fleck than at any other site (Table 4.5).

The mean probability of foraging during the midday period did not differ between years (means from GLMM: 2002, 0.36; 2003, 0.38; GLMM, $\chi^2_{1,12940} = 1.92$, P = 0.17, n = 14076). This was also the case for foraging effort between 10:00 and 11:30 BST, as determined from spot-checks of territorial attendance (GLM: $F_{1,130} = 1.72$, P= 0.19). In 2002, adults breeding at Ristie Marsh foraged for less time (mean probability of foraging = 0.31) than other sites (probability = 0.40) but this was not the case in 2003 (mean probability at all sites ~0.39) (GLMM year*site, $\chi^2_{5,12940} = 13.11$, P < 0.001, n = 14076). In 2003, the probability of adults exhibiting heat-loss behaviour was lower

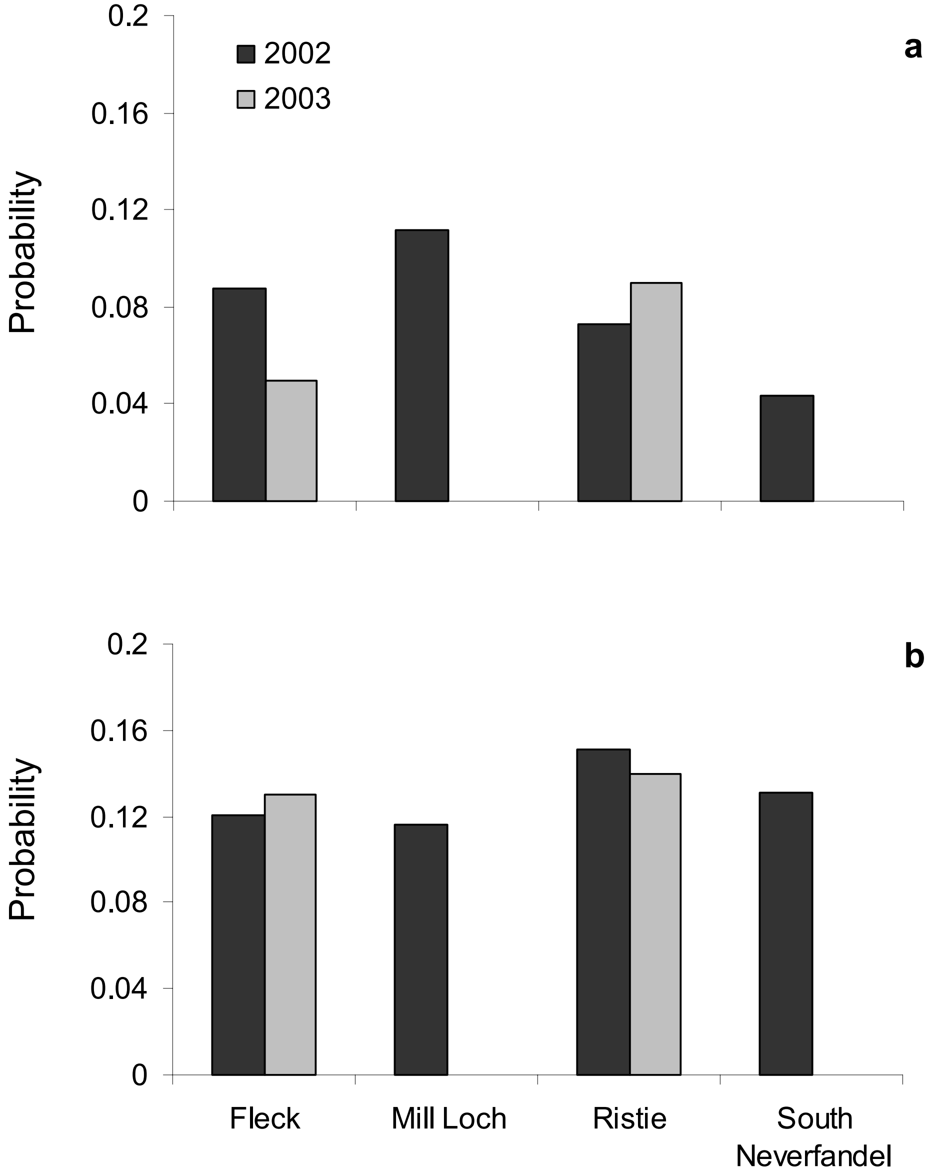

Figure 4.4 Predicted mean probability (from GLMM) of adult Great Skuas exhibiting (a) heat-loss and (b) bathing behaviour between 13:00 and 16:00 shown for all sites studied in 2002 (black) and 2003 (grey). Behavioural observations were limited to the Fleck and Ristie Marsh in 2003. Differences in the incidence of heat-loss and bathing between sites are significant (Table 4.4). In 2003, heat-loss probability was lower at Fleck than Ristie (GLMM: $\chi^2_{1,2147} = 5.51$, $P < 0.05$, $n = 2272$), but bathing probability was not significantly different (GLMM: $\chi^2_{3,4489} = 2.60$, $P = 0.11$, $n = 4766$).

Table 4.5 Probability of simultaneous nest desertion by a breeding pair at all sites in both years. Significance of site-specific differences are from GLMM. Overall, nest desertion was less frequent in 2003 than in 2002 (GLMM: $\chi^2_{1,6888} = 25.21$, $P < 0.001$, $n = 7038$). [a] for $\chi^2_{3,5087}$; [b] for $\chi^2_{3,2273}$.

						Site-specific differences	
Year	Fleck	Mill Loch	Ristie	South Neverfandel	Overall	Wald Statistic	P
2002	0.14	0.09	0.11	0.09	0.12	7.31^a	<0.001
2003	0.08	-	0.07	-	0.08	2.87^b	0.09

at Fleck than at Ristie but there was no difference in probability of bathing off-territory (Figure 4.4). Simultaneous absence of both pairs from breeding territories was also lower in 2003 (Table 4.5).

The probability of adults exhibiting heat-loss and bathing behaviour increased with operative temperature (Figure 4.5). If a bird was incubating or brooding it was far more likely to display heat-loss behaviour (mean probability from GLMM: incubating/brooding, 0.21; not incubating/brooding, 0.02; $\chi^2_{1,10619} = 524.9$, $P < 0.001$, $n = 10750$) and as a result, heat-loss behaviour was far more common during incubation (Figure 4.6).

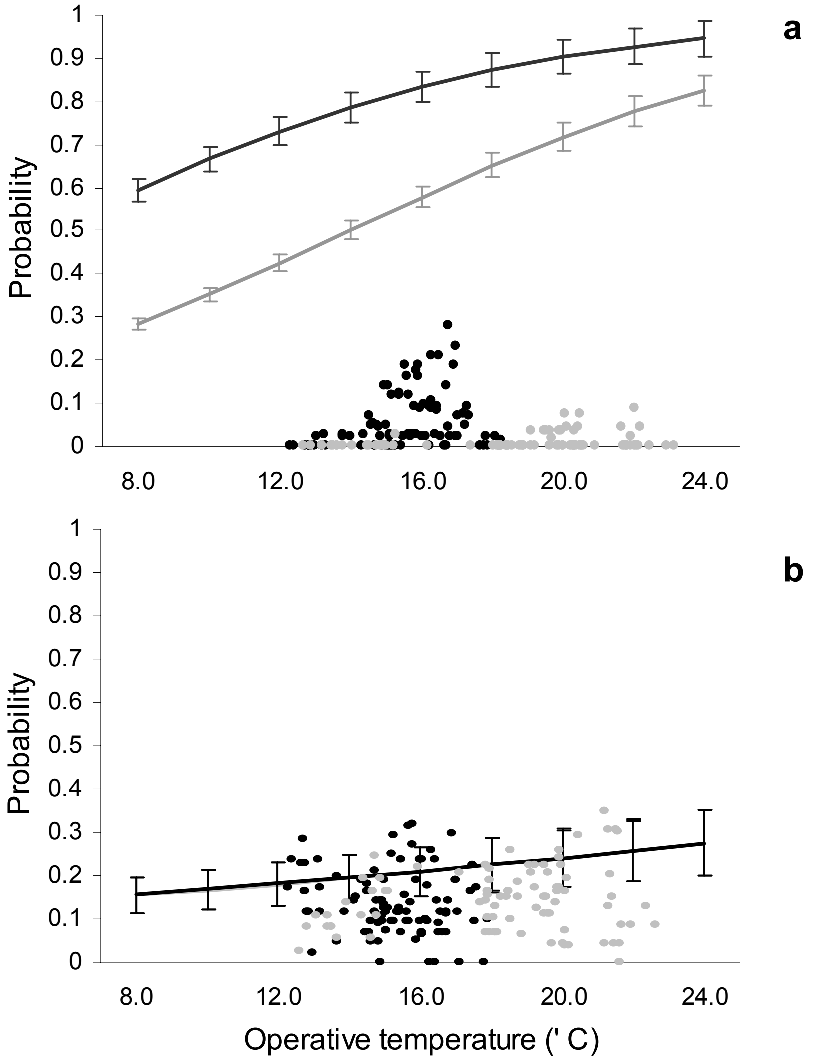

Figure 4.5 Mean probability of adult Great Skuas exhibiting (a) heat-loss and (b) bathing behaviour at different operative temperatures in 2002 (black) and 2003 (grey). Trend lines are probabilities estimated from components of the most parsimonious GLMMs and error bars are standard errors of the estimates. The effect of operative temperature was highly significant for both behaviours (heatloss GLMM: $\chi^2_{1,10619} = 44.74$, $P < 0.001$, $n = 10750$; bathing GLMM: $\chi^2_{1,12944} = 13.21$, $P < 0.001$, $n = 14076$). Predicted heat-loss trends are shown for actively incubating skuas breeding at Fleck once variability resulting from breeding stage was removed, although data are for all individuals at the Fleck at all times during the season. Consequently, observed probabilities are lower than those predicted for actively incubating individuals. Predicted bathing trends are shown for skuas breeding at Fleck once variability resulting from breeding stage, time of day and productivity covariates was removed, and data are for all individuals at the Fleck in all breeding stages, at all times of day and in all productivity categories (0-3 chicks fledged). The predicted trend line for bathing in 2003 is no different from that in 2003 (GLMM: $\chi^2_{1,12943} = 2.04$, $P = 0.15$, $n = 14076$). The effect of operative temperature was highly significant for both behaviours (heatloss GLMM: $\chi^2_{1,10619} = 44.74$, $P < 0.001$, $n = 10750$; bathing GLMM: $\chi^2_{1,12944} = 13.21$, $P < 0.001$, $n = 14076$).

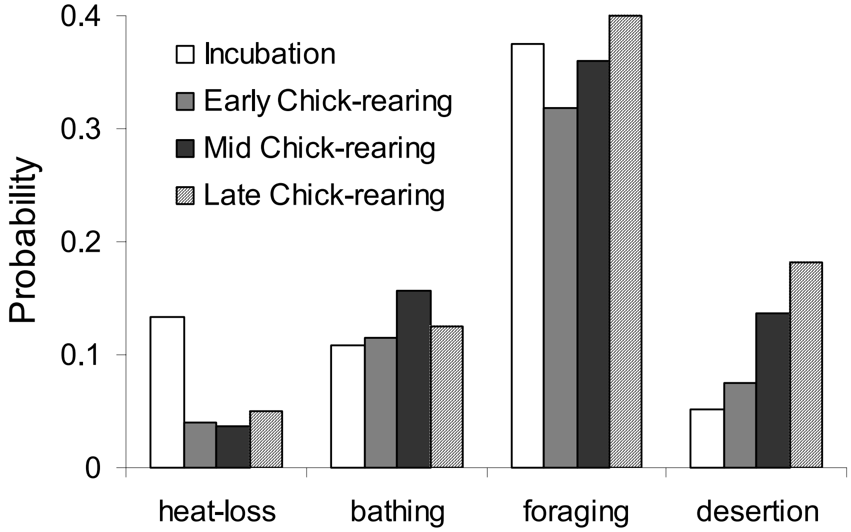

Figure 4.6 Differences in mean probability of skuas exhibiting heat-loss, bathing and foraging behaviours or pairs deserting an active breeding territories at different stages of the breeding season. Probabilities are predicted from GLMMs fitted with data from both years. All between-stage differences are significant (heat-loss GLMM, $\chi^2_{3,10620} = 279.02$, $P < 0.001$, $n = 10750$, bathing GLMM, $\chi^2_{3,12944} = 44.80$, $P < 0.001$, $n = 14076$, foraging GLMM, $\chi^2_{3,12941} = 31.55$, $P < 0.05$, $n = 14076$, desertion GLMM, $\chi^2_{3,6888} = 123.39$, $P < 0.001$, $n = 7038$). Heat-loss probabilities incorporate the influence of incubating/brooding behaviour, without which means are 0.056, 0.043, 0.080, 0.083, for the respective stages.

The prevalence of all behaviours varied significantly during the breeding season (Figure 4.6). Heat-loss behaviour was least common during early chick-rearing (0-12 days old), when foraging rate was also lowest (Figure 4.6). The incidence of foraging behaviour and territorial desertion increased as chicks grew, although foraging was also common during incubation (Figure 4.6). Bathing became more common for adults as their chicks grew but was curtailed just prior to fledging (Figure 4.6).

Breeding skuas that had a diet consisting of a high proportion of seabird exhibited heat-loss behaviour more often ($\chi^2_{1,2145} = 8.25$, $P < 0.01$, $n = 2272$), spent more time foraging ($\chi^2_{1,4447} = 33.1$, $P < 0.001$, $n = 4766$), and were more likely to be simultaneously absent from territories ($\chi^2_{1,2237} = 4.8$, $P < 0.05$, $n = 2383$). However, diet was not significantly different between sites, comprising 31.3 (± 7.2) % seabird at Fleck and 21.3 (± 6.6) % at Ristie (GLM: $F_{1,79} = 1.04$, $P = 0.3$).

4.4 Discussion

4.4.1 Effect of microclimate and nest-site on breeding performance

Despite consistent differences in microclimate between breeding sites, microclimate did not influence breeding success (hatching success or chick survival) or important breeding parameters (laying date, egg volume and clutch size). Altitude shaped the local microclimate of Great Skua breeding sites at Foula: operative temperature at Ristie Marsh (60 m above sea-level) was on average 3 C° more than at the Fleck (129 m above sea-level). Increased frequency of mist at higher elevations reduced exposure to solar radiation, although variation in nesting habitat was less pronounced, grasses being dominant at all sites. Mean global temperature is set to rise by 1.4-5.8 C° by 2100 and by up to 8 C° at higher latitudes (Houghton *et al.*, 2001). Given the relatively large within-colony variation in thermal exposure, an altitudinal shift of breeding sites would be likely to precede any range changes. Currently, however, differences in thermal exposure do not affect the breeding performance of Great Skuas.

Breeding success was below the long-term average at Foula in both years of this study (R.W. Furness unpubl. data). In 2003, breeding conditions were poorer than in 2002, reflected by retarded egg laying, reduced clutch sizes and slower wing growth of chicks, and most probably resulting from low availability of 1-group sandeels around Shetland (Mavor *et al.*, 2004). Operative temperatures were higher on average in 2003, but this difference was small in comparison to site-specific variation and so could not account for these differences in reproductive success. Differences between sites in breeding performance (hatching success, chick growth and survival) were probably obscured by low sandeel abundance (Mavor *et al.*, 2004) causing universally poor performance in this year (Ratcliffe, Furness & Hamer, 1998), especially given the extra reproductive costs imposed by experimentally enlarged broods. It is interesting that breeding success in this study was higher in 2003 (0.52 chicks pair^{-1}; Table 4.2) than that determined for a larger sample at Foula in the same year (0.1 chicks pair^{-1}; Mavor *et al.*, (2004). This probably resulted from experimental brood enlargement during this study because the mean size of broods at fledging was significantly larger in 2003 (1.65 chicks) than 2002 (1.27 chicks), when no brood manipulation was performed ($t_{43} = 2.15$, $P < 0.05$). Even so, no site-specific differences in breeding performance were observed in 2002 either, indicating that differences in microclimate at breeding sites were insufficient to affect breeding success and timing of Great Skuas in either year of the study. Unfortunately, only 19 of all adults studied were of known age so statistical comparison of age between sites was not possible, although the absence of differences in performance between sites suggests that there was no marked difference in the quality of breeders.

4.4.2 Effect of microclimate and nest-site on adult behaviour

Although breeding performance was unaffected, adults were found to be responding behaviourally to levels of thermal stress experienced at breeding sites.

In 2002, Great Skuas breeding at Ristie were significantly more likely than birds at other sites to leave their territories in order to bathe between 13:00 and 16:00 BST, hours of peak thermal stress (Chapter 3, Figure 3.2). These adults also spent less time foraging during this period (on average 25 % less than those at the Fleck) presumably in part resulting from the trade-off between time spent in both activities (Chapter 3). In 2002, however, heat-loss behaviour (panting and gullar fluttering) was not most frequent at Ristie, despite birds at this site experiencing significantly higher operative temperatures. In the same year, Great Skuas breeding at Fleck and Mill Loch, sites of significantly lower operative temperature, exhibited 33 % higher foraging rates and a 22 % lower incidence of bathing, but were observed panting at breeding territories more frequently (27 % more than birds at Ristie). This suggests that increased time spent bathing for birds at Ristie reduced thermal loads to a point where panting was no longer necessary but at Fleck and Mill Loch adults traded-off bathing for extra foraging time and reduced thermal loads by panting on territory. This latter strategy should be most advantageous in the Great Skua, for which territorial attendance prevents cannibalism of chicks by conspecifics (Caldow & Furness, 2000). At Mill Loch, however, both adults of a pair still temporarily deserted territories more often than those at Ristie. Absolute differences between sites were fairly small in comparison to individual differences: on average only a maximum of 11 % of the three hour watch period was spent panting (up to 74 % for some individuals), 14 % spent bathing (up to 68 % for individual birds), and mean differences in these two behaviours between sites was at most 2 % of the watch period (or 3.6 min), although this increased to 9 % (16.2 mins) on warm days. Consequently, it is unsurprising that the mean frequency of nest desertion was not necessarily related to differences in thermal exposure and that there were no overall differences in breeding performance between sites.

Heat loss behaviour (panting, gullar fluttering) and bathing were both most common at high operative temperatures (Figure 4.5) but only heat loss varied between years, being highest in 2002, despite lower mean operative temperatures. Foraging effort for Great Skuas on Foula was no different between years, as determined from observed territorial absence during midday watches and spot checks made between 10:00 and 11:30 BST (Caldow & Furness, 2000). However, the incidence of both birds of a pair being absent from territories was lower in 2003 and chick survival was 10 % higher in this year. This indicates that in 2003 the only breeders that managed to raise chicks were probably the best quality parents, that achieved better coordination of their individual foraging (Caldow & Furness, 2000) and bathing trips. In this year, the incidence of bathing and heat-loss at Fleck and Ristie reflected observed differences in thermal exposure, both being higher at Ristie. Poor breeding for other species in this year, particularly Kittiwakes (*Risa tridactyla*), Puffins (*Fratercula arctica*) and Guillemots (*Uria aalge*) (Mavor *et al.*, 2004), necessitated increased foraging effort for Great Skuas specializing on seabird prey, which is usually a less energetically costly foraging strategy (Votier *et al.*, 2004), although there were no differences in diet between sites.

4.4.3 Differences in susceptibility to microclimate at different breeding stages

Adult Great Skuas were most susceptible to thermal conditions during incubation and when their chicks were close to fledging. Heat loss behaviour was more frequently observed in actively incubating or brooding birds, presumably because these birds were restricted in their ability to alleviate heat stress by altering posture or position (Bartholomew & Dawson, 1979) or utilizing standing water on territory, e.g. Hand *et al.* (1981). Time spent bathing increased concurrently with foraging rate as chicks grew, probably as a result of thermal loading caused by increased metabolic heat-production of active adults (Chapter 2). Bathing activity was curtailed when chicks were close to fledging and panting on territory was common at this time, indicating that during this period bathing was probably traded off for extra foraging opportunity and birds pant to alleviate heat stress.

4.4.4 Impacts of changing climates on breeding Great Skuas

Altitude was the most important factor determining exposure to thermal stress at Foula and skuas at lower altitude sites were more regularly exposed to high operative temperatures. Currently, differences in microclimate seem to be influencing thermoregulatory decisions of breeding Great Skuas, particularly the probability of leaving territories to bathe at freshwater lochs. Behavioural budgets of breeding adults, however, appear sufficiently flexible to accommodate the consequential small reductions in foraging activity at sites of higher thermal stress without a reduction in breeding success. At cooler sites, or when foraging demands were highest, bathing activity was curtailed to increase foraging time and heat was lost instead by panting on territory. Consequently, breeding success was unaffected by differential exposure to heat stress.

Great Skuas at Foula, if temperatures regularly exceed those at which heat-loss by panting becomes insufficient (see Chapter 2), thermoregulation by bathing off-territory may restrict time available for foraging or guarding chicks and low altitude breeding sites will be first to suffer reductions in chick growth or survival. Currently, however, no such change has been observed and, because in the UK, air temperature is unlikely to rise by > 2 C° over the next 80 years (predictions from HadCM3 climate model (Gordon *et al.*, 2000)), direct thermal stress should not be a major problem at this colony.

There is evidence, however, that climate change is influencing the productivity of waters around Foula (Reid *et al.*, 1998; Reid, 2003) and poor food availability in recent years has caused widespread breeding failure for many seabirds around Shetland, including the Great Skua (Mavor *et al.*, 2004). Persistence of these conditions will lead to high levels of conspecific predation and low levels of breeding success at Great Skua colonies within the UK. For this species it appears that indirect effects of climate change, mediated by changes in food availability, are likely to be far more important than direct changes in thermal exposure.

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Chapter 5.

The influence of climate, food and habitat availability on the past, present and future spread of Great Skua breeding colonies within the United Kingdom

Summary

The breeding range of Great Skuas is expanding rapidly at its eastern margin in arctic Russia, but not at its southern margin within the UK. To examine whether the current UK distribution resulted from direct climatic requirements, habitat availability and distribution of food resources or a time lag in the spread from a previous bottleneck population, two different dispersal models were used: the incidence function model (IFM) and a spatially-realistic cellular automaton model (MIGRATE). IFMs were parameterised with colony data from a nationwide long-term population monitoring programme, and MIGRATE models were seeded with these data and parameterized from values in the literature. The UK was represented as a grid of 25 km^2 cells and, in each, suitability for supporting a breeding population of Great Skuas was determined from empirical data on habitat and climatic suitability and food availability. Models were seeded with observed distribution in 1969. Simulated breeding distributions from both models for the year 2000 were in good agreement with those observed. Simulations indicated that, in the absence of dramatic climate change, Great Skua colonies are predicted to spread southwards along the western Scottish seaboard, and to a lesser extent in north-east Scotland and Northern Ireland. A degree of uncertainty surrounded the extent of the expected spread because of difficulties in determining the flexibility of adult diets, although this pattern could be altered by changes in adult diets or prey availability.

5.1 Introduction

Breeding populations of birds are limited in their size and distribution by intrinsic demographic features (birth, death, immigration and emigration rates) and by extrinsic environmental factors (Newton, 1998). Extrinsic factors include inter-specific competition and predation, resource and habitat availability and climatic limitation (Newton, 1998), either acting directly (Turner, Lennon & Lawrenson, 1988) or influencing other factors (Davis *et al.*, 1998; Lennon, Greenwood & Turner, 2000). Seabirds are long-lived species with low annual fecundity, and changes in population size and distribution usually lag several years behind changes in demographic parameters. For instance, changes in adult survival effect population size far more rapidly and profoundly than changes in breeding success (Weimerskirch *et al.*, 2003). Climate has been implicated in many recent changes in the demography of Antarctic and temperate seabird populations (Veit & Hyrenbach, 2001; Croxall, Trathan & Murphy, 2002; Weimerskirch *et al.*, 2003). In Antarctic areas, changes in the annual retreat of sea-ice have led to changes in juvenile and adult survival and breeding success of several seabird species, although proximate causes differ (Wilson *et al.*, 2001; Croxall *et al.*, 2002; Weimerskirch *et al.*, 2003). In temperate areas, not dominated by ice dynamics, changes in sea-surface temperatures have been implicated in changing productivity regimes (Reid, 2003), prey abundance at low trophic levels (Reid *et al.*, 1998) and population dynamics (breeding success, survival and incidence of breeding) of seabirds (Montevecchi & Myers, 1997; Jones & Hunter, 2002; Durant, Anker-Nilssen & Stenseth, 2003; Harding, Piatt & Hamer, 2003;

Inchausti *et al.*, 2003). Such changes in food availability are thought to be the major factors affecting numbers of breeding seabirds (Cairns, 1989) and there is some evidence that competition for these resources has shaped the distribution of seabird colonies within the UK (Furness & Birkhead, 1984; Lewis *et al.*, 2001). Dietary variation within a species may complicate responses to climatically-forced changes in food availability with some individuals benefiting and some being adversely affected by an increase in some prey species at the expense of others (Pinaud & Weimerskirch, 2002; Inchausti *et al.*, 2003).

Great Skuas (*Catharacta skua*) are transequatorial migrants breeding in north-west and arctic Europe, Scandinavia, western Russia and wintering mainly off the coast of Spain and western Africa (Hamer, 2001; J. Crane unpubl. data). Given the high over-winter survival of adults (Ratcliffe *et al.*, 2002) and high natal philopatry (Klomp & Furness, 1992a), changes in breeding distributions are more likely to be determined by resource availability and suitability of breeding sites than by events outside the breeding season. Mortality of adults during the breeding season is low (Furness, 1977, 1978b; Klomp & Furness, 1992a) but there is some evidence of inter-colony dispersal, despite high site fidelity once established within a colony (Klomp & Furness, 1992a). For instance, Great Skuas ringed in Shetland have contributed greatly to the expanding colony at St. Kilda (Phillips *et al.*, 1999a) and one quarter of the birds breeding on Fair Isle in the mid-1970s were ringed as chicks on Foula (Furness, 1977, 1978b). The attractiveness of a colony should determine rates of immigration and emigration but because of the high philopatry of established breeders, colony extinction may have a generational lag time (Weimerskirch *et al.*, 2003).

A number of different dispersal models have been used to simulate the direction and rates of change of animal populations (e.g. Hanski (1994), Hill et al. (2002)). The incidence function model (IFM) is a stochastic patch occupancy model (SPOM) (Moilanen, 1999) relating occupancy of habitat patches (in this case breeding colonies) to the twin processes of extinction (a function of patch size) and colonisation (a function of dispersal). The main components of IFMs are detailed in Hanski (1994; 1998; 1999). Extinction probability is proportional to patch area (i.e. population size) given that all patches have the same "quality" and therefore equal equilibrium density (Hanski, 1994). Colonisation probability is a function of the yearly immigration to a specific patch which is directly related to patch connectivity (describing how dispersal declines with distance to each source patch (Wilson *et al.*, 2002)).

MIGRATE is a two-dimensional spatially-explicit model simulating migration over a gridded landscape, fully described by Collingham et al. (1996). The model has previously been used to simulate range expansion in a variety of species including birds and butterflies (Collingham *et al.*, 1996; Hill *et al.*, 2001). MIGRATE is sensitive to variation in dispersal (Collingham & Huntley, 2000) and also requires information on period of maturation, survival, reproductive output and breeding density (Collingham *et al.*, 1996).

The distribution pattern and recent northwards expansion of Great Skuas suggests that their southern range margin may be determined by climate (Furness, 1988; Hamer, 2001), even though available evidence indicates that breeding birds are not directly constrained by climate at their breeding colonies (Chapters 2, 3 & 4). The most widely observed constraint upon Great Skua breeding populations is food availability. Great Skuas have a very catholic diet (Hamer, 2001) which varies according to available food resources (Votier *et al.*, 2004b). In the UK, observed diets during the breeding season include sandeels (*Ammodytes marinus*) and fisheries discards as well as adult seabirds (Hamer, 2001) and recently changes in the availability of all these prey have been evident around Great Skua breeding colonies (Mavor *et al.*, 2003, 2004; Votier *et al.*, 2004b). Distribution may also be limited by the availability of suitable nesting habitat (Micol & Jouventin, 2001; Croxall, 2004), which may be affected by sea-level or floral changes associated with climatic warming (Houghton *et al.*, 2001).

This chapter examines whether range expansion in Great Skuas is most strongly influenced by direct climatic requirements, habitat availability, distribution of food resources or a time-lag in dispersal from a previous bottleneck population of ~40 pairs in 1900 (Chapter 1). Two models of population spread and dispersal were run for two contrasting diet scenarios and both models incorporated estimates of climatic and habitat suitability. These models were used to simulate future breeding distributions of Great Skuas within the UK.

5.2 Methods

Two spatially explicit dispersal models, the incidence function model (IFM) (Hanski, 1994) and a cellular automaton model (MIGRATE) (Collingham *et al.*, 1996), were used to simulate recent changes in UK Great Skua breeding distributions and most probable future distributions. Data for the sizes of all UK colonies were available for census years from the JNCC Seabird Colony Register.

5.2.1 Developing a gridded landscape for spatial modelling: variation in suitability of the UK landmass for breeding by Great Skuas

A landscape representing the entire UK landmass was developed for use with both dispersal models (Figure 5.1). This was as an equal-area grid, of 58176, 5 × 5 km cells, encompassing all UK landmasses between 9°58’48 W, 48°35’24 N, and 3°43’12 E, 61°30’00 N, but not the Republic of Ireland. An index of the suitability of each cell for supporting a Great Skua colony was calculated using three criteria: habitat suitability, food availability and climate suitability. The index of overall suitability was the lowest of these three values, i.e. the limiting factor. Figure 5.1 shows the cell suitability across the landscape for two different diet scenarios.

Habitat suitability was the proportion of the cell classified as either “mountain, heath, bog” or “semi-natural grassland” in the Land Cover Map of Great Britain 2000 (Aggregative Class codes 6 or 5; © Centre for Ecology and Hydrology 2001; www.ceh.ac.UK/data/lcm/index.htm) since these categories encompassed the nesting habitat of Great Skuas (Furness, 1987; Hamer 2001).

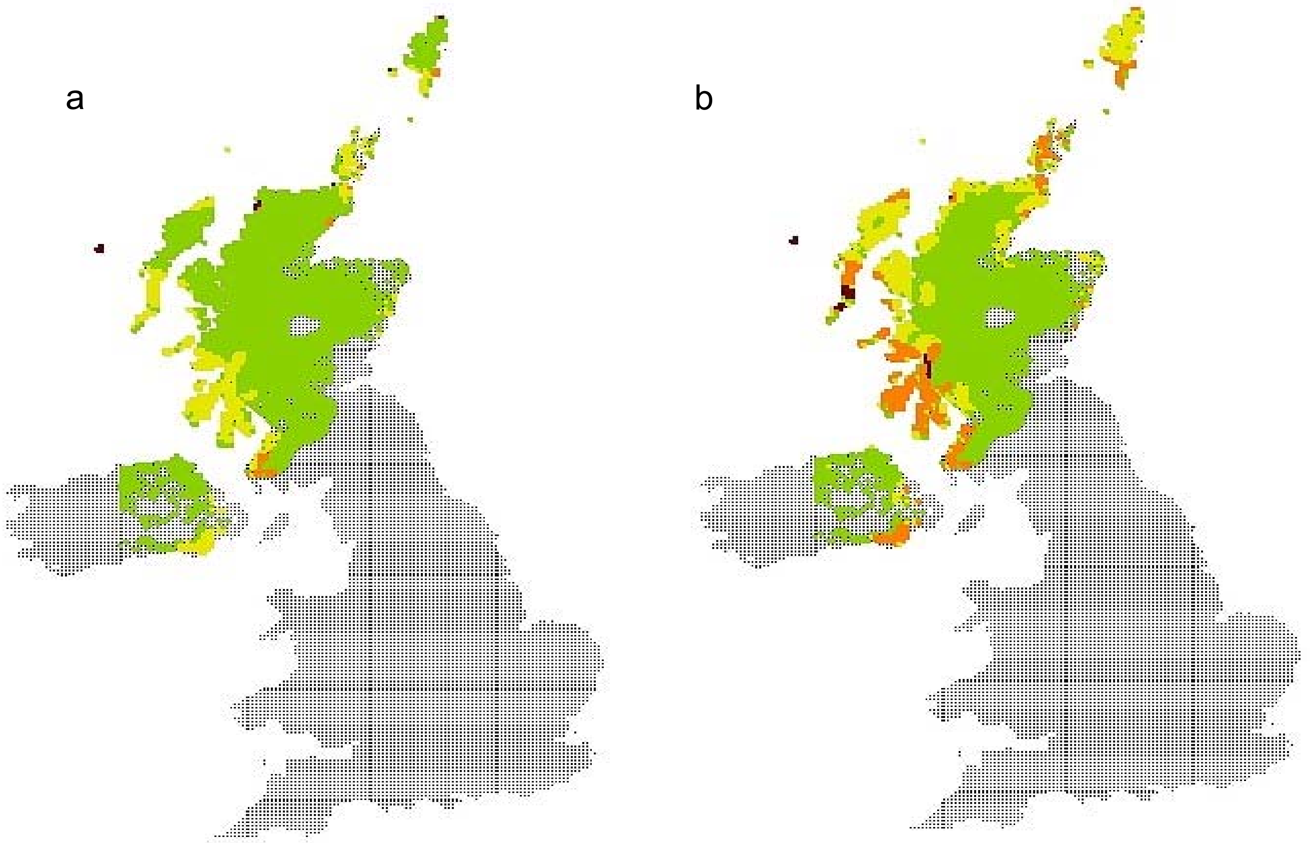

Figure 5.1 The relative suitability of each cell in the model landscape for breeding by Great Skuas (i.e. the proportion of a cell that is available for breeding relative to all other cells (see text)). Suitability varies when diet is modeled as (a) predominantly seabird (60 %) or as (b) predominantly pelagic (15 % seabird) and is determined from the relative availability of habitat, suitable climatic conditions or food resources, whichever is most limiting. Since cells are 5 km × 5 km, grey regions indicate none of the cells are suitable, green regions have 0.001-0.05 cell suitability, yellow 0.05-1.0 cell suitability, orange 0.1-0.2 cell suitability and red > 0.2 cell suitability. Cell suitability is used in the dispersal models to indicate the proportion of a 25 km^2 cell that is available for breeding (maximum population size = suitability / breeding density).

An index of food availability was calculated by combining data on the three food resources most commonly used by Great Skuas in the UK: small pelagic fish, fisheries discards and seabirds (Hamer, Furness & Caldow, 1991; Phillips *et al.*, 1997; Hamer, 2001; Votier *et al.*, 2004b). Mean cholorophyll-a concentration during chick-rearing (15th June – 31st July) in 1997 (averaged from daily means held by NERC Remote Sensing Data Analysis Service (RSDAS) (www.npm.ac.UK/rsdas)) was used as an index of the availability of small pelagic fish (Valavanis *et al.*, 2004). The relative availability of this prey in each cell was determined from kernel density estimation (e.g. Wood *et al.* (2000)) of mean cholorphyll-a values using a search radius of 50 km (the estimated maximum radius of foraging trips; Furness (1978a)). Density values for each cell were then converted to proportions of the maximum cell value observed within the landscape.

Data on fisheries discards (yearly means between 1988 and 2001) for Mackerel *Scomber scombrus*, Whiting *Merlangius merlangus*, Blue Whiting *Micromesistius poutassou* and Haddock *Melanogrammus aeglefinus* (the main species eaten by Great Skuas (Votier *et al.*, 2004b)) were taken from the International Council for the Exploration of the Sea (ICES) (www.ices.dk) for the 11 ICES fishing areas around the UK. The density of discards available in each cell was calculated using kernel analysis, and converted into a proportional value, as for chlorophyll density.

Population sizes of those seabird species eaten by Great Skuas were obtained from the Joint Nature Conservation Committee (JNCC) Seabird Colony Register (SCR) (www.jncc.gov.uk) as a mean of two years in which complete coverage was made (1969-70 and 1985-87). Numbers of breeding Puffins *Fratercula artica*, Common Guillemots *Uria aalge*, Razorbills *Alca torda*, Kittiwakes *Rissa tridactyla* and Fulmars *Fulmarus glacialis* were converted into energetic equivalents (multiplying numbers of individual birds by species-specific mean body masses (Dunning, 1993) and energy density (Phillips *et al.*, 1997)(Table 5.1)). Energy available from seabirds for a grid cell, calculated as the sum of energetic equivalents of all five species, was used to predict the maximum size of breeding Great Skua colony that the cell could support, by dividing by the energy requirement of a breeding skua (307,000 kJ per season; (Phillips *et al.*, 1999b)). Since Great Skuas do not consume entire breeding populations of these seabirds in a single year, realised skua populations will be smaller than those predicted in this way (Furness, 2004). To account for this,

Table 5.1 Mean body mass, energy density and content of the main seabird prey of Great Skuas, assuming all tissues to be consumed. ^{a} mean of values for males and females (from Dunning (1993)); ^{b} values from Phillips *et al.* (1999b).

Species	Mean body mass (g) ^{a}	Energy density ($kJ.g^{-1}$) ^{b}	Energy content of one bird (kJ)
Puffin	381.0	10.9	4152.9
Guillemot	992.5	10.9	10818.2
Razorbill	719.0	10.9	7387.1
Kittiwake	407.0	10.9	4436.3
Fulmar	544.0	10.9	5929.6

observed sizes of Great Skua colonies at Foula and St. Kilda, for which diet data were available, were multiplied by the mean proportion of seabird in the diet, to give the number of breeding individuals directly dependent on seabirds (Table 5.2). This value was then divided by predicted colony size, giving a calibration between predicted and observed colony size. Maximal colony sizes predicted from simple energy requirements were therefore multiplied by 0.156, the conservative estimate for St. Kilda (Table 5.2). Kernel analysis, with a search radius of 10 km was used to estimate the number of Great Skuas that could be supported by seabird populations in every grid cell, because birds specialising as seabird predators often maintain regular feeding areas not far from their breeding territories (Reinhardt, 1997; Mougeout, Genevois & Bretagnolle, 1998; Votier *et al.*, 2004a). This number was then converted to a proportion, as for chlorophyll density.

The diet of breeding Great Skuas varies widely between colonies (Phillips *et al.*, 1997) but reflects the relative availability of different food resources (Votier *et al.*, 2004b). Overall food resource availability in each cell was therefore calculated for two extreme scenarios based on documented diets at two colonies, St. Kilda (mean diet: 58.2 % seabird, 36.4 % fish, 5.4% other) and Foula, (mean diets: 10.4 % seabird, 84.9 % fish, 4.7 % other) (Phillips *et al.*, 1997). Fish diet was assumed to be split equally between discards and active fish predation, because when pelagic fish are scarce discards make up a higher proportion of the diet (S. Votier, pers. comm.), and the “other” component of the diet was ignored.

Table 5.2 Available seabird prey (1969 & 1986 JNCC censuses), overall energy, maximum predicted skua breeding population and dietary scenarios compared with observed population sizes at Hirta, St. Kilda, and Foula, Shetland. Data sources: [a] Phillips *et al.* (Phillips *et al.*, 1999a), [b] Klomp & Furness (1992b). Proportion observed/maximum predicted accounts for differences between realised population sizes and those estimated from bioenergetics, incorporating necessities of prey population persistence and predator searching and handling times.

	Mean numbers of seabird prey species									
Colony	Puffin	Guillemot	Razorbill	Kittiwake	Fulmar	Overall energy available from seabird prey (kJ)	Maximum number of bird-specialist skuas	Observed maximum breeding skua population (individuals)	Maximum proportion of seabird in diet	Observed (corrected for diet) /maximum predicted
St. Kilda	10,179	11,982	3,404	20,094	54,556	609,488,761.5	1,792	466 [a]	0.60	0.156
Foula	50,630	23,156	3,367	5,556	59,275	863,216,475.0	2,812	5090 [b]	0.10	0.181

For the scenario assuming a diet comprising mainly seabirds, food availability for each cell was calculated by multiplying the availability of seabirds, discards and chlorophyll-a by 0.6, 0.2 and 0.2, respectively, and summing the products. For the scenario assuming a diet comprising mainly fish, food availability was calculated in the same way but multiplying proportional availability of seabirds, discards and fish by 0.10, 0.45 and 0.45, respectively.

Climatic suitability of each cell was calculated from the probability of occupancy in climate response surface analysis (Chapter 6), interpolated for each 25 km^2 grid cell. Climate variables used in the response surface were those that best simulated current European distribution: mean temperature of the coldest month, growing degree days > 5 °C, and spring sea surface temperature (model H2, Kappa = 0.725; Chapter 6).

Overall cell suitability was the value for either relative habitat suitability, food availability or climate suitability, whichever was lowest, i.e. most limiting. The proportion of cells in the landscape for which overall suitability was dictated by habitat suitability, food availability or climatic suitability indicated the relative importance of these three factors in constraining the UK breeding distribution of Great Skuas during simulations.

Competition for resources may occur between closely-spaced breeding colonies of seabirds, especially when colonies are large (Ashmole, 1963; Lewis *et al.*, 2001). To incorporate the negative effect of large neighbouring colonies, the suitability of cells within 10 km of Great Skua colonies supporting over 15 pairs (data from 1969 & 1986 (Cramp, Bourne & Saunders, 1974; Lloyd, Tasker &

Partridge, 1991)) was reduced, depending on the proximity of the neighbouring colony (suitability was equal to $s \times (0.1d)$, where s is original cell suitability and d is distance (in km) from the large colony. This led to a halving of the suitability for neighbouring cells, 5 km distant).

5.2.2 Model parameterisation

Figure 5.2 details the IFM equations and Table 5.3 describes the individual parameters used in this dispersal model. All but two IFM parameters were estimated from data on the presence/absence of breeding Great Skuas for all cells in the landscape at four snapshots in time (colony size data from SCR, years 1969-70, 1982, 1985-7, and 1992). For 1982 and 1992, when coverage was incomplete, occupancy was assumed if patches were occupied during the previous census. Parameterization was performed with SPOMSIM software (Moilanen, 2003) using the Turnover Monte Carlo (TMC) method of Moilanen (2000) that allowed accurate estimation despite an observed increase in Great Skua breeding populations within this period. This estimated IFM parameters from observed trends in extinction and colonization during this 23 year period. Values of α and β, describing dispersal of offspring from their natal colony, were estimated independently from a negative power curve ($y = 1/[1 + \beta x^{\alpha}]$) in which 98 % of offspring returned to breed within 5 km of their natal colony and 2 % dispersed further (Figure 5.3), as observed empirically for Great Skuas from Shetland (Furness, 1978b; Klomp & Furness, 1992a). To investigate the variation in rates of change of Great Skua breeding populations, a separate IFM parameterization (for all parameters including α and β) was performed with

Dispersal kernel

$k(\ ) = 1 / (1 + \beta\, d_{ij}^{\ \alpha})$

98 % of post-natal dispersal is within the same colony (Klomp & Furness, 1992a).

Connectivity function

$S_i(t) = \Sigma[p_i(t)\ k(\ )\ (A_j^{\ b})]$

Connectivity of a patch depends on the size of a patch scaled by b (Wilson *et al.*, 2002) (b > 1 indicates differences in connectivity are larger than equivalent patch sizes) .

Colonization probability

$C_i(t) = [S_i(t)]^2 / (y^2 + [S_i(t)]^2)$

There is a sigmoidal increase in colonisation probability with increasing number of immigrants (Hanski, 1994) (when y is <1 colonisation can occur with very few immigrants)

Intrinsic extinction probability

if $A_i > e^{1/x}$, $E_i = e / A_i^{\ x}$

if $A_i \leq e^{1/x}$, $E_i = 1$

Below a patch size of $e^{1/x}$ extinction probability is 1. Otherwise it is scaled with patch area to the x (Hanski, 1994) (differences in extinction risk can be equal to, less than or greater than differences in patch size, depending on x).

Rescue effect

$E_i = E_i\ ([1 - C_i(t)])^{R}$

If colonisation probability is high, there is a good chance of patches being recolonised in the same year as going extinct (Hanski, 1994). The parameter R allows the rescue effect to have an exponential relationship with colonisation rate (R < 1 indicates a smaller effect than expected from a linear relationship with colonisation rate).

Figure 5.2 Equations and explanations of IFM components used to model Great Skua spread within the UK. Parameter definitions and values are given in Table 5.3.

Table 5.3 Parameters in the basic IFM model, with usual data source and typical values (for butterfly studies). Sources: [a] Hanski (1994); [b] Wilson *et al.* (2002). In this study, area of patch (cell) (A_i) = value for overall cell suitability × cell size (25 km^2).

Parameter	Description	Source	Typical values
α	Parameter describing distribution of migration distances	Estimated from mark-recapture, or pres/abs data	2[a] ; 2,3,4,5 [b]
β	Parameter describing distribution of migration distances	Estimated from mark-recapture, or pres/abs data	1
A_i	Area of patch *i*	Empirical maps	0.4-0.9 ha [a]
d_{ij}	Pair-wise distances between patches	Empirical maps	<1 km [b]
p_i	Presence or absence of species in year of survey	Empirical pres/abs or data	N/A
y	Colonization ability of species (smaller gives more migrants)	Parameter estimation	0-2.663 [a]
e	Threshold area for extinction	Parameter estimation	0.01-0.044 [a]
x	Extinction susceptibility with patch area	Parameter estimation	0.5-1.099 [a]

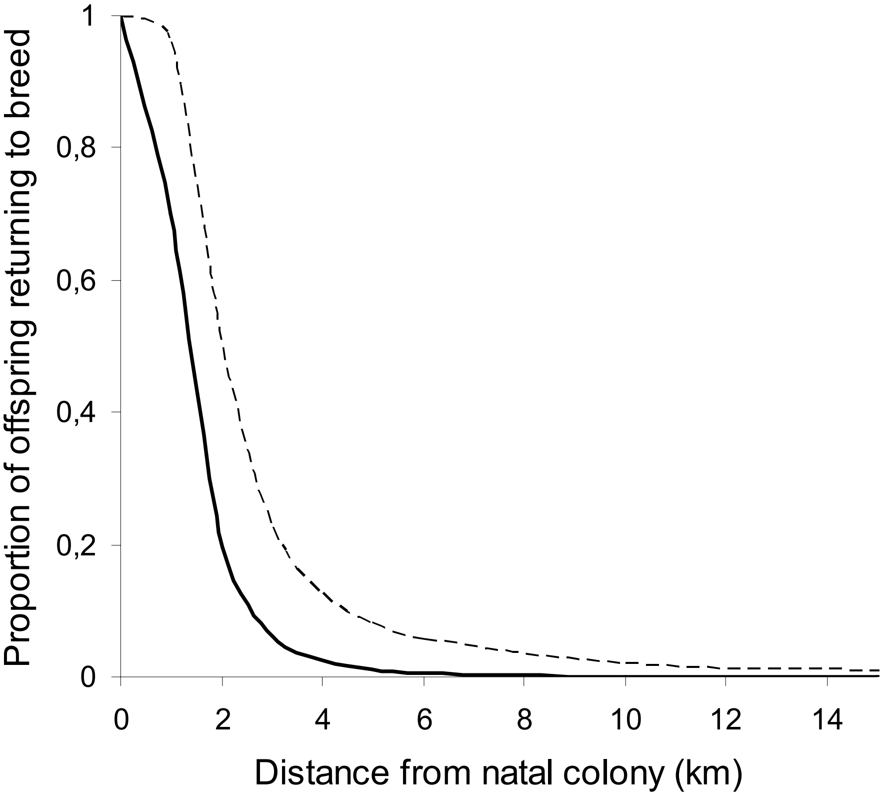

Figure 5.3 Dispersal kernels, used in both IFM (solid) and MIGRATE (dashed) models, predicting the proportion of offspring returning to breed at different distances from the natal colony. IFM curve derived from negative power function ($y = 1 / [\beta x \alpha]$), with $\alpha = 2.063$ and $\beta = 0.548$, MIGRATE curve also included long range dispersal (see text).

SPOMSIM for the period 1900-1960 (data for 1900, 1910, 1920, 1930, 1940, 1950, 1960 from Furness (1987)[Tables 13 & 14]).

Species-specific parameters used in MIGRATE simulations are given in Table 5.4. The proportion of each cell available for colonization was the overall cell suitability (section 5.2.1). Since 98 % of Great Skuas recruit to their natal colony, 0.98 of migrants were set to return to breed within the cell from which they originated. The dispersal function used in these simulations incorporated two different curves representing, medium- and long-range dispersal. Medium-range dispersal was estimated with the negative power function used in IFM parameterizations (Figure 5.3). This function alone may underestimate long-range dispersal (Collingham & Huntley, 2000) and so a separate negative power function ($\alpha = 1.0$ and $\beta = 0.01$), giving the cumulative probability of breeding observed for Great Skua colonies (0.02 for all distances > 5 km, i.e. 2 % long-distance dispersal)) (Klomp & Furness, 1992a), was incorporated to simulate long-distance dispersal.

5.2.3 Simulations and analyses

Both IFM and MIGRATE models were run for the two different diet scenarios (section 5.2.1), using the final parameters (IFM: Table 5.6, MIGRATE: Table 5.4). Runs for each scenario were made from starting distributions in 1969 (the first full census of Great Skua colonies in the UK) (Figure 5.4) and output was obtained for years 2000, 2050 and 2100 to provide model assessment and future predictions for the same periods as climate change analyses (Houghton *et al.*, 2001). Since both IFM and MIGRATE are subject to stochastic processes, each run was replicated (100 times for IFM; 10 times for MIGRATE simulations because each lasted many hours). Each replicate dataset was bootstrapped with replacement (Efron, 1982) to generate a sample of 1000 replicates for each run. Means were calculated for probability of occupancy (for IFM) and mean colony size (for MIGRATE) of each cell in 2000, 2050 and 2100 from these bootstrap datasets for each scenario. Mean probability of occupancy was also calculated for all outputs from MIGRATE scenarios by defining only cells with simulated colony size > 0 as occupied prior to bootstrapping.

Table 5.4 MIGRATE parameters, sources and values used to simulate recent spread of Great Skuas in the UK. [a] data collected at Foula, Shetland in 2002 and 2003 (Chapter 4).

Parameter	Description	Source	Value
	Probability of dispersal	98 % philopatry (Klomp & Furness, 1992a)	0.02
	Dispersal function	98 % philopatry (Klomp & Furness, 1992a)	$y = 1 / [\beta x^{\alpha}]$ where, $\alpha = 3.25$, $\beta = 0.43$
	Time to reach maturity	Conservative estimate (Furness, 1987)	8 years
L	Length of cell	Grid cell size	5 km
a	Area occupied by an adult	Mean density estimated from nearest neighbour distances at Foula in 2002 & 2003[a]	3631 m^2 (for a circular territory of radius 34 m)
K_{ij}	Proportion of each cell available for colonisation (carrying capacity)	Cell suitability (section 5.2.1)	range 0.00-0.54
T	Time step	Time taken for offspring to return to breed; (Furness, 1977, 1987)	8 years
S	No. offspring produced per generation	Calculated from intrinsic rate of increase	depends on colony size
P_0	Probability of offspring reaching maturity (8 years)	Calculated from yearly survival estimates (Klomp & Furness, 1992a; Ratcliffe *et al.*, 2002)	0.257
P_1	Probability of adults surviving a second generation (8 years)	Mean of yearly survival estimates (Ratcliffe *et al.*, 2002)	0.394
F	No. offspring produced per individual in a generation (8 years)	Mean of available productivity (× 8) data for Shetland and Orkney (Furness, unpublished data)	8

The Kappa statistic (Monserud & Leemans, 1992) was calculated by comparison of mean probability of occupancy from IFM and MIGRATE simulations for 2000 with observed data for that year (Mitchell *et al.*, 2004). Kappa is a quantitative index useful for the comparison of spatial data (Manel, Williams & Ormerod, 2001) and indicates, for all cells, the proportion of predicted presences/absences that were in agreement with those observed. To calculate this statistic, it is necessary to define a probability threshold, over which breeding colonies are predicted as being present for that cell. Thresholds for each comparison were chosen by simultaneously optimizing the sensitivity (proportion of observed presences that were simulated) and the accuracy (proportion of simulated presences/absences that coincided with those observed), following Huntley *et al.* (1995).

Figure 5.4 Observed distribution of Great Skua breeding colonies in the UK in (a) 1900 and (b) 1969. Data from 1969 were used as the starting point for IFM and MIGRATE simulations. Colony sizes (number of breeding pairs) are indicated in legend.

5.3 Results

5.3.1 Model Performance

Simulated Great Skua breeding distributions in 2000 from both IFM and MIGRATE were in good agreement with their observed distribution (Mitchell *et al.*, 2004) (Table 5.5, Figures 5.5 & 5.6).

Table 5.5 Agreement of simulated UK Great Skua breeding distributions for 2000 from dispersal models with those observed in the Seabird 2000 census for each diet scenario. Kappa in excess of 0.5 indicates good correspondence between predicted and observed distributions (Monserud & Leemans, 1992). Probability thresholds associated with maximum Kappa vales are given.

Dispersal Model	Main component in diet	Threshold	Max. Kappa
MIGRATE	Seabird	0.102	0.580
	Pelagic resources	0.140	0.641
IFM	Seabird	0.035	0.595
	Pelagic resources	0.966	0.561

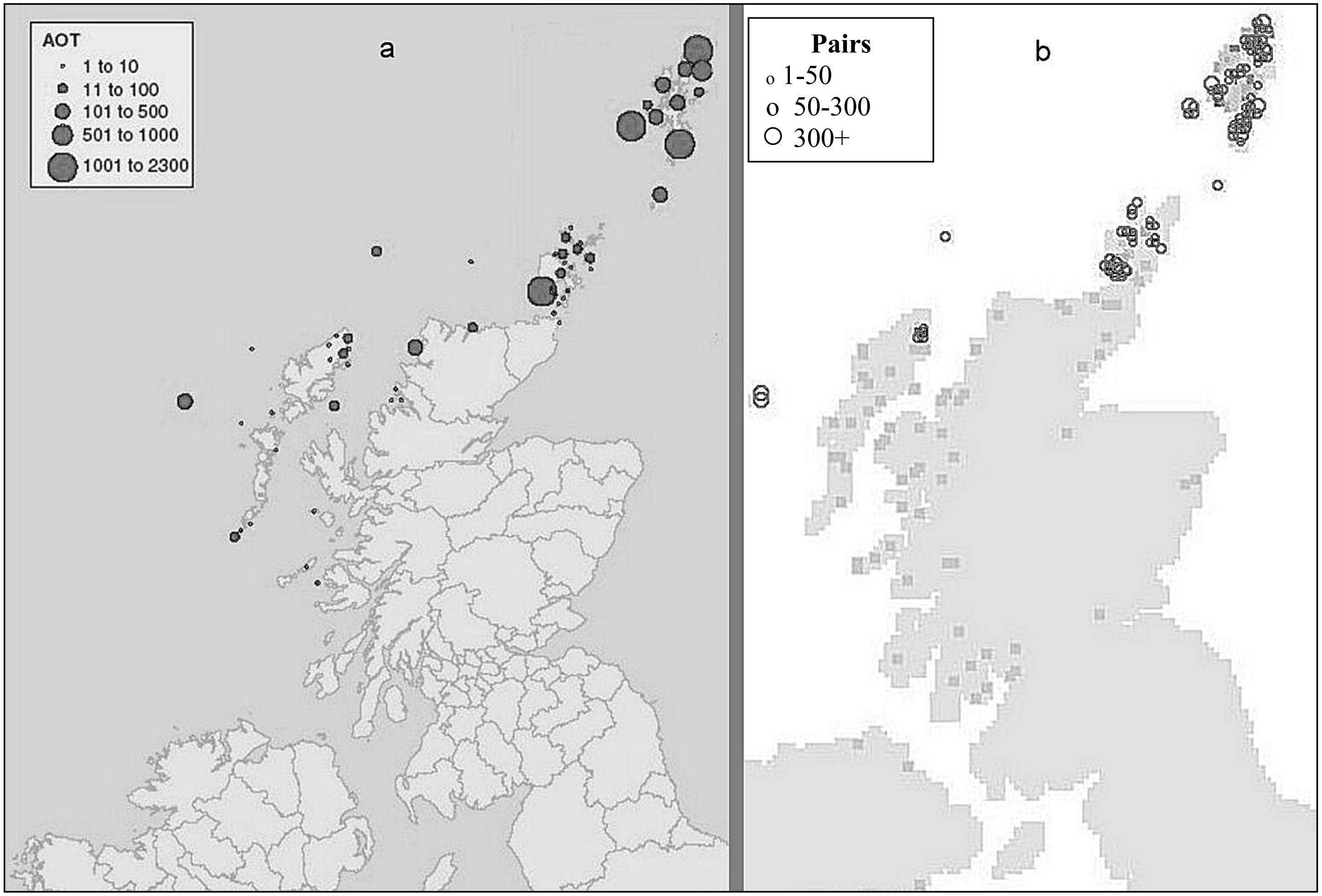

Figure 5.5 (a) Observed distribution and sizes of Great Skua colonies in the UK in 2000 and (b) simulated distribution from MIGRATE dispersal model for the same year. Filled circles in (a) are apparently occupied territories, open circles in (b) are predicted number of breeding pairs in cells where colonies are simulated in > 50 % of replicated simulations and shaded squares in (b) indicate colonies simulated in < 50 % of replicates, extensive light grey areas have zero probability.

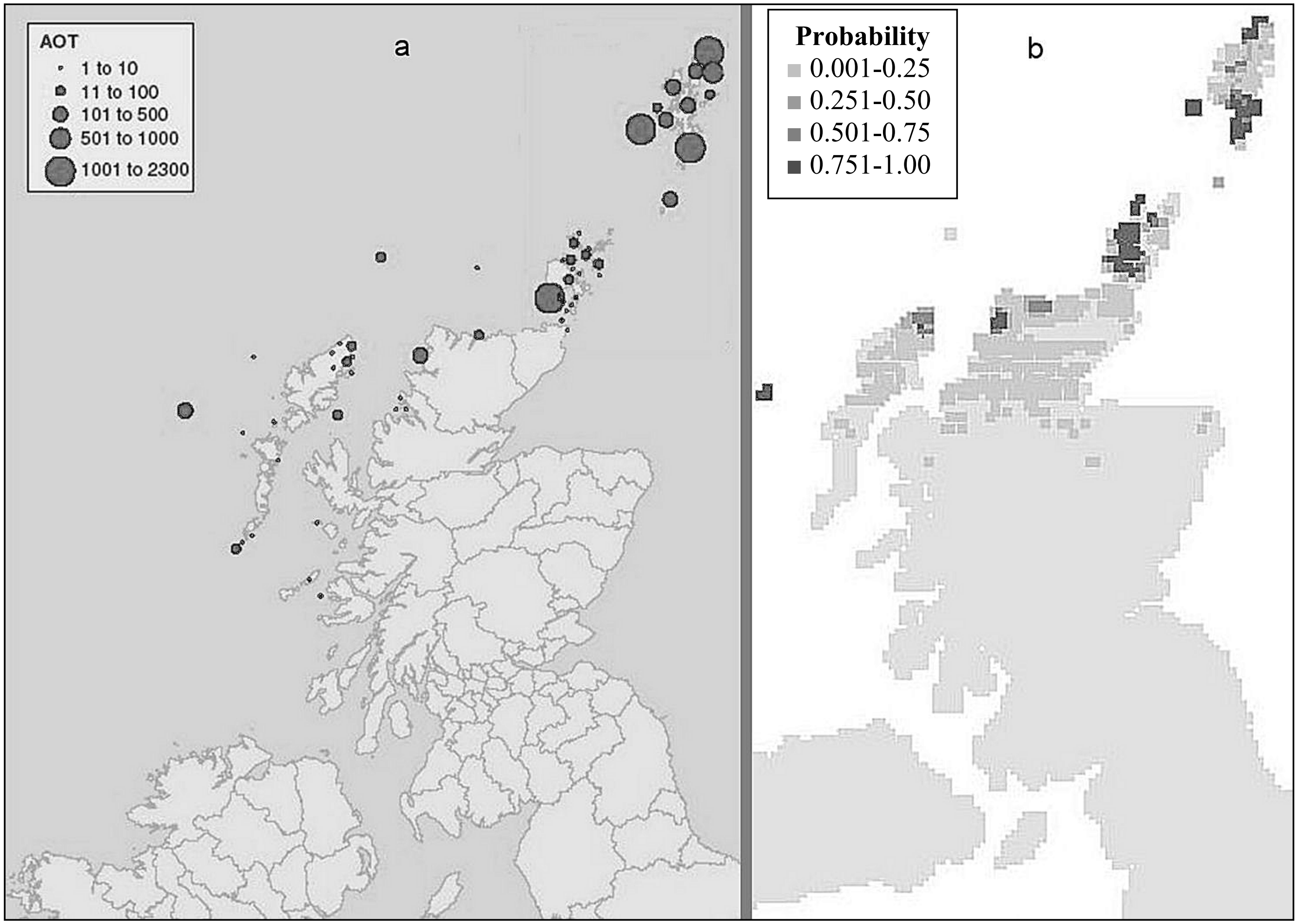

Figure 5.6 (a) Observed distribution and sizes of Great Skua colonies in the UK in 2000 and (b) simulated breeding probability from IFM dispersal model for the same year. Filled circles in (a) are apparently occupied territories, and shaded squares in (b) are simulated colonies in different proportions of simulation replicates, extensive light grey areas have zero probability.

5.3.2 Simulated future breeding distributions for the Great Skua within the UK

Simulated probability of supporting a breeding colony, for all cells in the landscape, is shown for 2050 (Figures 5.7 & 5.9) and 2100 (Figures 5.8 & 5.10) for MIGRATE and IFM models. Running MIGRATE models with two observed extremes of diet (60 % seabird and 15 % seabird) substantially influenced the rate of spread of breeding colonies but not the extent (Figures 5.7 & 5.8). MIGRATE simulations indicated extensive colonies to spread through all coastal regions of western Scotland and parts of eastern Scotland and Northern Ireland by 2100, although newly founded colonies only exceeded 300 pairs in simulations incorporating predominantly pelagic diets (Figure 5.8). Using the same extremes of diet in IFM models, however, affected both the rate and extent of spread. Simulations run with predominantly pelagic diet indicated a more rapid southward spread along coastal regions. IFM simulations incorporating predominantly pelagic diet predicted an extent of spread by 2100 similar to that seen in corresponding MIGRATE simulations (Figure 5.10). The rate of this simulated expansion, however, was much slower in IFM models (compare Figures 5.7 & 5.9) and, for the IFM model with a predominantly seabird diet simulated distribution in 2100 was barely any different from that observed in 2000 (compare Figures 5.6 & 5.10).

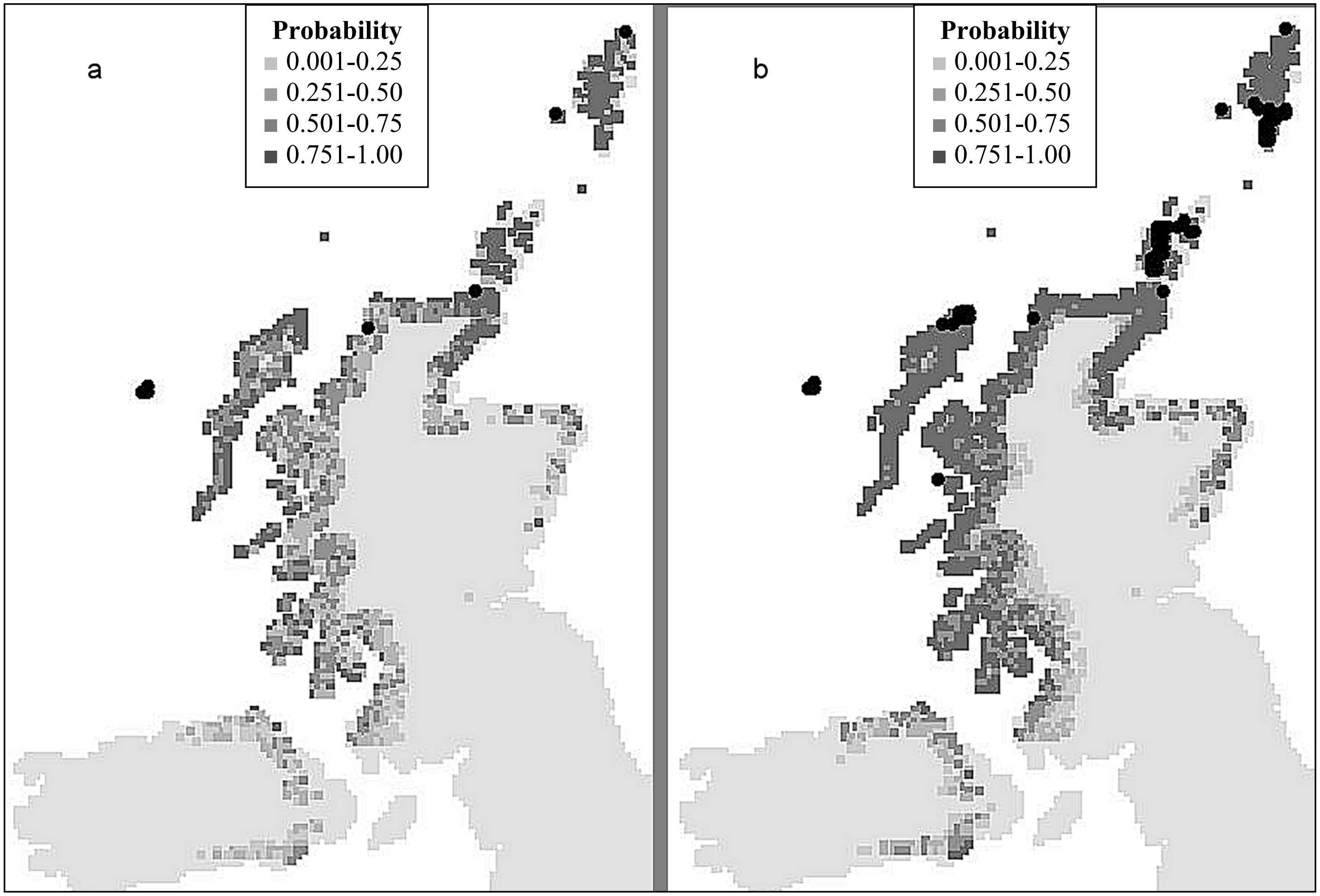

Figure 5.7 Simulated probability of Great Skuas breeding in all cells in 2050 from the MIGRATE model incorporating predominantly (a) seabird and (b) pelagic diets. Shading indicates the probability of a cell containing a breeding colony, extensive light grey areas have zero probability. Black circles indicate colonies of > 300 breeding pairs.

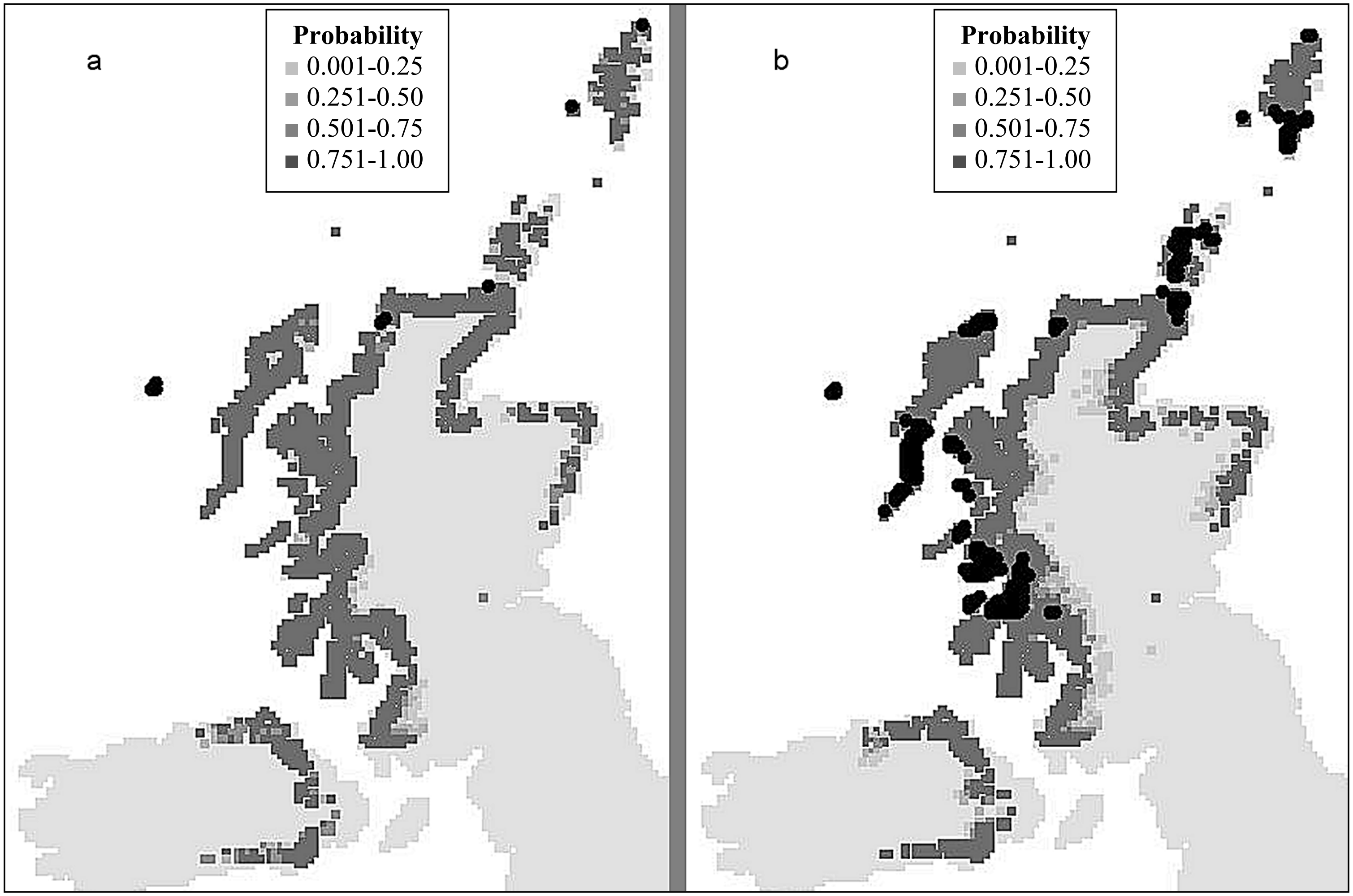

Figure 5.8 Simulated probability of Great Skuas breeding in all cells in 2100 from the MIGRATE model incorporating predominantly (a) seabird and (b) pelagic diets. Shading indicates the probability of a cell containing a breeding colony, extensive light grey areas have zero probability. Black circles indicate colonies of > 300 breeding pairs.

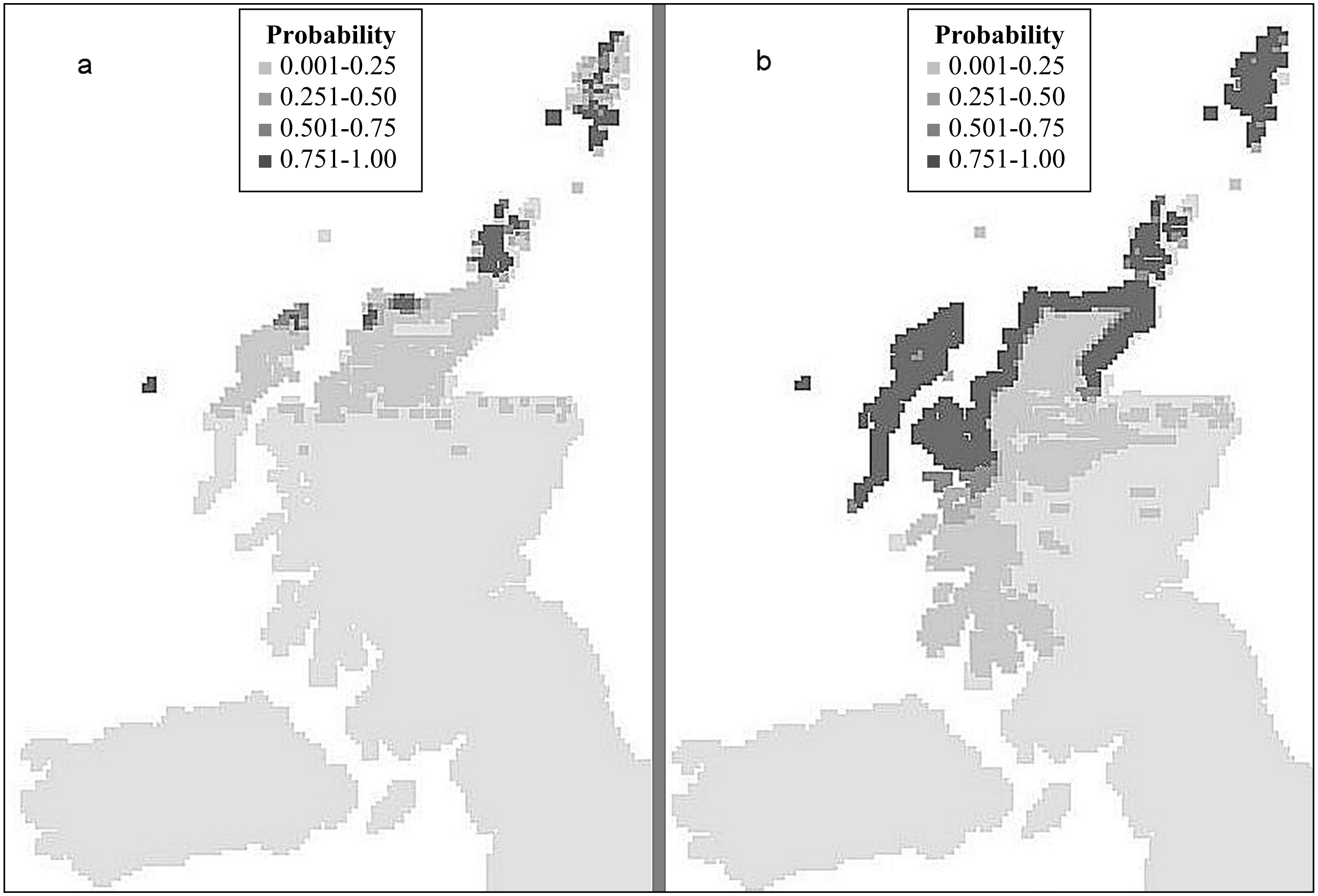

Figure 5.9 Simulated probability of Great Skuas breeding in all cells in 2050 from the IFM model incorporating (a) predominantly seabird and (b) pelagic diets. Shading indicates the probability of a cell containing a breeding colony, extensive light grey areas have zero probability.

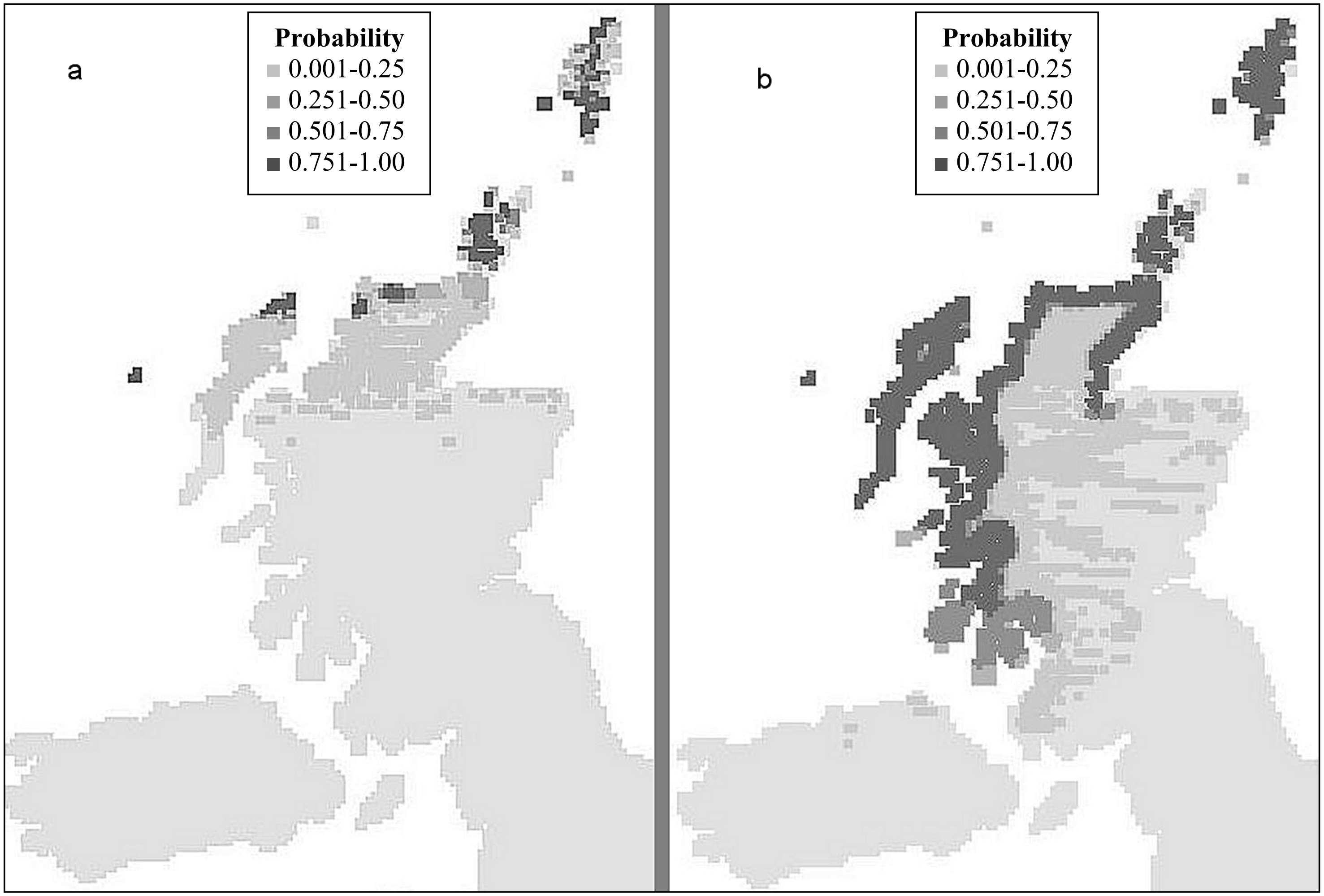

Figure 5.10 Simulated probability of Great Skuas breeding in all cells in 2100 from the IFM model incorporating (a) predominantly seabird diet (b) predominantly pelagic diets. Shading indicates the probability of a cell containing a breeding colony, extensive light grey areas have zero probability.

5.3.3 Recent and historical rates of spread

Compared to parameters estimated from colony occupancy between 1969 and 1992, populations expanding from the 1900 bottleneck were best simulated in IFM models by a three-fold increase in the survival of migrants (reduced α) plus an eight-fold increase in migration density (β) (Table 5.6). However, during this rapid phase of expansion (1900-1960) the colonization ability, a measure of how size and proximity to neighbouring colonies influences rates of colonization, was lower (as indicated by a large value of y).

Table 5.6 IFM parameter values estimated using Turnover Monte Carlo (TMC) estimation for years of rapid (1900-1960) and recent expansion (1969-1992). See Figure 5.2 & Table 5.3 for parameter definitions.

Parameter	Rapid expansion (1900-1960)	Recent expansion (1969-1992)
α	0.94	3.25
β	3.79	0.43
b	0.82	0.93
y	128.9	5.47
e	34.33	35.16
x	1.76	1.55
R	0.76	0.66

5.3.4 Relative importance of habitat, food and climate in limiting simulated suitability of sites for breeding by Great Skuas

Habitat suitability was the most limiting factor determining overall cell suitability in the model landscape (Table 5.7). Climatic suitability only restricted breeding sites for Great Skuas in ~ 7 % of the landscape and approximately 5 % of cells were restricted by food availability alone (Table 5.7). When more than one factor was limiting (Table 5.7), habitat suitability was part of this limitation in 62 % of cases, climatic suitability also in 62 % of cases but food availability only in 15 %.

Table 5.7 Proportion of all cells in study area in which the overall cell suitability for breeding Great Skuas is limited by climate, diet or habitat alone or by more than one of these factors. Proportions are given for the two extreme diet scenarios.

Main component in diet	Climate	Diet	Habitat	Multiple
Seabird	0.068	0.057	0.254	0.621
Pelagic resources	0.072	0.049	0.258	0.621

5.4 Discussion

5.4.1 Simulated breeding distributions of Great Skuas within the UK

Both IFM and MIGRATE models accurately simulated the observed breeding distribution of Great Skuas in 2000 when seeded with data for 1969. Several new colonies have been formed within this period and many established colonies have grown by > 10 % over the last ten years (Furness & Ratcliffe, 2004). Consequently, both dispersal models adequately incorporated observed trends in expansion and population increase over the past 30 years.

MIGRATE models assuming a predominantly pelagic diet produced the most accurate simulations but for IFM the most accurate simulation was for the diet comprising mainly seabirds. Small inaccuracies in simulated spatial dynamics are compounded the more years that simulations are run for and so predictive accuracy of these models declines for future simulations. IFM models run with a predominantly seabird diet simulated very little change in the breeding distribution of Great Skuas within the UK over the next 100 years (Figures 5.6b, 5.9a & 5.10a). IFM models assuming a predominantly pelagic diet simulated a range expansion similar to, although not as extensive as, that predicted by MIGRATE models with either diet specification (Figures 5.7 & 5.8). The influence of diet specification in MIGRATE models was to determine the rate at which breeding colonies spread southward, being much faster for models using predominantly pelagic diet. Neither of the diet scenarios truly represented observed flexibility in Great Skua diets, however, because diet appears to be largely a function of relative availability of food resources (Votier *et al.*, 2004b). Although, on average, Great Skua diets lie between the modelled extremes, both diet scenarios for MIGRATE models indicated a southward expansion of breeding colonies, as did the IFM model using a predominantly pelagic diet. Therefore, given the model assumptions, it is most likely that Great Skua breeding colonies will spread southward, particularly along the western Scottish seaboard over the next 50-100 years.

In addition to the inherent assumptions of the two models (section 5.4.3), simulations produced were dependent on there being no change in habitat or food availability or climatic conditions over the next 100 years. In the UK, temperature rise is predicted to be only moderate by comparison with global estimates (Houghton *et al.*, 2001). Considering that within current colonies, breeding sites may consistently differ in heat-stress by as much as 3 Celsius degrees (C°) (Chapter 4), direct impacts of this climatic warming are unlikely to impose new restrictions on the spread of breeding colonies. In both models food availability was found to be a limiting resource for at most 15 % of the whole study landscape. This is surprising since food availability is known to have major impacts on breeding success and adult survival in Great Skuas (Hamer *et al.*, 1991; Ratcliffe *et al.*, 2002) and is often the proximate cause of population changes in response to climatic change (Croxall *et al.*, 2002). This discrepancy exists because food availability data were from years in which food shortages at major colonies were not evident: chlorophyll data were from a snapshot in 1997 (Thompson, Brindley & Heubeck, 1988), seabird distributions from 1969 and

1986 (Cramp *et al.*, 1974; Lloyd *et al.*, 1991) and discard data from 1988-2001 (Votier *et al.*, 2004b). Therefore, all model simulations were based on food availability being sufficient throughout much of the breeding range. This assumption may lead to over-estimation of future distributions in view of future likely reductions in discarding rates (Furness, 2000), regime shifts in pelagic productivity (Reid, 2003) and sporadic widespread breeding failure of seabirds in areas of the UK (Proffit, 2004) .

5.4.2 Differences between recent and historical rates of spread of breeding populations

Expansion from an artificially low population in 1900 (~ 40 pairs (Furness, 1987)) was best represented by colonisation parameters that differed from those accurately describing recent population change (1969-2000). This former period was characterised by more migrants leaving existing colonies and being more likely to survive to breeding. Expansion during this time appeared to be predominantly local, because a high value for the parameter y indicated that connectivity, the influence of surrounding colonies, was much reduced. This is as observed: the majority of breeding range expansion between 1900 and 1960 was restricted to Shetland and, to a lesser extent, Orkney (Furness, 1987). Expansion since 1969 appears to have been less tightly focused, with new colonies being founded in the Hebrides as well as Orkney and Shetland (Cramp *et al.*, 1974; Lloyd *et al.*, 1991; Furness & Ratcliffe, 2004) and with fewer migrants leaving each breeding colony but there being many more colonies in existence.

5.4.3 Limitations of dispersal model simulations

One problem when parameterizing IFM models from observed colonisation and extinction dynamics of long-lived seabird colonies is that, even for data spanning > 20 years, extinction and colonisation events are relatively rare (only 6 colony extinctions were identified between 1969 and 1992). Thus, even with four or more snapshots of patch occupancy, model parameterization may under- or over-estimate rates of extinction and colonisation (Moilanen, 1999). Stochasticity eventually causes a network of colonies to become either fully occupied or empty (Hanski, 1998) and becomes more important the longer simulations are run for. Consequently, IFM simulations of Great Skua distributions for 2100 are probably far less accurate than those for 2000.

All models included competition from neighbouring large colonies, as suggested for other seabirds species (Ashmole, 1963; Lewis *et al.*, 2001), However, currently no studies show such competition at Great Skua breeding colonies and by 2100 simulated probabilities were moderate for most cells surrounding large colonies, suggesting that the influence of competition was minimal. All IFM predictions exhibited a steady cell-to-cell spread of breeding populations, in contrast with observed patchiness in the spread of Great Skua populations over the last 100 years (Furness, 1987; Furness & Ratcliffe, 2004). This difference arises because each cell is simulated as either occupied to capacity or empty (Hanski, 1994) but within real colonies growth is more gradual (e.g. Phillips *et al.* (1999a)). The observed spread of Great Skua colonies (Furness, 1987; Furness & Ratcliffe, 2004) is better described by low frequencies of long-distance migration, as simulated by MIGRATE (Collingham *et al.*, 1996), although figures 5.5, 5.7 & 5.8 were derived from many model runs and so show moderate probabilities for many cells that were not occupied in all simulations. Unfortunately, MIGRATE simulations are very dependent on the dispersal characteristics selected (Collingham & Huntley, 2000). Although long-distance dispersal can be described using a negative power curve (as here), this function assumes that the migrants that disperse furthest are fewer in number than those dispersing any shorter distances. For the Great Skua, detailed dispersal information is unavailable and while only 2 % of recruits breed away from their natal colony (Furness, 1978b; Klomp & Furness, 1992a), it may be that all of these individuals migrate over 50 km rather than spread across migration distances in the way simulated by negative power curves. Also, there was also considerable uncertainty in the variability of MIGRATE parameters such as adult and juvenile survival and breeding success throughout all UK colonies of different size and age. Whilst the parameters used in MIGRATE simulations were from robust studies at certain colonies (e.g. Ratcliffe *et al.*, 2002), it is unlikely that all colonies will exhibit similar dynamics, and so further uncertainty surrounds the accuracy of simulated distributions. Finally, migration rates are much lower in landscapes in which suitable habitats, or aggregations of habitat, are isolated (Collingham & Huntley, 2000). However, in the current study, spatial suitability was determined using empirical data and while cells of the highest suitability were aggregated, especially when a predominantly seabird diet was assumed (Figure 5.1a), migration between these was possible by spreading through cells of lower, but still positive, habitat suitability.

5.4.4 Implications of probable future Great Skua breeding distributions within the UK

Great Skuas were one of the only UK seabird species to exhibit large population expansions over the past 30 years (Mitchell *et al.*, 2004) but the rate of growth of breeding populations within the UK has slowed substantially since expansion from artificially low levels at the beginning of the twentieth century. Dispersal simulations indicate that substantial spread of breeding populations of Great Skuas is also liable to occur throughout northern and western Scotland and Northern Ireland within the next 50-100 years; the first Great Skua breeding in Northern Ireland was recorded in 2003 (R. W. Furness, pers. comm.). Although, current UK breeding distributions are associated with the 13 °C mean July isotherm (Furness, 1988), simulations indicate that UK distributions are still expanding from previous population bottlenecks and are not yet in equilibrium with the observed climatic tolerances of Great Skuas (Chapters 2 & 6). The rate of spread of populations, however, will depend on the diet of Great Skuas at breeding colonies which is very flexible and dependent on available resources (Votier *et al.*, 2004b).

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Chapter 6.

Climatic mechanisms limiting the breeding distributions of skuas and other high-latitude seabirds

Summary

To simulate the consequences of climate change for breeding distributions of long-lived seabirds, it is necessary to determine the most probable mechanisms by which species are restricted to observed climatic conditions at current breeding sites. Climate response surfaces were constructed for the four European species of skua (Stercorariidae), selecting climatic variables based on three mechanisms by which climate could be limiting the breeding distribution of these species. Simulated distributions using these surfaces were compared to observed distributions to determine the performance of each model and therefore the most likely mechanisms restricting skuas to their observed climate envelopes. The breeding distributions of *Catharacta pomarinus*, *Stercorarius longicaudus* and *S. parasiticus* were most accurately simulated by surfaces constructed with climatic variables related to the timing of snow melt during the arctic breeding season. The breeding distribution of the Great Skua (*Catharacta skua*) was best simulated by surfaces constructed with variables associated with habitat and pelagic food availability. Mechanistic models for skuas were found to apply only to gull and tern species with similar distributions. Simulated future distributions using forecast European climate in these response surfaces suggested that in the next 60-90 years most high latitude seabirds would suffer range contractions with core European breeding populations shifting to the east.

6.1 Introduction

Responses to climatic change have been recorded for a wide range of taxonomic groups with diverse geographical distributions (Walther *et al.*, 2002). For long-lived taxa, available data indicate changes in the phenology (reviewed in Root *et al.* (2003)) and distributions of individual species (e.g. Winkel & Hudde (1997)) and in the composition of ecological communities (McCarty, 2001; Walther *et al.*, 2002). However, because species respond in individualistic ways to changing climate it is important to determine the proximate mechanisms driving such responses (Huntley, 1991, 1995). Forecast rates of climate warming are greatest in polar regions (Houghton *et al.*, 2001) and it is imperative to determine the climatic limitations for breeding in high-latitude species to be able to estimate the impacts of climate change on important seabird populations.

Many recent models exploring biological responses to climate change have utilized a ‘climate envelope’ approach (Berry *et al.*, 2002; Erasmus *et al.*, 2002; Midgley *et al.*, 2002; Pearson *et al.*, 2002; Hill, Thomas & Huntley, 2003; Thomas *et al.*, 2004) whereby a species is assumed to be restricted in its distribution to the climatic conditions under which it presently persists (Pearson & Dawson, 2003). Ecological response surfaces are bioclimatic modeling tools developed to relate the presence/absence of species in geographical space to measured climatic variables at the same locations (e.g. Bartlein *et al.* (1986)). Multiple regression of these variables produces a ‘climate response surface’ defining the combination of climatic variables most strongly associated with the occurrence of a species (Huntley, 1995). Response surfaces can be used to assess the extent to which a species' distribution is limited by climate (Beerling, Huntley & Bailey, 1995; Huntley *et al.*, 1995) and, by selecting appropriate climatic variables, the mechanism(s) behind climatic limitation can be explored (Lenihan, 1993). Response surfaces can be used to simulate distributions of species from observed climate variables in different regions (Beerling *et al.*, 1995) or in historical (Bartlein *et al.*, 1986; Huntley, 1993) or future time periods (Huntley *et al.*, 1995; Sykes, Prentice & Cramer, 1996). When modeling migratory and homeothermic species, such as birds, it is essential to consider possible mechanisms by which climate may constrain their distributions and choose climatic variables accordingly (Huntley, 1995). Use of mechanistic variables reduces the risk of defining a climatic envelope based purely on correlative variables that are related to the current distribution by chance and would provide erroneous estimations of future distributions (Pearson & Dawson, 2003).

Bioclimatic models, such as response surfaces, have often been criticised because they may not be useful for some species for several reasons. Biological interactions such as competition and predation can influence how a species responds to climate change (Davis *et al.*, 1998), yet bioclimatic models often work well over continental scales, indicating that climate is the dominant factor at these scales (Pearson & Dawson, 2003). For species with slow rates of dispersal, the observed climatic envelope may not reflect current climatic restrictions (Woodward, 1990) and substantial barriers to dispersal may prevent climatically suitable areas from being colonised (Peterson, Soberon & Sanchez-Cordero, 1999), reducing the ability of bioclimatic models to estimate actual climatic envelopes (Pearson & Dawson, 2003). In addition, the extent to which species can track these conditions as climate changes determines the speed with which they will respond to climate change by changing their distribution or, where their response is insufficient, their rate of extinction (Walther *et al.*, 2002; Thomas *et al.*, 2004). Therefore, future distributions derived from bioclimatic models may not necessarily be the realized distributions, only potential distributions given the forecast magnitude of climatic change (Huntley *et al.*, 1995; Pearson & Dawson, 2003).

Consequently, it is important to confine bioclimatic analyses to species that have high rates of dispersal such as Skuas (Family Stercorariidae) that are transequatorial migrants, capable of long-range dispersal events (Furness, 1987; Klomp & Furness, 1992). In addition, three out of four northern hemisphere skuas exhibit a circumpolar distribution suggesting that their distribution is in equilibrium with climate. It is possible, however, that the current breeding distribution of Great Skuas may not be at equilibrium with climate since this species probably colonized the northern hemisphere within the last 500 years (Furness 1987). Data detailing the recent spatial distribution of the four species that breed in Europe are readily available from several atlases (Hagemeijer & Blair, 1997; Snow & Perrins, 1998) and the most complete time-series' of climatic variables are also available for this region (e.g. CRU Mean Monthly Terrestrial Climatology (New, Hulme & Jones, 1999)).

Much recent research has found that breeding success, survival and distribution of seabirds in polar areas is influenced by climate (via changes in sea-ice and resulting food availability) (Croxall, Trathan & Murphy, 2002; Weimerskirch *et al.*, 2003). There are several mechanisms potentially restricting the breeding distributions of high-latitude seabirds to particular climatic conditions. Since skuas nest among short vegetation and are adapted for breeding at high latitudes by virtue of their morphology and physiology (Furness, 1988), they may be limited by direct physiological effects of prevailing climatic conditions whilst breeding. For instance, correlations of the southern limits of breeding distributions of Great (*Catharacta skua*) and Arctic Skuas with mean July air temperatures could indicate a climatic constraint imposed by thermoregulatory requirements (Furness, 1988). For Long-tailed, Arctic, and Pomarine Skuas nesting in arctic Europe, the breeding season is restricted by climatic conditions through the availability of nest-sites, prey and days on which foraging is possible (Maher, 1974), and such restrictions may influence breeding distributions. The availability of suitable habitat may also be important in limiting exposure to thermal extremes (Salzman, 1982; Buttemer & Astheimer, 1990; Stokes & Boersma, 1998).

To select between the most likely mechanisms by which climate may limit breeding distributions of high-latitude seabirds, response surfaces were constructed for the four skua species breeding in Europe using climatic variables that reflected heat stress conditions, habitat and food availability and limits on the timing of breeding. The accuracy of these response surfaces was estimated by comparison of simulated with observed distributions. To examine whether the narrow geographic distribution of Great Skuas in the northern hemisphere was directly related to climate suitability, surfaces were constructed for southern hemisphere *Catharacta* species and used to simulate the distributions of Great Skuas in Europe. The best performing response surfaces for all skuas were used to estimate future distributions of these species within Europe using forecast climatic variables from GCM scenarios. The applicability of these mechanistic response surfaces for other seabird species was then assessed by using them to simulate the distributions of other seabird species with contrasting morphology, distribution and habitat requirements.

6.2 Methods

6.2.1 Climate data

European breeding records (presence/absence) were taken from the European Atlas of Breeding Birds (EBBC) (Hagemeijer & Blair, 1997) for 16 seabird species (four skuas, six terns and six gulls; Table 6.2). These data were on a ~ 50 km × 50 km UTM grid adapted from *Atlas Florae Europaeae* (AFE) (Jalas & Suominen, 1972).

Climate data were extracted from the Climate Research Unit (CRU) 1960-1991 mean 30-year climatology (New *et al.*, 1999). These data relate to the climate normal period 1961-1990 and include 30 year monthly means for temperature, solar radiation, precipitation and wind speed (New *et al.*, 1999). Thirty-year means for sea surface temperature (SST) were calculated from GISST2.2 (1° resolution) data (Parker, Jackson & Horton, 1995) for the same period.

Future climate data for the period 2061-2090, summarized as 30 year monthly means, were taken from simulations of the HadCM3 global climate circulation model (Gordon *et al.*, 2000; Pope *et al.*, 2000) for all variables except sea surface temperature, which was derived from simulations of the CGCM2 (Flato & Boer, 2001). All climate variables were interpolated to the adapted AFE UTM grid as a mean value at the centre of each grid cell.

6.2.2 Constructing response surfaces

Three climatic variables were used to derive a single response surface from climate data and bird distributions. The main hypotheses and their associated variables are listed in Table 6.1 and reflect possible constraints of climate through direct physiological effects (heat stress), indirect physical effects (snow melt) and indirect biological effects (vegetation and marine productivity). Thermoregulatory requirements during breeding may result in the observed correlation between summer air temperatures and skua distributions (Furness, 1988). Therefore, one surface (H1, Table 6.1) was constructed with variables reflecting the frequency and intensity of heat stress above the anticipated thermal threshold (13 ºC, Chapter 2) during the breeding season (May to June) and other variables important in heat-transfer (solar radiation and wind speed (Monteith & Unsworth, 1990). An index of pelagic productivity was derived by subtracting mean sea surface temperature (SST) in March from the mean of sea surface temperatures for April and May, since the timing and extent of the spring bloom in phytoplankton productivity in arctic seas is reflected to some extent by differences in sea surface temperatures between early and late spring (Engelsen *et al.*, 2002; Edwards & Richardson, 2004). Such regions of high marine primary productivity are often associated with the best feeding grounds for pelagic seabirds (Chown & Gaston, 1999) and spring plankton blooms have a strong influence on the availability of sandeels (Wright & Bailey, 1996), which is an important determinate of breeding success for Great and Arctic Skuas (Hamer, Furness & Caldow, 1991; Phillips, Furness & Caldow, 1996). The SST index was combined with the mean temperature of the coldest month and growing degree

Table 6.1 Hypothesized mechanisms limiting the distribution of skuas in Europe and the variables used to explore these hypotheses.

No.	Hypothesized mechanism	Description	Variable 1	Variable 2	Variable 3
H1	Heat stress	Heat-gained through convection and radiation with convective heat-loss	Temperature sum over 13˚ C during breeding season	Mean solar radiation during breeding season	Mean wind speed during breeding season
H2	Vegetation and pelagic food availability	Vegetation growth and survival and pelagic food availability	Mean temperature of the coldest month	Growing degree days over 5 ˚C	Spring sea surface temperature index
H3	Timing of spring snow melt	Amount of snow fall and timing and extent of spring snow melt	Mean temperature of the coldest month	Mean precipitation (snow fall) in winter and spring	Mean spring temperature

days over 5 ºC (variables important for plant growth (Huntley *et al.*, 1995)) to create a surface (H2, Table 6.1) reflecting the indirect effect of climate via both habitat and food availability. A surface corresponding to the timing and extent of the breeding season in arctic regions (H3, Table 6.1) incorporated variables determining the extent of snow fall (Stone *et al.*, 2001): mean winter/spring precipitation amount (December to May), mean temperature of the coldest month (reflecting the severity of winter, without requiring the definition of the exact winter period) and the intensity of the spring melt (mean air temperature from March to May). This hypothesis accounted for importance of known delays in the onset of breeding for skuas at high-latitudes caused by snow cover (Maher, 1974).

Solar radiation and wind speed were calculated as means of monthly values for May, June and July directly from the CRU climatology. Mean air temperature during spring (March to April) and winter/spring mean precipitation (snow fall) amount (December to May) were computed in a similar way. The SST index was calculated for coastal cells only, since foraging ranges for the Great Skua, the European species that is most dependent on pelagic food resources (Furness, 1987), are commonly < 50 km (Furness, 1978). Mean temperature of the coldest month (MTCO) was the mean temperature of the coldest month in the year averaged over the 30 year period. Growing degree days above 5 ˚C was the sum of air temperature above this threshold throughout the year and mean temperature sum above 13 ºC was the air temperature sum during the breeding season (May to July). Future climatological variables were calculated in the same way but using HadCM3 data, or CGCM2 data for SST.

For each of the three hypotheses (Table 6.1), the response surface was fitted with three climatic variables using the LOWESS (locally-weighted regression) method (Cleveland & Devlin, 1988), following Huntley *et al.* (1995).

6.2.3 Simulations of current and future breeding distributions of skuas

Fitted surfaces were used to simulate the probability of occurrence of Long-tailed Skua (*Stercorarius longicaudus*), Arctic Skua (*S. parasiticus*), Pomarine Skua (*Catharacta pomarinus*) and Great Skua (*C. skua*) separately throughout the AFE grid. The probability threshold for simulation was determined by assessing the concurrency of simulated with observed distribution (data from Hagemeijer *et al.* (1997)). Predicted presences and absences were derived from probabilities produced by response surfaces and the performance of each response surface was given by the Kappa statistic (Landis & Koch, 1977): a value < 0.4 indicated poor predictive ability, between 0.4 and 0.55 moderate, between 0.55 and 0.7 good, between 0.7 and 0.85 very good, and over 0.85 excellent (Monserud & Leemans, 1992).

Potential future distributions within Europe were simulated for each skua species by substituting future climatic data for 2061-2090 into the response surface that best simulated the current breeding distribution, following Huntley *et al.* (1995). Since GCM data were at a coarser resolution, simulated future distributions were smoothed using LOWESS smoothing splines (Cleveland & Devlin, 1988) to aid visual interpretation of major trends.

6.2.4 Determining the generality of mechanistic response surfaces

Response surfaces were also constructed for six species of gull (Family Laridae) and six species of tern (Family Sternidae). Each species was chosen because of its particular habitat requirements, latitude of breeding, or body size (Burger & Gochfeld, 1996; Gochfeld & Burger, 1996)(Table 6.2), so that performance of the models for species of varying ecology/morphology could be assessed. Simulations from these models were compared to observed distributions of these species (Hagemeijer & Blair, 1997) and model performance was determined from maximized Kappa (section 6.2.3). Distributions for 2061-2090 were simulated by substituting GCM data into the best performing response surfaces. These simulations were made only for species for which model performance was high (Kappa > 0.75).

To determine if the climatic envelope observed for breeding Great Skuas was representative of the range of breeding conditions observed for congeners, simulations of Great Skua distributions in Europe were performed using models constructed for southern hemisphere *Catharacta* species. Mechanistic models were constructed with CRU and GISST2.20 (sea surface temperature) data (at the same resolution) for the southern hemisphere (spanning all longitudes between -30˚ and -60˚ latitude, for which climate data were readily available). Variables calculated for winter (December to May), spring (March to April) or summer (May to July) during the construction of the response surface (section 6.2.2), were derived using the corresponding months for the austral season (e.g. summer was November to January). Model performance was assessed by correspondance

Table 6.2 Gull (Family Laridae (L)) and tern (Family Sternidae (S)) species for which response surfaces were constructed to determine the generality of hypothesis developed for skua species. Body mass, mid-point between extremes of breeding latitude and breeding habitat preferences are given to aid interpretation of model performance. "No veg." Indicates that this species prefers no vegetation. Data sources: mass Dunning (1993); latitude, habitat and breeding range, Burger & Gochfeld (1996); Gochfeld & Burger (1996).

Species	Common Name	Family (L/S)	Mass (g)	Mid-point of breeding latitude (˚)	Breeding habitat preference	Main habitat features
Larus ridibundus	Black-headed Gull	L	284	51.2 N	Open ground or low bushes in wetlands	Wet
Rissa tridactyla	Black-legged Kittiwake	L	407	59.2 N	Cliffs	No veg.
Larus fuscus	Lesser Black-backed Gull	L	766	58.2 N	Dry vegetation	Long
Larus argentatus	Herring Gull	L	1135	57.0 N	Short, drv vegetation or bare rock	Short
Larus hyperboreus	Glaucous Gull	L	1413	68.6 N	Cliff ledges, short vegetation or beaches	Short
Larus marinus	Greater Black-backed Gull	L	1659	57.3 N	Short vegetation or bare rock or sand	Short
Sterna albifrons	Little Tern	S	57	12.2 N	Sand and shingle beaches	No veg.
Childonias nigra	Black Tern	S	65	48.7 N	Vegetation or logs within wetlands	Wet
Sterna paradisaea	Arctic Tern	S	110	59.2 N	Gravel islands, beaches or tundra vegetation	Short
Sterna hirundo	Common Tern	S	120	37.7 N	Low vegetation or beaches	Short
Thalasseus sandvicensis	Sandwich Tern	S	208	6.2 N	Short vegetation or beaches	Short
Sterna caspia	Caspian Tern	S	655	11.8 N	Low sand or short vegetation	Short

of simulated distributions with observed combined breeding distributions of all southern hemisphere *Catharacta* species within these latitudes (distribution maps in Furness (1987)) using Kappa. These response surfaces were substituted with corresponding climate data from Europe to give simulations of *Catharacta* distributions in the northern hemisphere. Coincidence between simulated distributions and observed Great Skuas distributions was determined with Kappa and two other statistics indicating accuracy of prediction at the probability threshold determined for *C. skua* (Huntley *et al.*, 1995).

6.3 Results

6.3.1 Simulating current distribution of breeding skuas

Table 6.3 details the performance of response surface models constructed with variables reflecting three possible mechanisms by which breeding distributions of northern hemisphere skuas might be constrained to their observed climate envelopes. The breeding distributions of *Stercorarius* species were best simulated by surfaces constructed with variables that determined the timing and extent of the spring snow melt (H3) (Figures 6.1d, 6.2b). This model was also excellent at simulating the breeding distribution of Pomarine Skuas (*C. pomarinus*) (Figure 6.2a). Surfaces using variables reflecting the timing of snow melt were relatively poor at simulating the breeding distribution of Great Skuas (*C. skua*) which was estimated more accurately by surfaces reflecting the combined influence of the availability of habitat and pelagic food resources (H2) (Table 6.3; Figure 6.3 d). This surface (H2) performed less well for Arctic Skuas (*Stercorarius parasiticus*), predicting more breeding colonies southwest Scotland and the Baltic coasts (compare Figures 6.1c & d). Models including pelagic food availability (H2) also performed relatively poorly for Long-tailed (*S. longicaudus*), Pomarine and Arctic Skuas (Table 6.3).

Surfaces constructed with variables important in determining heat stress during the breeding season (H1) performed less well for all four species (Table 6.3). Figure 6.1b illustrates the distribution simulated for Arctic Skuas by this model, indicating that although this species is largely confined to coastal areas in Scandinavia and the UK (Figure 6.1a), thermal conditions suitable for breeding exist further inland.

Table 6.3 Kappa values indicating coincidence of simulated distributions from response surfaces constructed following three mechanistic hypotheses with observed breeding distributions of European skua species. Kappa values between 0.55 and 0.7 indicate good agreement, 0.7-0.85 very good agreement, > 0.85 excellent agreement (Monserud & Leemans, 1992).

No.	Hypothesis	Performance of model (Kappa)			
		S. parasiticus	*S. longicaudus*	*C. pomarinus*	*C. skua*
H1	Heat stress	0.673	0.571	0.707	0.530
H2	Vegetation and pelagic food availability	0.657	0.452	0.577	0.725
H3	Timing of spring snow melt	0.784	0.761	0.970	0.596

Climatic envelopes for breeding colonies of the four skua species are shown in Figure 6.4. The three smaller species showed similar climatic preferences at the northern edge of their range, breeding in areas where winter temperatures regularly dropped below -17 ºC but only where winter precipitation (snow fall) was low. The distribution of Pomarine Skuas was restricted to these

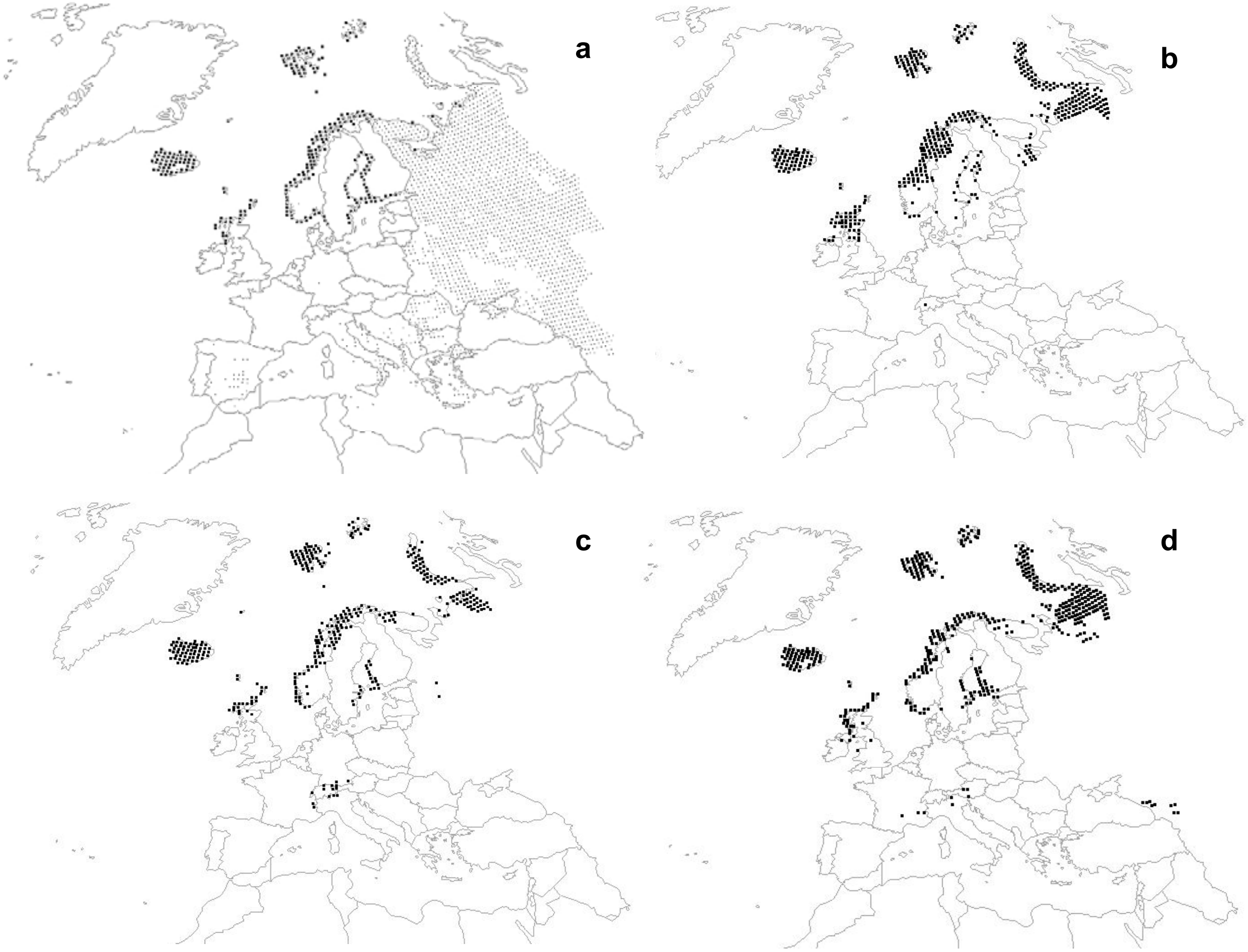
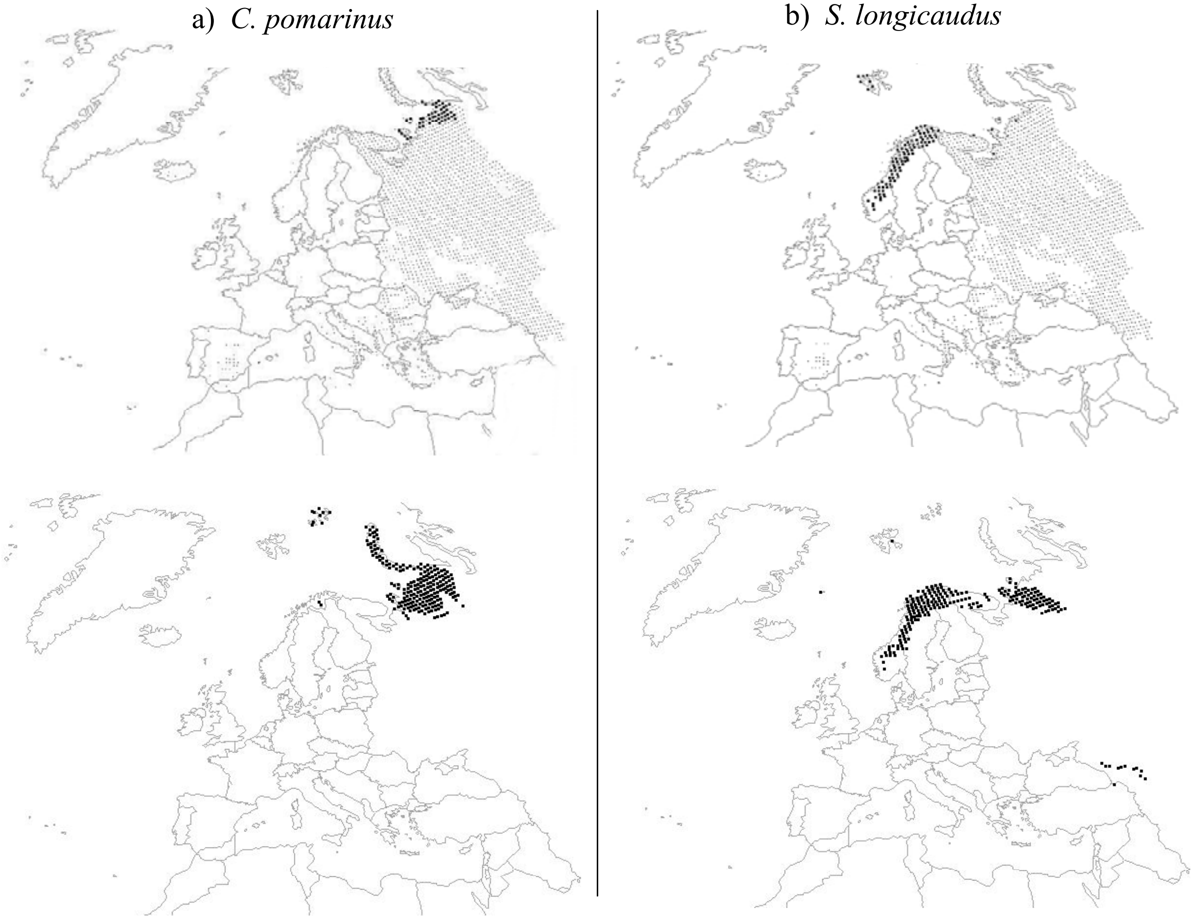


Figure 6.1 Observed breeding distribution of *S. parasiticus* (a), and distributions simulated for this species using response surfaces constructed with climatic variables related to (b) heat stress (H1), (c) vegetation growth and pelagic food availability (H2) and (d) timing of snow melt (H3). Observed maps: (■) confirmed breeding, (·) no data. Simulated maps: (■) simulated breeding.



a) *C. pomarinus*

b) *S. longicaudus*

Figure 6.2 Observed breeding distributions (top panels) and distributions simulated using response surfaces constructed with variables relating to the timing of spring snow melt (H3) (bottom panels) for (a) *Catharacta pomarinus* and (b) *Stercorarius longicaudus*. Observed maps: (■) confirmed breeding, (·) no data. Simulated maps: (■) simulated breeding.

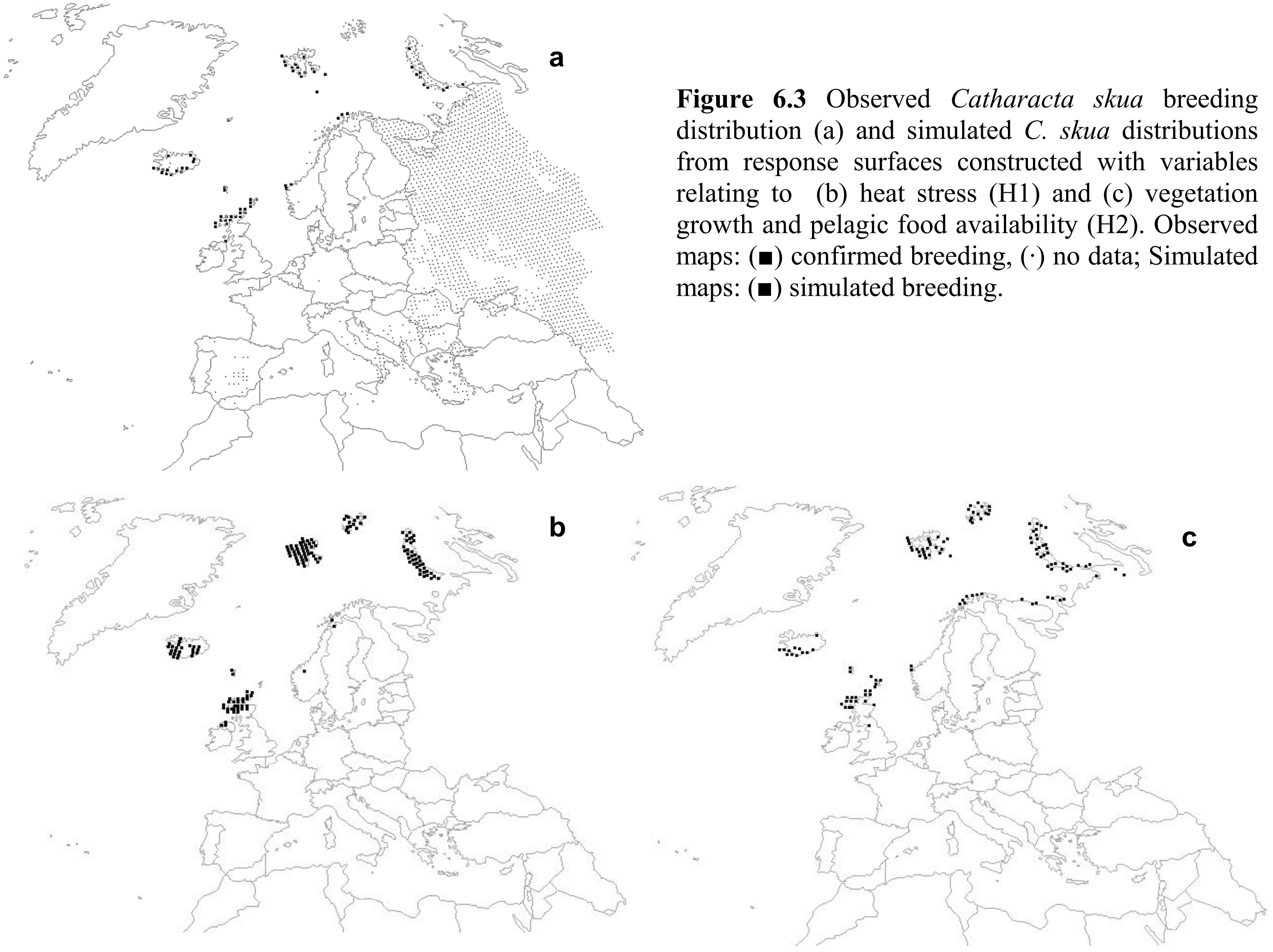


Figure 6.3 Observed *Catharacta skua* breeding distribution (a) and simulated *C. skua* distributions from response surfaces constructed with variables relating to (b) heat stress (H1) and (c) vegetation growth and pelagic food availability (H2). Observed maps: (■) confirmed breeding, (·) no data; Simulated maps: (■) simulated breeding.

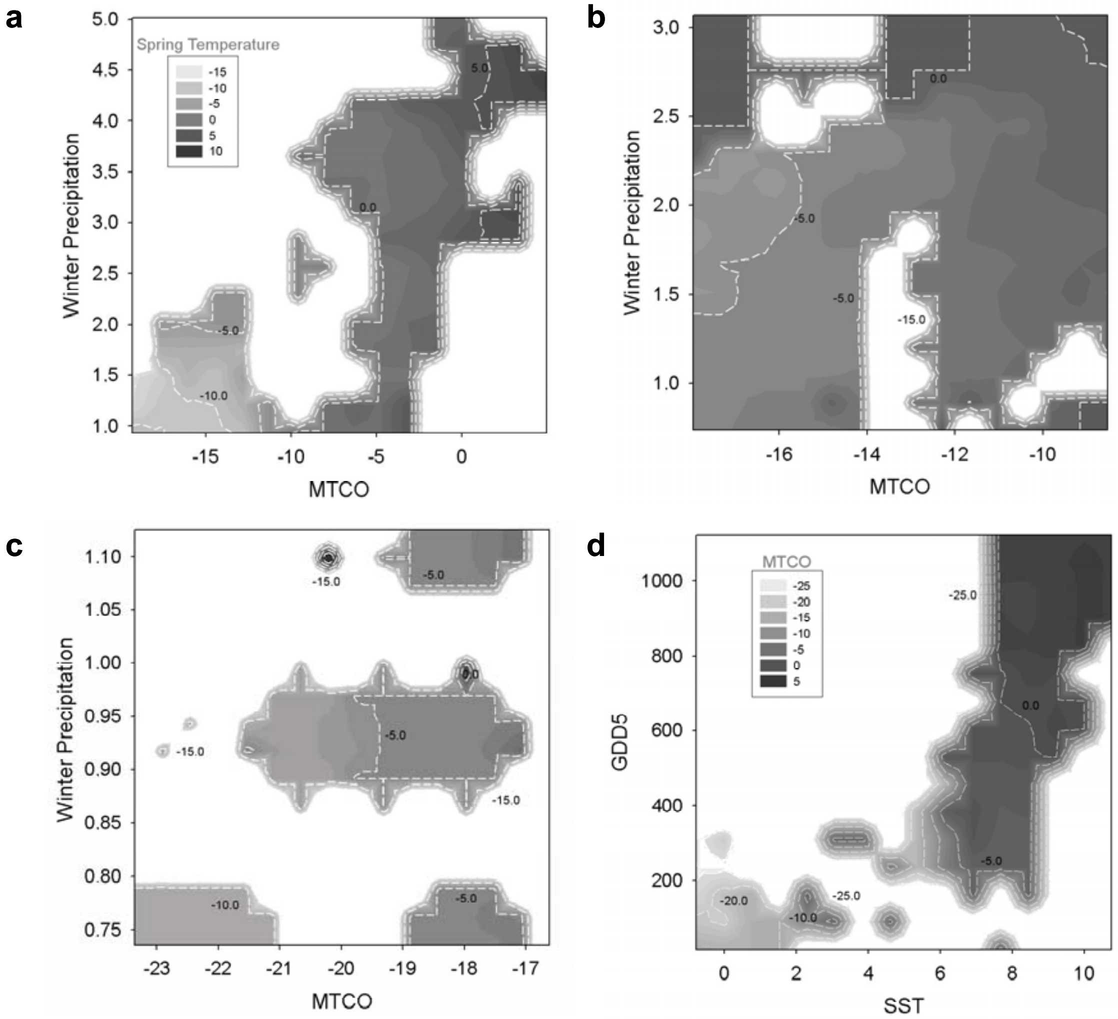


Figure 6.4 Climate envelopes for breeding populations of the four northern hemisphere skua species within Europe derived from the most accurate mechanistic response surfaces. Surfaces were constructed with variables related to the timing of spring snow melt (H3) for (a) *Stercorarius parasiticus*, (b) *S. longicaudus* and (c) *Catharacta pomarinus*, and habitat pelagic food availability (H2) for (d) *C. skua.* Variables on axes are winter precipitation (mm/month), mean temperature of the coldest month (MTCO) (ºC), growing degree days over 5 ºC (GDD5) (ºC) and sea surface temperature index (SST) (ºC). For each surface the third variable [spring temperature (ºC) in (a), (b) and (c), MTCO in (d)] is contoured (dashed contour lines, with labels, at 5 ºC intervals). Blank regions indicate that the species was not observed breeding under this particular combination of climatic variables.

areas (Figure 6.4c) but Long-tailed Skuas bred in areas of higher winter snowfall so long as the spring-temperatures were above freezing (Figure 6.4b) as did Arctic Skuas (Figure 6.4a). Great Skuas exhibited a dichotomous climate envelope, breeding in areas of similar mean winter temperatures as the other species (the high arctic zone, with corresponding short growing season (low GDD5) (Figure 6.4d)) but also in regions where the spring sea surface temperature index was 6-12 ºC (sharp increases in temperature between March and April/May, suggesting higher marine productivity) (Figure 6.4d).

6.3.2 Generality of mechanistic response surfaces constructed for skua species

58% of response surface simulations for terns and gulls gave a ‘good’ level of agreement (Monserud & Leemans, 1992) with observed distributions (Table 6.4). Incorporating climatic variables that determined the timing of snow melt (H3) produced surfaces that gave, on average, the best match with observed distributions (mean Kappa (± SD): 0.673 (± 0.13)). The performance of H3, however, was negatively correlated with breeding range, i.e. data prevalence (r_s = -0.96, n = 12, P < 0.01). Response surfaces constructed with variables related to the combined influence of habitat and pelagic food availability (H2) were, on average, less accurate (mean Kappa (± SD): H2, 0.452 (± 0.18)) (Table 6.4). The performance of this model, but not H3, was independent of species’ breeding latitude (Table 6.4) and simulation accuracy for terns and gulls was not related to the body size or habitat requirements of these species (Table 6.4).

Table 6.4 Measures of fit (maximum Kappa) between observed breeding distributions and distributions simulated for 12 species of gull (Laridae) and tern (Sternidae) using response surfaces constructed with variables relating to vegetation growth and pelagic food availability (H2) and timing of snow melt (H3). Data are ranked by mid-point of breeding latitude. Species, family, body mass and main habitat requirements are given for comparison. Only latitude showed a significant correlation with model performance (H3: $r_s = 0.89$, $n = 12$, $P < 0.01$). *n* = breeding range (km) (i.e. data prevalence). Data sources: mass Dunning (1993); latitude, habitat and breeding range, Burger & Gochfeld (1996); Gochfeld & Burger (1996).

Species	Family	H2	H3	Mass (g)	Mid-point of breeding latitude (˚)	Main habitat requirements	*n*
Thalasseus sandvicensis	Sternidae	0.551	0.446	208	6.2 N	No vegetation	136
Sterna caspia	Sternidae	0.654	0.613	655	11.8 N	No vegetation	83
Sterna albifrons	Sternidae	0.368	0.480	57	12.2 N	No vegetation	509
Sterna hirundo	Sternidae	0.213	0.614	120	37.7 N	Short	1520
Childonias nigra	Sternidae	0.291	0.702	65	48.7 N	Wet	698
Larus ridibundus	Laridae	0.207	0.660	284	51.2 N	Wet	1682
Larus argentatus	Laridae	0.350	0.731	1135	57.0 N	Short	824
Larus marinus	Laridae	0.493	0.726	1659	57.3 N	Short	481
Larus fuscus	Laridae	0.434	0.692	766	58.2 N	Long	527
Rissa tridactyla	Laridae	0.621	0.714	110	59.2 N	Short	241
Sterna paradisaea	Sternidae	0.435	0.773	407	59.2 N	No vegetation	642
Larus hyperboreus	Laridae	0.802	0.926	1413	68.6 N	Short	72

Response surfaces constructed for *Catharacta* species in the southern hemisphere performed well between 30 and 60 °S but poorly simulated the breeding distribution of Great Skuas in Europe (Table 6.5). The most accurate simulations were from surfaces constructed with variables related to habitat and pelagic food availability (H2) (Table 6.5, Figure 6.5). Surfaces constructed with variables reflecting heat stress during breeding only predicted three European grid cells as suitable for breeding and Great Skuas bred in none of them (Table 6.5).

Table 6.5 Accuracy of simulated distributions from mechanistic response surfaces (Table 6.3) constructed for *Catharacta* species in the southern hemisphere (30-60 °S). Simulations were made of current breeding distributions of all *Catharacta* species between 30-60 °S and for Great Skuas in Europe. Kappa, the number of observed and simulated presences, the proportion of observed presences that are correctly predicted (P1) and the proportion of all simulated presences that are correct (P2) are included for model assessment.

		Simulations between 30 and 60 °S	Simulations within Europe				
No.	Hypothesis	Performance of model (Kappa)	No. observed	No. simulated	P1	P2	Performance of model (Kappa)
H1	Heat stress	0.254	69	3	0.00	0.00	0.000
H2	Vegetation and pelagic food availability	0.679	69	42	0.36	0.61	0.416
H3	Timing of snow melt	0.637	69	76	0.17	0.17	0.159

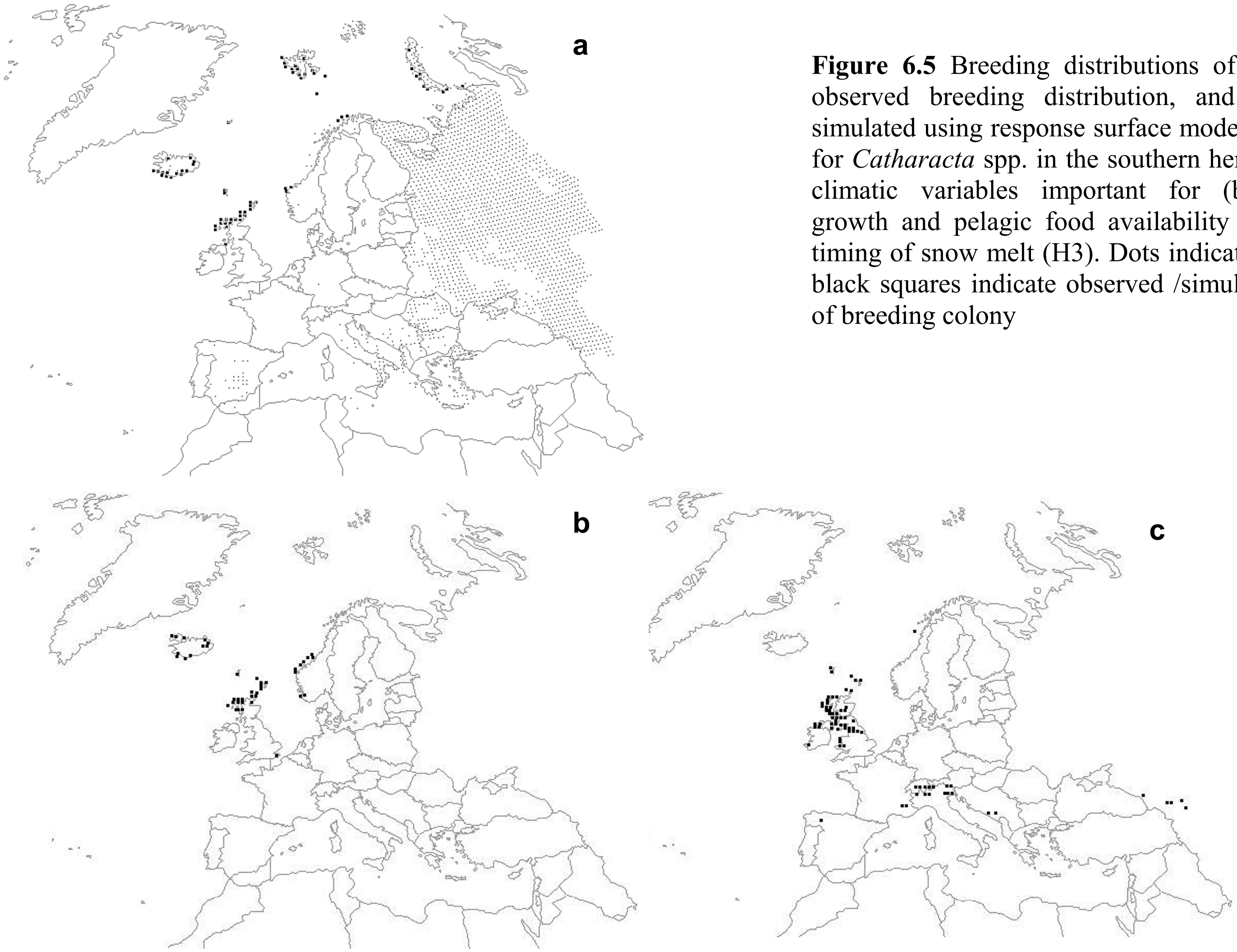


Figure 6.5 Breeding distributions of *C. skua*: (a) observed breeding distribution, and distributions simulated using response surface models constructed for *Catharacta* spp. in the southern hemisphere with climatic variables important for (b) vegetation growth and pelagic food availability (H2) and (c) timing of snow melt (H3). Dots indicate no data and black squares indicate observed /simulated presence of breeding colony

6.3.3 Simulations of the future distribution of skuas and other high-latitude seabirds

Simulated breeding distributions throughout Europe, derived from the three best performing mechanistic response surfaces, are given in Figures 6.6-6.7 for each European skua species, and in Figure 6.8 for two high-latitude gull and tern species. These simulations suggest radical changes in distribution for all these high-latitude seabird species over the next 60-90 years.

Breeding Pomarine Skuas were predicted to shift out of Europe and west Russia over the next 60-90 years (Figure 6.7a). Great Skuas were simulated as being lost as a breeding species in Iceland, the Faroes and the UK and shifting to the most favourable climatic conditions in the south Baltic Sea (Figure 6.7b). Breeding Long-tailed skuas were simulated as being lost from the mountain areas of Norway and Sweden and retracting to the coast and continent of west arctic Russia (Figure 6.6b). Simulated changes in the distribution of Arctic Skuas and Arctic Terns (*Sterna paradisea*) were similar, with general range retractions eastward within Europe, through Scandinavia and the continental north-east (Figures 6.6a & 6.8b). The future strongholds of Arctic Skuas are projected as the arctic islands of Spitsbergen, Franz-Joseph Land and Nova-Zemlya, whilst Arctic Terns are simulated as breeding only in the Baltic States and continental arctic Russia, respectively (Figures 6.6a & 6.8b). The simulated breeding distribution Glaucous Gulls (*Larus hyperboreus*) within Europe showed the least change of all species examined (Figure 6.8a), with slight eastward retractions from colonies in Spitsbergen and Iceland over the next 60 to 90 years.

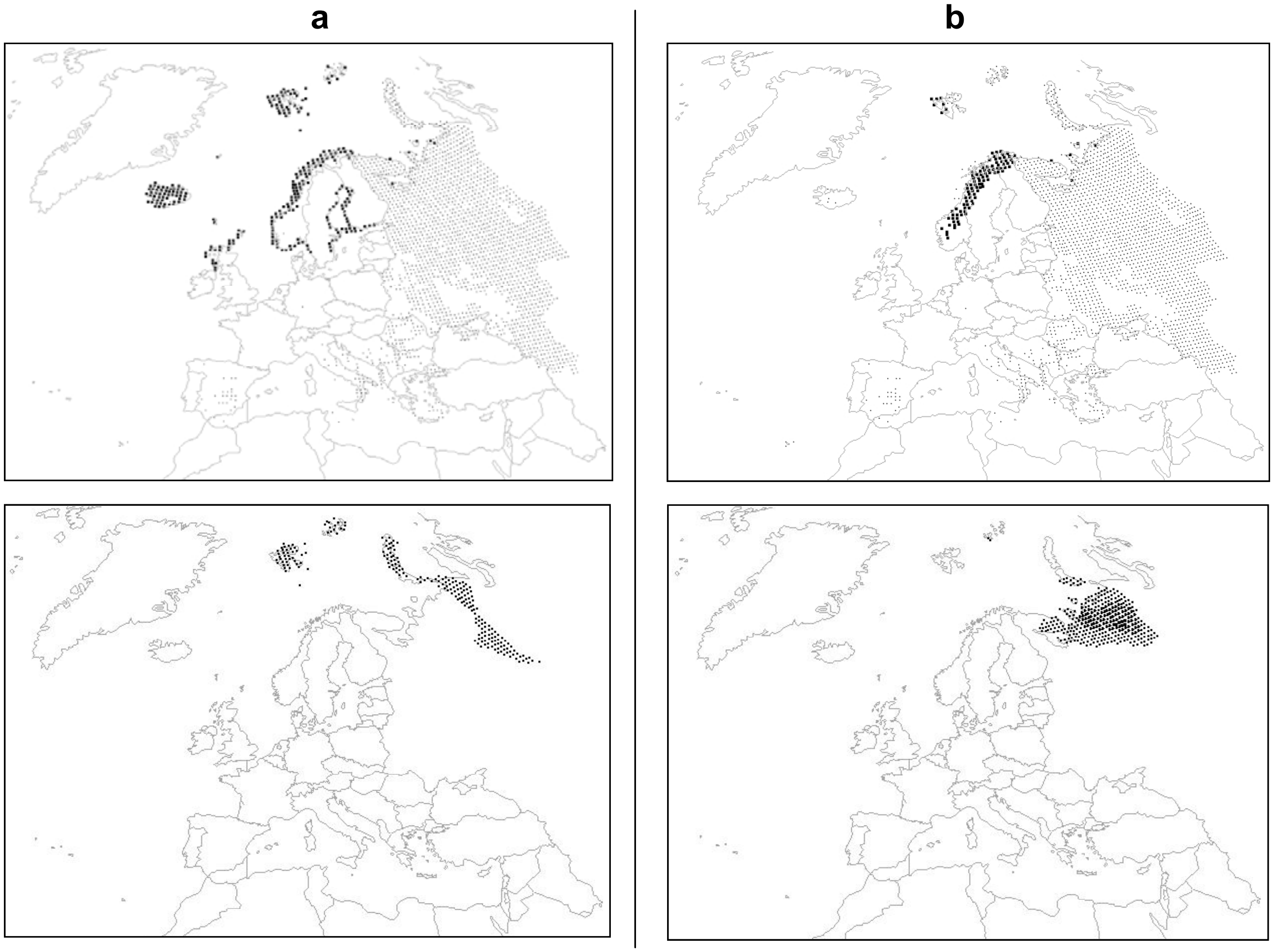


Figure 6.6 Observed breeding distributions (top panels) and future distributions simulated for 2061-2090 from response surfaces constructed with climatic variables relating to timing of snow melt (H3) (bottom panels) for (a) *Stercorarius parasiticus* and (b) *S. longicaudus*. Observed/simulated breeding (■, heavy shading indicates very high probabilities (> 0.75)), no data (·).

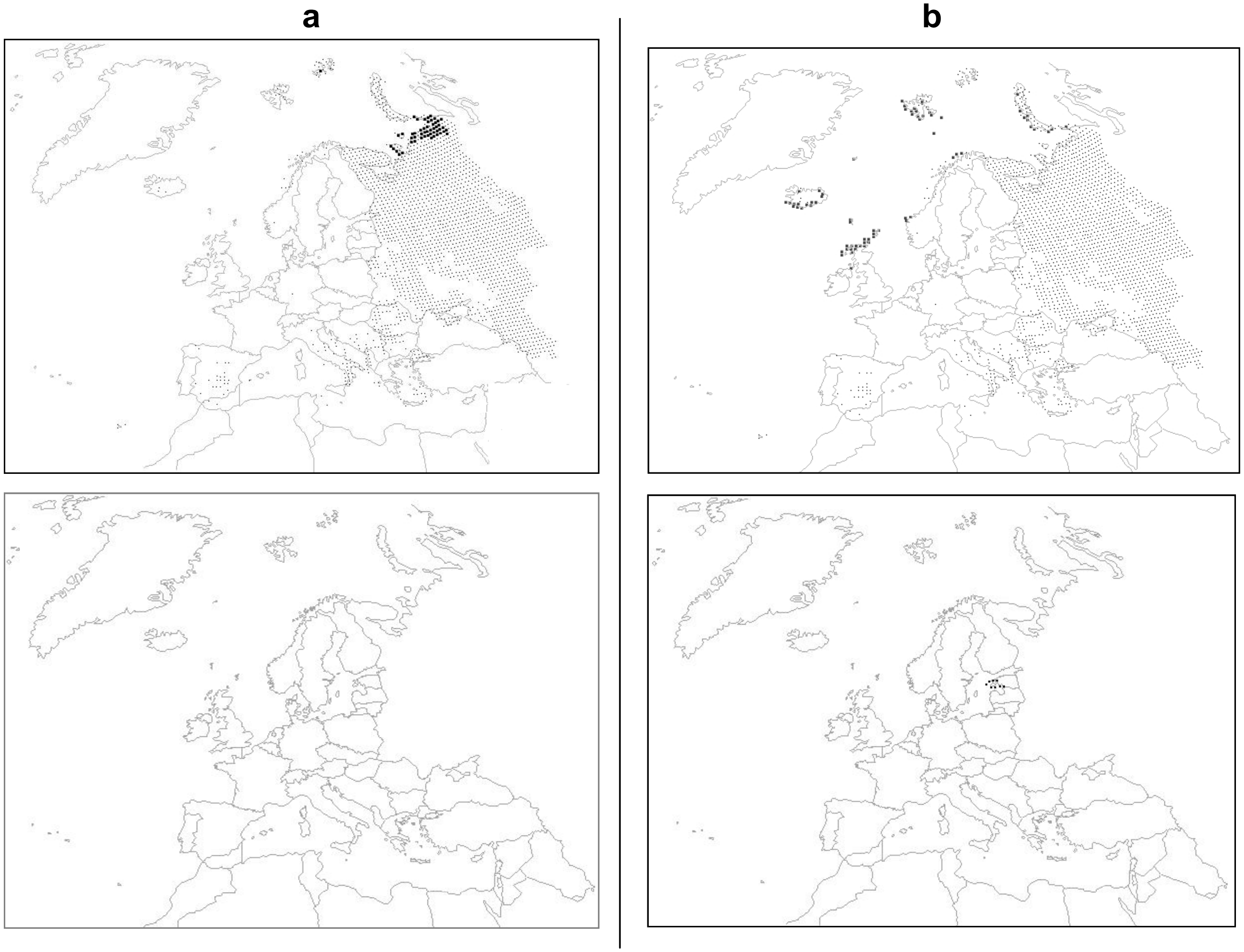


Figure 6.7 Observed breeding distributions (top panels) and future distributions (bottom panels) simulated for 2061-2090 from response surfaces constructed for (a) *Catharacta pomarinus* with climatic variables relating to timing of snow melt (H3) for and (b) *C. skua* with climatic variables important for vegetation growth and pelagic food availability (H2). Observed/simulated breeding (■), no data (·).

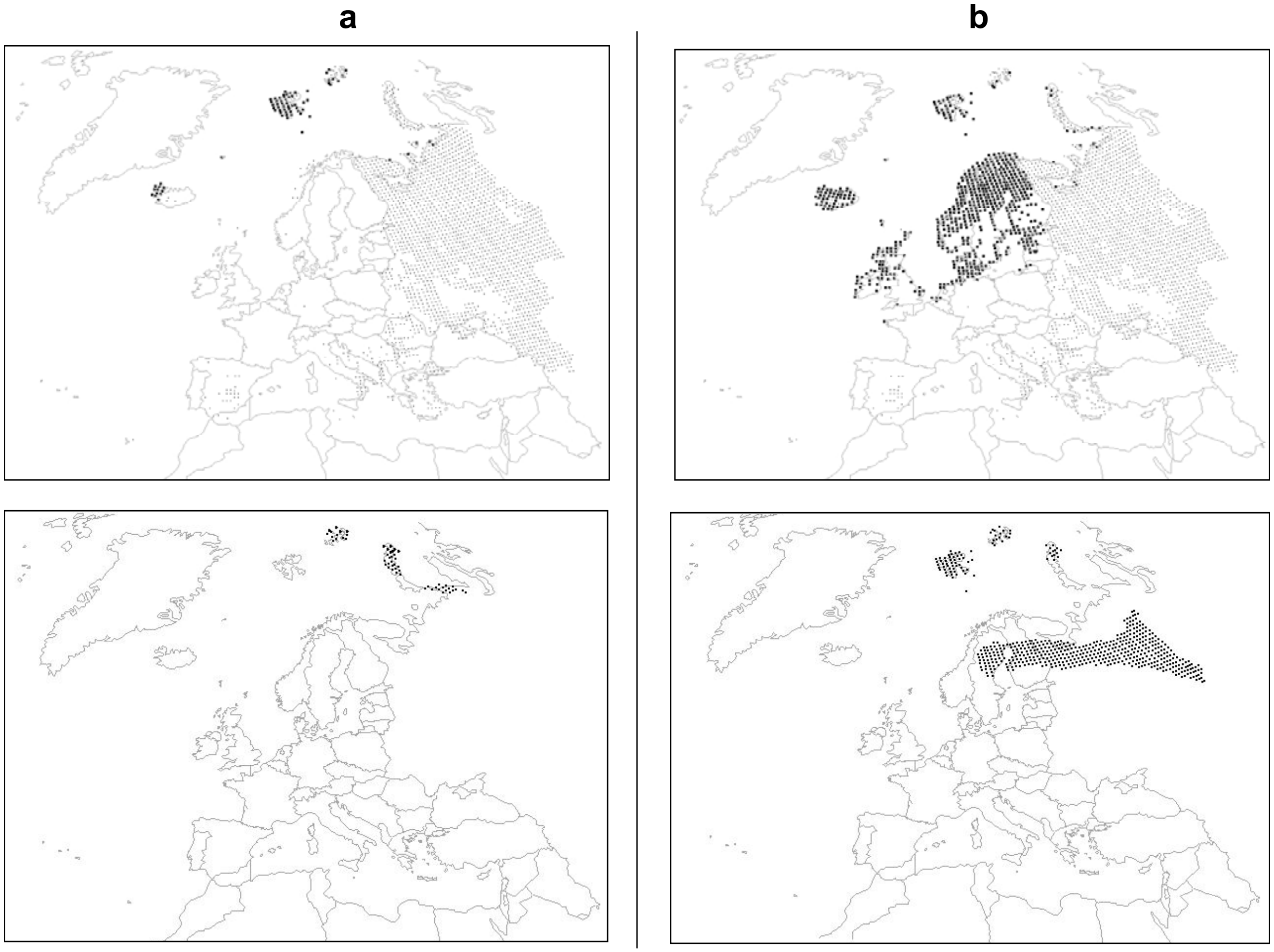


Figure 6.8 Observed current breeding distributions (top panels) and distributions simulated for 2061-90 from response surfaces constructed with variables relating to timing of snow melt (H3) (bottom panels) for (a) *Larus hyperboreus* and (b) *Sterna paradisea*. Observed/simulated breeding (■), no data (·).

6.4 Discussion

6.4.1 Climatic mechanisms restricting the distribution of skuas in Europe

Breeding distributions of all three small species of skua (*Stercorarius parasiticus*, *S. longicaudus* and *Catharacta pomarinus*) were most accurately simulated by response surfaces constructed with climatic variables important in determining the timing of spring snow melt (H3). Actual climate envelopes for each species differed though, with *C. pomarinus* being restricted to the coldest, most arid regions whilst the other two species bred in these regions and, if mean spring temperatures were around 0 ºC, in warmer areas with higher winter snow fall. Breeding is probably inhibited by the presence of snow on the ground on arrival at the breeding grounds (Maher, 1974; Furness, 1987) and this appears to be the main climatic factor determining the European breeding distribution of these species. Southern range margins, however, will not be constrained by the length of the breeding season, although changes in thermal stress, prey availability, predation pressure and competition linked to the timing of snow melt may limit breeding here.

Surfaces constructed following the hypothesis that skua distributions were restricted by thermal conditions during breeding (Furness, 1988) performed poorly for all species, indicating this hypothesis probably only holds, if at all, at southern range margins (Furness, 1988). Surfaces constructed with sea surface temperature (H2) also performed relatively poorly for Pomarine, Long-tailed Skuas, that feed mainly on terrestrial prey during the breeding season (Maher, 1974; Furness, 1987). Arctic Skua distributions were poorly defined by sea surface temperatures, presumably because, within Europe, there are many continental breeding populations also feeding on predominantly terrestrial prey. Difficulty in defining the influence of climate on terrestrial prey availability consequently limits the accuracy of mechanistic bioclimatic models for these species, although the entire European distributions seem associated with the timing of spring snow melt.

Timing of snow melt was far less important for Great Skuas (*C. skua*) and surfaces constructed according to habitat and pelagic food availability (H2) simulated the breeding distribution of this species most accurately. Although Great Skuas were found to breed within two distinct climatic regimes, the high arctic of Spitsbergen and the warmer regions near the North and Baltic Seas, the majority of the population bred in these warmer areas, where distribution was associated with habitat availability and marine productivity and not timing of snow melt. Response surfaces accurately simulating distributions of *Catharacta* species in the southern hemisphere did not correctly simulate the breeding distribution of Great Skuas in Europe. The closest correspondence was achieved by the model constructed with variables related to vegetation and pelagic food availability (H2). This model failed to predict breeding in arctic areas because only data from between 30 and 60 °S had been used in its construction (climate data at higher latitudes was incomplete). Consequently, the southern breeding margin of Great Skuas in Europe probably reflects the constraint of current habitat suitability and food availability, not a continuing expansion from recent colonization ~ 500 years ago (Furness, 1987).

6.4.2 Mechanistic response surfaces as a tool for predicting changes in breeding distributions of high-latitude seabirds

Response surfaces developed with mechanistic variables important for skuas simulated breeding distributions of other seabird species relatively well. The most general surface was constructed with variables determining the timing of spring snow melt (H3) and its simulations were accurate for arctic and sub-arctic seabirds. Surfaces constructed according to habitat and pelagic food availability simulated breeding distributions well for species breeding on isolated islands, e.g. the Glaucous Gull (*Larus hyperboreus*), but poorly for seabirds with continental distributions, e.g. the Common Tern (*Sterna hirundo*). Accuracy of this model, however, was also correlated with data prevalence as found for other European taxa (Huntley *et al.*, 2004). Species' body size and estimates of habitat requirement did not influence the performance of response surfaces, indicating response surface models were not influenced by characteristics of secondary importance for the distributions of these species.

Simulated breeding distributions for the period 2061-2090 were derived for the four skua and one gull and one tern species. Models simulated large changes in European breeding range for all six species within the next 60-90 years with all expected to shift east of their current distribution (Figures 6.6-6.8). Seabirds are generally long-lived and the species for which simulations were performed exhibit strong breeding site fidelity (Furness, 1987; Burger &

Gochfeld, 1996; Gochfeld & Burger, 1996). Consequently, shifts in distribution simulated from these bioclimatic models are likely to be over-estimates of actual rates of change (Pearson & Dawson, 2003) although, unless a species can adapt to new climatic regimes, these changes will eventually occur.

The simulated distribution for breeding Great Skuas in 2061-2090 was restricted to southern Baltic coasts, with breeding colonies being lost from Iceland, the UK and arctic areas. This simulation is unlikely to be realized for several reasons. Firstly, models constructed to reflect habitat and pelagic food availability, although the best performing model for this species, produced less accurate simulations than those using snow melt variables to simulate the distribution of other species. Secondly, the timing of the spring phytoplankton bloom is only weakly related to sea surface temperature in arctic areas (Engelsen *et al.*, 2002), differs in strength for different plankton species (Edwards & Richardson, 2004) and the sea surface temperature index used was too broad to determine the exact timing of plankton bloom events at different latitudes. Additionally, changes in fisheries discards within important areas of this species' range should lead to shifts in diet (Votier *et al.*, 2004), possibly lessening the dependence of breeding distributions on areas of high marine productivity. Since Great Skua distributions do not appear to be restricted by thermal stress during breeding, this species may be able to respond to such changes in food availability by colonizing areas south of its current breeding range.

Mechanistic response surfaces developed for skuas have provided insights into climatic mechanisms that might be limiting breeding distributions. The applicability of these models, however, is restricted to other high-latitude species.

Consequently, individual differences in ecology and distribution appear to limit the generality of mechanistic models, even though more correlative surfaces perform well for a wide range of taxa, e.g. Huntley et al. (2004).

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Chapter 7.

General Discussion

7.1 Introduction

There is increasing evidence that the rate of recent change in global and regional climate does not only exceed any since the end of the last glacial period, 10,000 years ago (Sundquist, 1993; Huntley, 1995), but is affecting individuals, communities and species at all trophic levels (Parmesan & Yohe, 2003; Root *et al.*, 2003; Thomas *et al.*, 2004). Species are predicted to respond in individualistic ways to changing climatic regimes (Huntley, 1991) depending on their life-histories (Hill *et al.*, 2002), ecological requirements (Warren *et al.*, 2001) and community dynamics (Davis *et al.*, 1998). At lower trophic levels, species are often directly influenced by climate (Huntley, 1991, 1995), since solar radiation and temperature influence the rate of photosynthetic processes and therefore plant and phytoplankton growth. For higher predators or highly mobile species, however, direct climatic limitations are not so clear (Huntley, 1995) and indirect effects of climate, such as restrictions in food or habitat availability, may be more important (Huntley, 1995) and could obscure direct impacts. Changes in food or habitat availability often lag behind underlying changes in climate (Huntley, 1991) but any direct effect of climate upon an animal species would increase the immediacy of its response and the risk posed by forecast rapid climate change. To estimate the potential impacts of forecast climate change on migratory higher predators it is therefore important to determine the mechanisms by which climate may be currently limiting the reproduction, survival and spread of these species (Huntley, 1995).

Great Skuas (*Catharacta skua*) are long-lived seabirds, adapted for breeding at high-latitudes, but restricted to small areas of northern and Arctic Europe, Scandinavia and Russia (Hamer, 2001) (Chapter 1). The worldwide breeding population is only ~14,000 pairs and because 60 % of these nest in the UK (Hamer, 2001) this species is of important national and international conservation concern. Since climate warming is forecast to be greatest at high-latitudes (Houghton *et al.*, 2001) the threat posed to this species by climate change needs to be quantified. Recent spread and distribution of Great Skua breeding colonies suggest that climate may be directly restricting breeding via heat stress at breeding colonies (Furness, 1988). To date, however, most observed impacts of climate warming on high-latitude seabirds have been mediated by changes in food availability in response to shifts in the timing and extent of sea-ice (Micol & Jouventin, 2001; Croxall, Trathan & Murphy, 2002; Weimerskirch *et al.*, 2003). Great Skuas commonly breed in areas where the influence of sea-ice is negligible, as do many European seabird species. These and other aspects of their ecology, e.g. long-distance migration, high philopatry (Chapter 1, section 1.6), complicate the detection of climate-induced responses but also make the Great Skua an ideal model species to study responses to climatic change that may be generally applicable for a wide range of marine predators.

7.2 Current responses of Great Skuas to climate

For the Great Skua, a high-latitude seabird adapted for breeding in cool arctic and sub-arctic climates, observed rapid climatic warming (Houghton *et al.*, 2001) may be expected to directly impair breeding success and survival by increasing the probability of overheating during foraging or constraining time budgets by increased demand for thermoregulatory activities (Furness, 1988). Substantial variation in heat stress exposure was predicted throughout the entire breeding range (Chapter 2). Both frequency and intensity of estimated heat stress decreased with latitude suggesting that the probability of over-heating was highest for lower-latitude colonies, such as Foula, Shetland (60 ˚N), and any negative reproductive consequences should be evident at these colonies. Observations and experiments at Foula, one of the largest Great Skua breeding colonies, indicated that the effects of food shortage were far more important than thermal stress in determining adult time budgets, chick growth and consequent breeding success (Chapters 3 & 4). This was not because heat stress at breeding colonies was unimportant, since breeding adults often traded-off time that could have been spent foraging or guarding chicks to bathe in freshwater when thermal conditions were challenging. This trade-off was more commonly observed for birds breeding at low-altitude sites, at which operative temperature, an index of heat stress, was found to be consistently higher (Chapter 4). Experimentally supplementing the diet of breeding adults reduced the time they spent foraging and increased bathing activity, again indicating a trade-off between bathing and foraging activities (Chapter 3). Despite these behavioural responses, breeding performance (laying dates, hatching success, chick growth and survival) of Great Skuas was unaffected because adults exhibited considerable behavioural flexibility: when thermal stress and energetic demands of growing chicks were high but food availability was scare, adults maintained territorial attendance (to guard chicks) but traded-off bathing for increased foraging time, and instead panted at territories to reduce thermal loading (Chapter 4). As a result of this behavioural flexibility, Great Skuas breed successfully in regions where air temperatures during chick-rearing regularly exceed the predicted upper limit of their thermoneutral zone but only occasionally rise above 20 ºC, where panting and gullar fluttering are no longer sufficient for heat loss (Chapter 2). Currently, there is no evidence that climate is directly restricting the breeding success, and consequently distribution, of Great Skuas by one of the most plausible mechanisms: heat stress at breeding colonies.

Large scale analyses indicated that the dependence of breeding adults on predominantly marine prey that varies according to climatic conditions was the most probable mechanism by which climate may have shaped European Great Skua breeding distributions (Chapter 6). It is not certain, however, that Great Skua distributions are currently restricted by climate, in part because climatic mechanisms affecting productivity in marine systems are unclear and variable (Reid *et al.*, 1998; Edwards & Richardson, 2004) and consequently difficult to model (Chapter 6). Also, recent changes in the breeding distributions of Great Skuas in Europe are evident (Hamer, 2001) and many new colonies have been founded in the UK during the last 30 years (Chapter 5). During this period of expansion, Great Skua colonies in Shetland, accounting for over 70 % of the UK population (Furness & Ratcliffe, 2004), experienced several years of low breeding success as a result of poor food availability ((Hamer, Furness & Caldow, 1991; Ratcliffe, Furness & Hamer, 1998; Caldow & Furness, 2000). Such poor food availability dictated time budgets for breeding adults during recent food shortfalls at Foula, Shetland, leading to lower than average breeding success (Chapter 4) and has also been found to reduce survival of fledglings (Hamer *et al.*, 1991) and adults (Ratcliffe *et al.*, 2002). Population expansion over the last 30 years suggests that periodic low food availability at UK breeding colonies did not restrict the breeding distribution of this species (Chapter 5), even though models indicate that, throughout Europe, breeding distribution is more likely to be shaped by food availability than expansion from historical distributions (Chapter 6).

7.3 Responses of Great Skuas to forecast climatic change

A bioclimatic model for the Great Skua indicated that active thermoregulation by panting or gullar fluttering was necessary at air temperatures above 10.6 ˚C, while above 20.6 ˚C additional behavioural modifications were required to maintain homeothermy and prevent over-heating (Chapter 2). In high-latitude regions, mean air temperatures are forecast to rise by as much as 8 Celsius degress (C°) over the next century, even in conservative scenarios (B2 SRES scenario, HadCM3 global climate model (Gordon *et al.*, 2000; Pope *et al.*, 2000)). Great Skua breeding populations are currently expanding in arctic Russia and it is in these areas where the highest levels of climate warming are expected (Houghton *et al.*, 2001). At these, and any new colonies at south-eastern range margins, higher altitude breeding territories should be occupied preferentially to limit exposure to heat stress. Even so, time available for foraging may still become restricted by the need for heat loss by bathing off-territory (Chapter 3). Other heat-loss behaviours are likely to be exhibited more often, especially wing-drooping, drinking freshwater, bathing, standing in water and shading chicks

(Lustick, 1984) or flying at high altitudes (Piersma, 2002), all of which were observed at breeding territories at Foula in 2002 and 2003. These behaviours and trade-offs will be most evident at times when heat stress is intense, particularly during incubation and late chick-rearing (Chapters 2 & 4), and chicks or eggs may become exposed to conspecific predation, the main cause of breeding failure in this species (Caldow & Furness, 2000; Hamer, 2001).

In the UK, where temperature rise predicted from these same models is only ~ 2 C° in the next 80 years, changes in frequency and intensity of heat stress can probably be accommodated by selection of high altitude nesting sites or by small alterations of time budgets by breeding adults (Chapter 4). Dispersal models simulated rapid colonization of western Scotland and Northern Ireland by breeding Great Skuas over the next 50-100 years (Chapter 5). These models, however, made no provision for changes in climate or food availability. Drastic changes in availability of pelagic food resources, especially sandeels (Proffit, 2004) and consequent breeding failure for gulls and auks (Oro & Furness, 2002), coupled with future restrictions in whitefish discard (Furness, 2000) are all likely to lead to an increasing frequency of food shortfall for breeding Great Skuas at many UK colonies. In the UK, climate change has been implicated in recent reductions in sandeel availability (Proffit, 2004), and phytoplankton data indicate that marine productivity has responded to changing climate (Reid, de Fatima Borges & Svendsen, 2001), with subsequent effects on marine productivity (Solow & Beet, 2005). Persistent food shortfall around large breeding colonies, seen in Shetland since 2002 (Mavor *et al.*, 2003, 2004; Parsons, 2004), would reduce breeding success and post-fledging (Hamer *et al.*, 1991) and adult survival

(Ratcliffe *et al.*, 2002) at these sites. Breeding populations may decline if food shortage continues through successive years and, if philopatry remains high (Klomp & Furness, 1992), fewer migrants would spread to new breeding sites.

Future simulations from response surface models, incorporating the effect of changing climate on pelagic food sources, indicated large reductions in breeding range for Great Skuas within the next 100 years (Chapter 6). Uncertainty surrounding estimations of marine productivity from climatic variables, coupled with observed flexibility of Great Skua diet (Votier *et al.*, 2004), however, limit the reliability of these predictions. Additionally, changes in distribution are likely to lag behind causal mechanisms, as a result of the longevity and high philopatry of Great Skuas, and will be preceded by successive seasons of poor breeding success in areas of food shortage.

7.4 Responses of Great Skuas to climate: consequences of climate change for high-latitude seabirds

Great Skuas had much potential as a model for determining the consequences of climate change for a variety of high-latitude seabirds because of their adaptations for breeding at high-latitudes (Furness, 1988), observed thermal preferences (Furness, 1988), high trophic level and varied diet (Hamer, 2001). Climate was found to be most likely to limit breeding success and distribution of this species indirectly, by influencing the availability of food resources: chiefly, small pelagic fish and other seabird species. Available evidence indicates that the effect of climate change on other high-latitude seabirds is also most commonly mediated by the availability of food (Croxall *et al.*, 2002; Durant, Anker-Nilssen &

Stenseth, 2003; Weimerskirch *et al.*, 2003). The breeding distribution of the Great Skua within Europe was accurately simulated by climatic variables thought to represent marine productivity (Chapter 6). Unfortunately, this model performed poorly at simulating observed breeding distributions of other seabird species, probably resulting from difficulties in defining climatic influences on marine productivity and interspecific differences in foraging ecology (Chapter 6). The observed influences of heat stress frequency and intensity were insufficient to restrict Great Skua breeding success or distributions (Chapters 4 & 6), despite morphological, physiological and ecology adaptations for limiting heat loss in this species (Furness, 1988) (Chapter 1). Consequently, it is unlikely that other high-latitude seabirds will be directly affected by heat stress, unless they exhibit more restricted time budgets or experience additional problems concurrently, such as parasitism (Gaston, Hipfner & Campbell, 2002). Although the Great Skua illustrates the most probable responses of high-latitude seabirds to climate change, interspecific differences in life-history, foraging ecology and diet preclude any direct application of observed responses for other species.

Response surface models indicated that the timing of spring snow melt was important in determining the distribution of seabirds that are largely restricted to breeding in polar regions (Chapter 6). The length of the breeding season is very critical for these species (Maher, 1974; Furness, 1987) and egg-laying cannot begin until areas of the breeding site are free from snow cover (Maher, 1974). Any change in the timing of snow melt will directly affect breeding success and eventually breeding distributions. Although global temperatures are projected to rise over the next 100 years, regional estimates vary and snow fall is expected to increase in areas of western Europe (Houghton *et al.*, 2001). Easterly range shifts are therefore predicted for all these species since temperature rise may cause migration of competitors or predators from lower latitudes and force these seabirds northwards (Chapter 6). As a result, changes in marine productivity and food availability may not be the only factors determining the responses of high-latitude seabirds to changing climates, especially in high-arctic regions, where meteorological phenomena can directly limit breeding success.

7.5 References

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Appendices.

Appendix 1 (see Chapter 2 for references)

A1.1 Calculating solar radiation (Qs) indirectly

$Qs = Qs^{*} \times TCA$ eqn.A1.1

where, TCA is total cloud amount (proportional) and Qs^{*} is global radiation reaching the surface:

$Qs^{*} = S \cos Z$ eqn.A1.2 (Monteith & Unsworth, 1990)

where, S is the direct solar radiation on a horizontal perpendicular to the solar beam (1025.25 Wm^{-2} (Xue *et al.*, 2000)) and Z is the zenith angle of the sun:

$Z = \phi - \delta$ eqn.A1.3 (Monteith & Unsworth, 1990)

where, ϕ is latitude and δ is the declination angle of the sun.

$$\delta = 0.006918 - 0.399912 \cos(\theta_d) + 0.070257 \sin(\theta_d) - 0.0067518 \cos(2\theta_d) + 0.000907 \sin(2\theta_d) - 0.002697 \cos(3\theta_d) + 0.001480 \sin(3\theta_d)$$

eqn.A1.4 (Hartmann, 1994)

which is a simple expansion of the Fourier series where, θ_d is the time of year (in radians) given by:

$\theta_d = (2 \pi d_n)/ 365$ eqn.A1.5 (Hartmann, 1994) where, d_n is the time of year as a Julian Date.

A1.2 Constants used in biophysical model

Parameter	Value	Units	Source
Specific heat capacity of soil (Cp)	1.921	$Jg^{-1}K^{-1}$	Jury (2004)
Specific heat capacity of plumage (Cp)	1.7	$Jg^{-1}K^{-1}$	http://www.engineeringtoolbox.com/24_393.html
Mass of soil absorbing surface (mc)[1]	715	g	see footnote 1
Mass of plumage absorbing surface (mc)[1]	0.419	g	see footnote 1
Vapour pressure under standard conditions[2] (VP_{std})	1.0092	kPa	Monteith and Unsworth (1990)

Table A.1 Constants and fixed parameters of the model: values, units and source.

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[1] Assuming, mc = surface area × view factor × penetration × (plumage mass/plumage volume). Data: plumage mass (210.67 g) Furness (1988), surface area and view factor (Table 4.1), plumage volume (empirical: 0.0073 m^3), penetration (0.00055 m) Wolf & Walsberg (2000), soil values from Jury (2004).

[2] 60 % relative humidity and 25 °C air temperature.