



Sex differences in the T-cell-mediated immune response in wintering great tits *Parus major*

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Although sex differences in immune response have been reported in domestic animals, in which females generally show greater immune responses than males, studies of such differences in wild organisms including birds are still scarce. Most such studies of immune responses in wild birds have been carried out on nestlings and breeding adults, while few have reported on immune responses in wintering birds. Here, we report sex differences in the cell-mediated immune response assessed by the phytohaemagglutinin injection assay in a population of great tits *Parus major* during winter. Females showed higher level of immune response than males. As far as we know this is the first time that cell-mediated immune response has been reported in wintering birds.

Key words: Immune response, great tit, *Parus major*, phytohaemagglutinin test, sexual dimorphism.

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Studies of immunocompetence, i.e. the ability of an organism to mount an immune response to a pathogen, in wild birds have undergone a great increase in recent years, giving rise to the new discipline of ecological immunology (see Sheldon & Verhulst 1996, Norris & Evans 2000 and references therein). One of the reasons for this is that the immune system provides a possible mechanism relating biological performance to condition (Møller & Saino 1999) and can be considered as a valuable measure of bird fitness in terms of survival and reproduction (Saino et al. 1997, Soler et al. 1999). However, in spite of the increase in the number of studies, most have been carried out on nestlings (i.e. Saino et al. 1997, Brinkhof et al. 1999, Hørak et al. 1999, Tella et al. 2000). Studies of immune responses in adults are less frequent and have been carried out mainly during the breeding season (Moreno et al. 1998, Ots & Hørak 1998, Moreno et al. 1999, Moreno et al. 2001) with the exception of Hasselquist et al. (1999) and Ots et al. (2001). Information about immune responses during winter is scarce.

Work on sex differences in immune response in domestic animals generally shows that females have

greater immune responses than males (Terres et al. 1968, Grossman 1984) but such differences in wild organisms, including birds, have rarely been investigated. The level of immune response in winter is interesting mainly for two reasons: first, because parasitaemia has been reported to be reduced in winter (Applegate & Beaudouin 1971) and second, because sex differences in immune function may be mediated at least partially by the suppressive effects of androgens on the immune system (Alexander & Stimson 1988). In winter the level of sex hormones such as testosterone is lower than during breeding season (Hasselquist et al. 1999), so that sex differences in immunity could be affected. Data from the winter period can therefore help provide information about the fundamental differences between sexes in their immune responses.

There are three major facets of the immune system in birds: phagocytosis, antibody response and T-cell mediated immunity (Wakelin & Apanius 1997). Here we address the likely sexual differences in the latter by means of the phytohaemagglutinin injection assay (PHA) test. This technique has been used in several studies in wild birds, providing a good measure of immu-



ne response (Lochmiller et al. 1993, Moreno et al. 1998, Saino et al. 1998, Moreno et al. 1999, Moreno et al. 2001) without detrimental effects (Merino et al. 1999). As far as we know, no study has investigated sexual differences in T-cell mediated immune responses in wintering wild birds. The aim of this paper is to test for such differences in great tits *Parus major* at a time when levels of parasitaemia and sex hormones are expected to be reduced.

Material and Methods

Fieldwork was carried out during January 2001 in a 6 ha mixed forest of *Pinus sylvestris*, *Castanea sativa*, *Acer* spp and *Populus* spp at El Ventorrillo Field Station (1500 m a.s.l.) in the Sierra de Guadarrama, Madrid. Great tits (15 males and 8 females) were captured by means of funnel traps and were individually colour ringed. After capture, birds were injected with phytohaemagglutinin for assessment of their immune response (see below). Body mass was measured with an electronic balance to the nearest 0.1 g.

Blood samples were taken from the brachial vein of all individuals with a heparinised capillary tube (0.75 µl), which was later centrifuged at 12,000 rpm for 10 min to obtain a haematocrit index. The haematocrit index, the relative percentage of red blood cells in the total volume (i.e. red blood cell volume + plasma volume), may indicate condition and pathologies such as anaemia due to diseases and parasites (Barnes 1986, Merino & Barbosa 1997, Wanless et al. 1997).

Immunocompetence assessment

T-lymphocytes are considered major components of the avian immune system. An index of the ability to mount a T-lymphocyte cell-mediated immune response can be evaluated, *in vivo*, by injection of phytohaemagglutinin (PHA) (Cheng & Lamont 1988). Subcutaneous injection with PHA produces a complex physiological response that is seen macroscopically as a local inflammation due to macrophage infiltration and dense perivascular accumulation of lymphocytes (Goto et al. 1978), producing a thickening in the zone where PHA was injected. We injected 0.04 ml of a solution of phosphate buffered saline (PBS) containing 0.2 mg PHA (Sigma, L-8754) in the bird's right wing web. Usually

in other studies, the left wing web is injected with phosphate buffered saline (PBS) and the differences between the thickness in each wing web after 24 h is used as a measure of immune response. However, we have used the method proposed by Smits et al. (1999), which avoids injection of PBS as control, thereby reducing any stress due to handling and the probability of errors. The thickness of the right wing web was measured before inoculation with a spessimeter with constant pressure (Mitutoyo 7/547, Tokyo, Japan), with an accuracy of 0.01 mm. After injection, birds were kept in an outdoor aviary (2 m high x 2 m x 3 m) with an *ad libitum* diet of peanuts, sunflower seed and water. Twenty-four hours after injection we again measured the thickness of the wing web at the site of inoculation. The immune response index was calculated as the difference between pre- and post-injection measures of thickness on right wing web point (PHA injected).

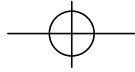
The repeatability of the measure of PHA-inoculated web thickness was determined by measuring the wing webs of 10 individuals three times before and three times 24 h after injection.

Results

Our measurements of wing web thickness were highly repeatable (initial wing web, $r = 0.95$, $F_{9,20} = 66.10$, $P < 0.00001$; final wing web, $r = 0.94$, $F_{9,20} = 53.1$, $P < 0.00001$; Lessels & Boag 1987). Body mass before injection did not show any relationship with wing web thickness ($r = -0.19$, $p = 0.39$, $n = 23$). Females had a higher immune response (wing web thickness) than males (ANOVA, $F_{1,21} = 5.41$, $P = 0.03$, Table 1). We did not find differences between the sexes in haematocrit index ($F_{1,21} = 0.62$, $P = 0.44$; males 48.76 %, s.e. = 0.70; females 49.75 %, s.e. = 1.09)

Table 1. Sex differences in T-cell-mediated immune response (wing web index) measured with the phytohaemagglutinin skin test in great tits.

	Mean	Standard deviation	n
Male	0.15	0.13	15
Female	0.27	0.08	8



Discussion

Female great tits showed a higher level of cell-mediated immune response in winter than males. Sex differences in immune response involving different components of the immune system have been reported several times in different organisms. The general pattern found is that females have higher immunity than males (Terres et al. 1968, Grossman 1984), including the humoral response in breeding v. non-breeding red-winged blackbirds *Agelaius phoeniceus* (Hasselquist et al. 1999), differences in mass of organs involved in immunity (bursa of Fabricius and spleen) (Møller et al. 1998), and cellular responses (Moreno et al. 2001). There are some exceptions, however, where no differences in cell-mediated immunity between sexes have been found, as in chinstrap penguins *Pygoscelis antarctica* (Moreno et al. 1998).

Although it has been suggested that sex differences in the immune system could be a consequence of the immunosuppressive effect of testosterone in males (Alexander & Stimson 1988, Schuurs & Verheul 1990), an alternative explanation has been suggested by some authors, in which sex differences could arise due to an enhanced immune response in females rather than a suppression in males (Grossman 1985, Olsen & Kovacs 1996, Hasselquist et al. 1999). During winter, sex hormones such as testosterone have a lower level than in spring (Hasselquist et al. 1999). Our results show that sex differences in immune response arise even in winter, so that it is not necessarily an increase in levels of sex hormones that gives rise to these differences. Although we do not have direct data on sex hormone levels, we assume that they were not as high as during the breeding season because no great tits during the study were engaged in territorial behaviour, singing or other behaviour related to reproduction.

Sex differences in immune response have also been explained on the basis of differences in reproductive costs (Moreno et al. 1999). Our results show that such differences in immune response can arise even when such reproductive costs are not operating, such as occurs during winter (see Moreno et al. 2001 for a similar result).

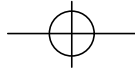
Differences in immune response between the sexes could appear if individuals of one sex were parasitised or sick. Because immune responses can arise in response to a great variety of pathogenic agents (Wakelin

& Apanius, 1997) and it is not possible to check for all of them, we used the haematocrit index as an indirect measure of possible disease. The absence of differences in haematocrit indices between the sexes suggests that sex differences in immune response due to disease can be excluded, at least for those diseases affecting haematocrit.

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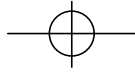
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The annual breeding cycle of unbanded king penguins *Aptenodytes patagonicus* on Possession Island (Crozet)

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All previous studies of the breeding cycle of king penguins *Aptenodytes patagonicus* have been based on the use of flipper bands. Although time consuming, this method has been the only practical way to study penguins but has induced some substantial bias. Moreover, few data were ever collected outside the summer period and winter activities of penguins remain poorly known. We present here the first study of the king penguin breeding cycle based on the automatic monitoring of unbanded birds. This new approach allows penguins to be followed throughout their annual cycle without disturbance and detects each time they come ashore or leave the colony. Fifty birds were studied from March 1998 to March 2001. Forty other birds (20 males and 20 females) were followed during the 1999/2000 season, during which they managed to fledge a chick. These birds provide the first data on the winter activities of non-breeding and unsuccessfully breeding birds. King penguins, contrary to other species of penguins and seabirds, come ashore several times during winter even if they have failed or not attempted to breed. Our data on the winter cycle of successful birds differ from previous data and show that all chicks were fed several times during winter. Parental investment was no different between males and females in terms of the time devoted to the chick and number of feeds.

Key words: king penguin, *Aptenodytes patagonicus*, breeding cycle, automatic identification, Crozet Islands.

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The breeding cycle of the king penguin *Aptenodytes patagonicus* is unusual because it exceeds one year (Stonehouse 1960, Barrat 1976) and is not synchronised in a population. Birds successful in fledging a chick one year can only be late breeders the next season (Stonehouse 1960, Barrat 1976, Jouventin & Lagarde 1995, Olsson 1996). Previous studies have focused mainly on the summer part of the breeding cycle, from courtship to brooding (Olsson 1997, 1998, Gauthier-Clerc et al. 2000, 2001, in press), or on the relationship between two successive breeding cycles (Weimerskirch et al. 1992, Van Heezik et al. 1994, Jouventin & Lagarde 1995, Olsson 1996, Jiguet &

Jouventin 1999, Gauthier-Clerc et al. 2002). For the autumn and winter period, two studies have described the chick growth curve (Van Heezik et al. 1994, Adams 1990) and it has been estimated that chicks are fed less than twice during the winter (Weimerskirch et al. 1992). Consequently it was assumed that they undergo a long period of fasting during that time (Stonehouse 1960, Barrat 1976, Cherel et al. 1987, Cherel et al. 1988, Weimerskirch et al. 1992, Van Heezik et al. 1994, Jiguet & Jouventin 1999). In June and July, king penguin colonies are full of adults (Gauthier-Clerc et al. 1998), yet no study has described in detail the autumn and winter cycles, or the relative contributions of males



and females over the complete breeding cycle. Moreover, previous studies relied on visual observations based on the use of flipper bands. Because visual observations are time-consuming, they do not permit describing all the movements of penguins between their breeding site and the sea, especially during winter when penguins may be absent for long periods. In addition, a large part of the penguin activity occurs during the night (Challet et al. 1994). Human presence around the breeding site could stress the birds and modify their behaviour (Wilson et al. 1989, Culik & Wilson 1991, Regel & Pütz 1997). Furthermore, the use of flipper bands to identify penguins induces some bias. Penguins cannot be banded with traditional foot rings due to the form of the leg joint and up to now flipper banding has been the most practical way to mark them. Because penguins propel themselves in water with their flippers, flipper bands interfere with aquatic locomotion and foraging (Culik et al. 1993) and have an adverse effect on survival and reproductive success (Ainley et al. 1983, Fraser & Trivelpiece 1994, Froget et al. 1998, Stonehouse 1999, Jackson & Wilson 2002). Because of the band's effects on life-history traits of penguins, especially during periods of low food availability (Gauthier-Clerc et al. unpublished data), previous results on the breeding cycle of king penguins might be called into question (Jackson & Wilson 2002).

The purpose of this study was therefore to reconsider previous data on the king penguin breeding cycle during the summer and to determine the winter activities of successful, unsuccessful and non-breeding birds using an automatic identification system, i.e. without any human disturbance. We also compare the parental investment of males and females in chick rearing over the whole cycle.

Study area and methods

Stonehouse (1960) first described the breeding cycle of king penguins at South Georgia. Pre-breeding moult starts in early spring and is followed by courtship and egg-laying. The laying period (only one egg is laid) extends from November to February on the Crozet Islands (Barrat 1976). Birds are considered as early breeders if incubation begins in November or December and as late breeders if it begins in January or February. Hatching takes place between January and April 54 days after

laying and both parents regularly feed the single chick from hatching until the beginning of winter. From May to August, food availability drops in areas where king penguins forage in summer (Foxton 1956, Cherel et al. 1993). Penguins reach the pack-ice limit and foraging trips are longer (Moore et al. 1999, Charrassin & Bost 2001). King penguins catch mainly myctophid fishes and squid at a depth of 50 to 400 m (Pütz & Bost 1994, Bost et al. 1997, Charrassin et al. 1998). During the summer, adults rely almost entirely on myctophid fish taken in the region of the Antarctic Polar Front, the convergence of Subantarctic and Antarctic waters located 400–500 km south of the Crozet Islands (Bost et al. 1997). At the end of spring, chicks begin moulting before leaving the colony and adults go to sea to feed before beginning a new breeding cycle.

Study area and monitoring system

The study was conducted from March 1998 to March 2001 in a colony of c. 25 000 breeding pairs at the Baie du Marin, Possession Island (46°25'S, 51°45'E), Crozet Archipelago (Weimerskirch et al. 1992, Froget et al. 1998). A part of this colony, comprising some 10 000 pairs of breeding king penguins, is connected to the sea by only three pathways. Two antennas allowing detection of transponder tags (TIRIS, Texas Instrument Recognition and Identification System) were buried permanently in the ground on each pathway and connected to a computer, which collected the data. The transponder tags, implanted under the skin of the bird's leg, weighed 0.8 g and worked without batteries. These tags have no adverse effect (Michard et al. 1995, Froget et al. 1998). The tags were activated electromagnetically by the antennas at a distance of 70 cm to permit individual identification of the tagged birds throughout their lifetime. The sequence of signals emitted by the two antennas determined whether the birds were entering or leaving their breeding site without the need for capture or visual observation. For the present study, 50 birds were fitted with transponders in February 1998. The birds to be fitted were randomly chosen from among the breeding penguins of the study area and were caught on the beach when departing after having been relieved by their partner. Bill and flipper lengths were measured as indices of body size. Five of these birds disappeared during the first year, and five others during the second breeding season. None of the birds wore any visible



mark and only one of them was handled again by mistake after transponder implantation. This single bird was only caught and weighed, and considering that this manipulation was short, the bird has not been removed from the present analysis.

A video camera was installed on the most important of the three pathways, i.e. where 90 % of penguin passages occurred. Recordings were taken when the transponded birds passed the antennas in order to determine their body and plumage condition. This provided information about their status and particularly about the date of moult.

Parental investment

To study the investment of males and females in chick rearing, we used 40 other birds (20 males and 20 females) fitted with transponders during the 1998/1999 breeding season. These birds were sexed by analysis of their breeding cycle. We used data from the 1999/2000 season, when all of these 40 birds were successful, for comparing parental investment.

Data interpretation

The breeding cycle of the birds was established from their movements between the study site (breeding area) and the sea. At the beginning of the breeding cycle, males remain on shore for about one month to display and provide the first long incubation shift (shift 2). Females leave the colony just after courtship and shift 1 (the initial short shift of the female, who then gives the egg to the male a few hours after laying, Barrat 1976). By analysis of the TIRIS data, we were able to sex most of the transponded birds. Especially during moult and display, some birds make many short round trips between different places in the colony, and they may also stay outside the study site but ashore (on the beach for example). To reduce the chance of wrongly interpreting the birds' activities (such as considering a bird to be at sea when it is actually ashore), we assumed that a bird leaving the study site for less than 2.5 days was still ashore.

To study the period between the return ashore after the post-moult trip and laying, we used data from females only. Females do not leave their breeding area between courtship and laying. They did not pass the antennas and so we could not determine the duration of

shift 1 separately (about several hours, see Stonehouse 1960), which is therefore included as part of the overall length of this period. For the studies of incubation and brooding, when parents alternate on the egg or the chick, we took into account only birds successful during these stages. Data from 1998 could not be used because most of the birds were fitted with transponders during brooding and the hatching date could not be determined. We considered that incubation corresponded to shifts 2 to 5 and brooding to shifts 6 to 9.

For the study of the winter period (from the end of brooding to renewal of feeding), only those birds that later appeared to be successful in fledging a chick (i.e. those continuing to feed their chick until November) were taken into account. This is because during this period both unsuccessful and successful birds frequented the colony and it is not possible to tell which birds had chicks. We considered that the winter fast of a chick started when its transponded parent made its first long winter trip (> 20 days). The fast finished with the last trip longer than 20 days (which corresponded to the beginning of the second period of short foraging trips).

Statistical analyses

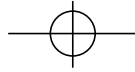
Statistical tests were carried out using the SYSTAT package (Wilkinson 1996). Values are reported as means \pm s.e.

Results

Breeding success

Breeding success did not differ significantly between the three breeding seasons (Table 1). The average breeding success over the three seasons was 27 % if we include only birds that laid. If we consider only early breeders (24 birds in 1998/1999, 23 in 1999/2000), their success in fledging a chick was 38 % in 1998/1999 and 39 % in 1999/2000. Ten birds in 1998/1999 and six in 1999/2000 did not attempt to breed or failed during courtship. If we include these birds, breeding success was 20 % in 1998/1999 and 23 % in 1999/2000.

Eight birds were successful twice during the three breeding periods, 17 were successful once during the three years and 15 birds never succeeded in fledging a chick. The ten other birds disappeared between 1997

**Table 1.** Breeding success of king penguins in three seasons.

^a chi-square tests were carried out on the three breeding seasons combined for overall breeding success and on the 1998/99 and 1999/00 seasons for success during incubation, brooding and crèching.

^b the crèche period corresponds to the period between chick emancipation (end of brooding) and chick fledging.

	All seasons	1997/1998	1998/1999	1999/2000	Chi-square test ^a
Number of breeding birds	119	50	35	34	
Success during incubation (%)	72		74	71	$\chi^2_1 = 0.12$, ns
Success during brooding (%)	70		69	71	$\chi^2_1 = 0.02$, ns
Success during the crèche period ^b (%)	52		50	53	$\chi^2_1 = 0.03$, ns
Overall breeding success (%)	27	30	26	26	$\chi^2_2 = 0.23$, ns

and 1999. Seven of the nine birds successful in the third breeding season (1999/2000) had been successful two years before (1997/1998).

One bird was successful in 1997/1998 and again in 1998/1999. Unless it had lost its chick during the winter of 1999 and adopted another, as has been recorded in emperor penguins *Aptenodytes forsteri* (Jouventin et al. 1995), this would be the first observation of success in two consecutive seasons by a king penguin.

Duration of chick rearing

Chick rearing (from hatching to fledging) lasted from 285 to 365 days in 1998/1999 and 1999/2000. The average duration for these two seasons was 324 ± 5 days

($n = 24$). The duration of chick rearing was not significantly different between these two seasons (Table 2a, b; t-test: $t_{16} = 1.0$, $P = 0.34$). The last feed of the chick was significantly earlier in 1997/98 than in 1998/99 (Table 2b; Mann-Whitney $U = 26.5$, $n = 24$, $P = 0.01$). There was no significant difference in last feeding date between 1998/99 and 1999/00 (Table 2b; $U = 43.0$, $n = 18$, $P = 0.83$).

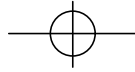
Moult

Few transponded birds passed through their future breeding area during moult, and because of too small a sample size, the date and the duration of the moult could not be determined in 1999 or 2000. In 1998, unsuc-

Table 2. Timing and duration of events in the breeding cycle of king penguins in three seasons. Values are means \pm s.e. (n). All durations are in days.

(a) from moult to chick emancipation

		1998/1999	1999/2000	2000/2001	All seasons
Moult	Beginning	Oct-16 ± 10.2 (15)	Oct-24 ± 5.6 (16)	Oct-05 ± 2.7 (8)	Oct-17 ± 4.6 (39)
	Duration	22.2 ± 1.1 (15)	22.9 ± 0.9 (16)	24.3 ± 0.6 (8)	22.9 ± 0.6 (39)
Post-moult trip	Duration	15.6 ± 0.5 (27)	16.6 ± 0.6 (27)	19.8 ± 1.4 (21)	17.1 ± 0.5 (75)
Courtship and shift 1	Beginning	Nov-22 ± 4.9 (32)	Dec-04 ± 4.6 (27)	Dec-05 ± 5.9 (26)	Nov-30 ± 3.0 (85)
	Duration	17.5 ± 3.4 (14)	16.7 ± 2.6 (12)	21.6 ± 4.9 (10)	18.4 ± 2.1 (36)
Incubation	Shift 2	18.0 ± 1.6 (7)	16.1 ± 0.5 (9)	16.7 ± 1.0 (8)	16.9 ± 0.6 (24)
	Shift 3	15.7 ± 0.7 (8)	18.2 ± 0.9 (6)	18.1 ± 1.1 (12)	17.4 ± 0.6 (26)
	Shift 4	14.5 ± 0.6 (7)	14.1 ± 0.9 (9)	15.2 ± 0.9 (7)	14.6 ± 0.5 (23)
	Shift 5	11.8 ± 0.6 (8)	10.4 ± 0.2 (6)	13.2 ± 0.6 (11)	12.1 ± 0.4 (25)
Brooding	Shift 6	8.0 ± 0.9 (7)	8.7 ± 0.7 (9)	11.8 ± 2.2 (8)	9.5 ± 0.9 (24)
	Shift 7	6.9 ± 0.5 (8)	7.9 ± 2.4 (6)	6.7 ± 0.7 (9)	7.1 ± 0.7 (23)
	Shift 8	7.2 ± 1.3 (7)	6.9 ± 0.8 (9)	6.3 ± 0.7 (1)	6.9 ± 0.6 (22)
	Shift 9	6.2 ± 0.6 (8)	4.3 ± 0.5 (4)	8.6 ± 1.3 (6)	6.6 ± 0.6 (18)

**Table 2** (continued).

(b) crèche period

	1997/1998	1998/1999	1999/2000	All seasons
First feeding phase		n = 8	n = 9	n = 17
Total duration		68.0 ± 7.7	82.6 ± 12.7	75.7 ± 7.6
Time at sea (%)		85.5 ± 2.2	75.7 ± 3.5	80.3 ± 2.4
Number of trips		7.4 ± 1.2	8.0 ± 1.2	7.7 ± 0.8
Duration of stays ashore		1.4 ± 0.2	2.6 ± 0.4	2.0 ± 0.3
Duration of trips		7.8 ± 0.8	7.9 ± 0.4	7.9 ± 0.4
Fasting period	n = 15	n = 9	n = 9	n = 33
Total duration	147 ± 5.1	148 ± 8.9	129 ± 10.5	143 ± 4.5
Time at sea (%)	84.8 ± 1.2	87.6 ± 2.3	87.2 ± 2.9	86.2 ± 1.
Number of trips >20 days	2.5 ± 0.1	2.6 ± 0.2	2.0 ± 0.2	2.4 ± 0.1
Number of stays ashore	3.9 ± 0.5	3.8 ± 0.8	3.5 ± 1.0	3.8 ± 0.4
Duration of stays ashore	8.3 ± 1.8	8.5 ± 3.4	10.1 ± 3.9	8.8 ± 1.6
Trip duration	23.4 ± 2.1	24.8 ± 2.0	27.3 ± 4.1	24.9 ± 1.5
Longest trip	62.3 ± 3.1	69.1 ± 5.7	67.2 ± 2.0	65.5 ± 2.7
Last feeding phase	n = 15	n = 9	n = 9	n = 33
Duration	79.6 ± 5.6	89.2 ± 10.7	83.5 ± 7.7	83.3 ± 4.3
Beginning	Sept-12 ± 4.3	Sept-16 ± 6.8	Sept-22 ± 7.5	Sept-16 ± 3.3
End	Dec-01 ± 3.6	Dec-14 ± 4.4	Dec-12 ± 8.6	Dec-07 ± 3.2
Number of stays ashore	10.5 ± 0.6	9.9 ± 1.2	10.1 ± 1.0	10.2 ± 0.5
Duration of stays ashore	1.4 ± 0.1	1.7 ± 0.3	1.8 ± 0.3	1.6 ± 0.1
Trip duration	6.8 ± 0.3	8.5 ± 0.7	7.5 ± 0.7	7.5 ± 0.3

successful penguins began moulting earlier than successful birds (Table 2a; successful: 27 December ± 23.4 d, n = 3; unsuccessful: 28 September ± 11.3 d, n = 12; Mann-Whitney U = 0.0, n = 15, P = 0.009) and had a longer moult (Table 2a; successful: 16.9 ± 2.3 d, n = 3; unsuccessful: 23.5 ± 1.0 d, n = 12; $t_{13} = 3.0$, P = 0.01). There was no difference between the post-moult trip duration of the unsuccessful and the successful birds (Table 2a; 1997/98: unsuccessful: 16.0 ± 0.5 d, n = 23; successful: 13.3 ± 1.8 d, n = 4; $t_{25} = 1.9$, P = 0.07; 1998/99: unsuccessful: 16.5 ± 0.5 d, n = 23; successful: 17.4 ± 2.8 d, n = 4; $t_{25} = 0.6$, P = 0.59; 1999/00: unsuccessful: 20.9 ± 1.5 d, n = 17; successful: 15.1 ± 2.1 d, n = 4; $t_{19} = 1.7$, P = 0.10). The date of the moult and length of the post-moult trip were significantly different according to year for the unsuccessful birds (Table 2a; date: Kruskal-Wallis H = 29.6, n = 35, P < 0.001; post-moult trip: ANOVA, $F_{2,60} = 9.1$, P < 0.001).

End of the post-moult trip to departure of the females

This period, which includes courtship and incubation shift 1, began between October and February and was earlier for unsuccessful birds (1998/99: Mann-Whitney U = 0.0, n = 32, P < 0.001; 1999/00: U = 0.0, n = 27, P = 0.005; 2000/01: U = 0.0, n = 26, P < 0.001). Its duration did not differ according to previous reproductive success (Table 2a; 1998/99: $t_8 = 2.1$, P = 0.06; 1999/00: insufficient data; 2000/01: $t_5 = 0.03$, P > 0.9). The maximum duration of this period was 60 days in 1998/1999 and 2000/2001, and 44 days in 1999/2000, but birds that had such a long display phase made one or more foraging trips during this period. Year had a significant effect on the beginning of this period for unsuccessful birds (Table 2a; Kruskal-Wallis test: H = 22.3, n = 69, P < 0.001), and tended to have an effect for successful birds but was not significant (Kruskal-Wallis H = 5.6, n = 16, P = 0.06).

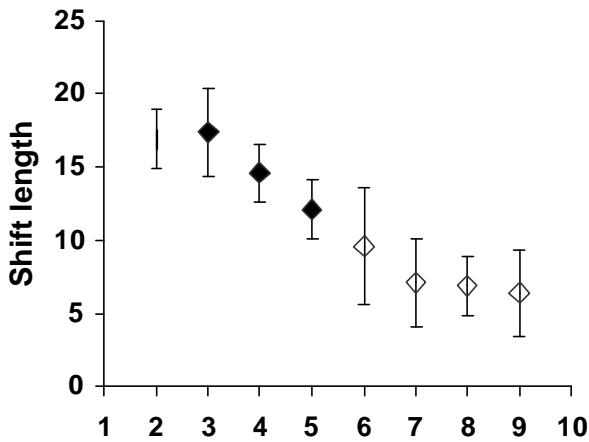
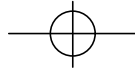


Figure 1. Shift lengths (mean \pm s.d.) of king penguins during incubation (solid points) and brooding (open points); data pooled over three seasons. Shifts 1, 3, 5, 7, 9 are carried out by the female; shifts 2, 4, 6, 8, 10 by the male.

If we disregard females that had a very long pre-laying period (more than 20 days), which could correspond to two or more successive courtships with different partners and which usually included at least one foraging trip, the average duration of this period over the three seasons was 13.8 ± 0.4 days ($n = 30$). There was no difference between the three years (1998/1999: 13.6 ± 0.6 d, $n = 12$; 1999/2000: 14.2 ± 0.9 d, $n = 11$; 2000/2001: 13.7 ± 0.8 d, $n = 7$; ANOVA: $F_{2,27} = 0.2$, $P = 0.80$).

Incubation and brooding

From incubation shift 3 to the second brooding shift (shift 7), shift duration decreased significantly (Fig. 1; three years pooled: shift 3 – shift 4: $t_{47} = 3.6$, $P = 0.001$; shift 4 – shift 5: $t_{46} = 4.1$, $P < 0.001$; shift 5 – shift 6: $t_{47} = 2.7$, $P = 0.01$; shift 6 – shift 7: $t_{38} = 2.2$, $P = 0.03$). After shift 7, the duration of the brooding shifts did not decrease (Table 2a; ANOVA: 1998/99: $F_{2,20} = 0.4$, $P = 0.69$; 1999/00: $F_{2,16} = 1.4$, $P = 0.27$; 2000/01: $F_{2,18} = 1.6$, $P = 0.24$).

From chick emancipation to crèching

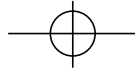
About one month after hatching (shifts 6 to 9), parents were no longer constantly with the chicks and trips at

sea were longer than the stays ashore (Table 2b, Paired t-test with 1998/1999 and 1999/2000 data: $t_{16} = 10.5$, $P < 0.001$). Year had a significant effect on duration of stays ashore (Table 2b; $t_{15} = 2.5$, $P = 0.03$).

Winter activities of breeding king penguins

The period between the first and the last 'long winter trip' (> 20 days), as well as the time passed at sea and the number and duration of stays ashore during this period, did not differ significantly by year (Table 2b; period between first and last trips: ANOVA, $F_{2,30} = 1.8$, $P = 0.19$; time at sea: ANOVA, $F_{2,30} = 1.9$, $P = 0.17$; number of stays ashore: Kruskal-Wallis $H = 1.2$, $n = 33$, $P = 0.54$; length of stays ashore: ANOVA, $F_{2,30} = 0.1$, $P = 0.12$). Nevertheless, the first 'long winter trip' was significantly shorter in 1998/1999 (Table 2b; ANOVA, $F_{2,30} = 4.4$, $P = 0.02$) and tended to begin later in 1999/2000 (Table 2b; Kruskal-Wallis $H = 5.6$, $n = 33$, $P = 0.06$). Among the 33 successful birds over the 1997/1998, 1998/1999 and 1999/2000 breeding seasons, 13 made three long winter trips (> 20 days), 19 birds made two and one bird made a single trip. The number of long winter trips tended to differ according to year (Table 2b; Kruskal-Wallis $H = 5.2$, $n = 33$, $P = 0.08$).

During the period between 1 May and 31 August (for comparison with results of Cherel et al. 1987 and Weimerskirch et al. 1992), we found that chicks received on average 4.7 visits from their transponded parent (1997/1998: 4.3 ± 0.5 visits, $n = 15$; 1998/1999: 3.9 ± 0.5 visits, $n = 9$; 1999/2000: 6.1 ± 1.4 visits, $n = 9$). During this period, the foraging trips of adults lasted for about 25 days (1997/1998: 24.7 ± 2.5 d, $n = 15$; 1998/1999: 28.0 ± 3.9 d, $n = 9$; 1999/2000: 21.5 ± 4.7 d, $n = 9$) and they stayed ashore for about 7 days (1997/1998: 7.1 ± 1.5 d, $n = 15$; 1998/1999: 6.5 ± 1.7 d, $n = 9$; 1999/2000: 7.1 ± 2.6 d, $n = 9$). The adults spent on average 83 % of their time at sea (1997/1998: 81.8 ± 1.4 %, $n = 15$; 1998/1999: 84.4 ± 3.0 %, $n = 9$; 1999/2000: 82.1 ± 2.8 %, $n = 9$). Females made fewer sea trips than males that were longer than 10 days (three years pooled: females: 2.3 ± 0.1 , $n = 12$; males: 3.1 ± 0.4 , $n = 16$; T-test: $t_{28} = 1.9$, $P = 0.01$. Considering each year separately, the tendencies are the same but not significant).



Time at sea and ashore during winter according to breeding status

Over the period 1 March –1 September, the mean trip duration and the total time spent at sea did not differ significantly by year between successful and non-breeding birds (Table 3; Successful birds, trip duration: ANOVA, $F_{2,30} = 1.2$, $P = 0.32$; time at sea: $F_{2,30} = 0.4$, $P = 0.70$; Non-breeding birds, trip duration: $F_{1,11} = 0.1$, $P = 0.75$; time at sea: $F_{1,11} = 2.4$, $P = 0.15$). For penguins that bred unsuccessfully, there was a significant effect of year (Table 3; ANOVA: trip duration: $F_{2,71} = 6.7$, $P = 0.002$; time at sea: $F_{2,71} = 6.4$, $P = 0.003$). Unsuccessful and non-breeding birds spent on average 46 days on shore between 1 March and 1 September (unsuccessful: 46.2 ± 2.5 d, $n = 74$; non-breeding: 46.2 ± 5.4 d, $n = 13$, three years pooled).

Between 1 March and 1 September in all three years, successful birds made more trips and therefore more stays on shore than unsuccessful and non-breeding birds (Table 3; 1997/1998: U-test: $U = 97.5$, $n = 45$, $P = 0.002$; 1998/1999: Kruskal-Wallis $H = 8.6$, $n = 40$, $P = 0.01$; 1999/2000: $H = 10.0$, $n = 35$, $P = 0.007$). In 1997/1998 and 1999/2000, the average duration of trips was significantly shorter among successful birds (Table 3; 1997/1998: $t_{43} = 3.2$, $P = 0.003$; 1999/2000: ANOVA, $F_{2,32} = 8.5$, $P = 0.001$). In 1998/1999, the tendency was the same but not significant (Table 3): non-breeding

birds made longer trips than unsuccessful birds, which made longer trips than successful ones. In 1998/1999, the total percentage of time spent at sea differed according to breeding status: successful penguins spent more time at sea than other penguins (Table 3; ANOVA, $F_{2,37} = 5.2$, $P = 0.01$). In all three years, successful birds made shorter stays ashore than others (Table 3; 1997/1998: $t_{43} = 2.6$, $P = 0.01$; 1998/1999: ANOVA, $F_{2,37} = 5.3$, $P = 0.01$; 1999/2000: ANOVA, $F_{2,32} = 8.7$, $P = 0.001$).

To summarise, during the winter period, successful breeding penguins were more often on shore than other birds but still spent more time at sea. Unsuccessful and non-breeding penguins made longer stays ashore during winter than successful birds. Successful penguins made shorter foraging trips than non-breeding and unsuccessful ones.

Renewal of feeding

After a winter period of long trips and long stays ashore, feeding starts again. The beginning and the duration of the period between the end of the last long winter trip and the end of chick feeding did not differ significantly according to year (Table 2b; beginning of the second feeding period: Kruskal-Wallis $H = 1.8$, $n = 33$, $P = 0.41$; duration of the second feeding period: ANOVA, $F_{2,30} = 0.4$, $P = 0.67$), though year tended to

Table 3. Activities of king penguins in winter (1 March to 1 September) according to their breeding status (S = successfully breeding birds; U = unsuccessful birds; NB = non-breeding birds). Values are means \pm s.e. (n).

^a The product 'Number of trips * Trip duration' could be more than the 184 days between 1 March and 1 September because the last foraging trip could finish after 1 September.

		1997/98	1998/99	1999/2000
Number of trips ^a	S	10 \pm 1 (15)	10 \pm 1 (9)	12 \pm 1 (9)
	U	7 \pm 1 (30)	7 \pm 1 (22)	8 \pm 1 (22)
	NB		7 \pm 1 (9)	5 \pm 1 (4)
Trip duration (days) ^a	S	16.1 \pm 1.0 (15)	16.0 \pm 1.4 (9)	13.6 \pm 1.4 (9)
	U	30.6 \pm 3.2 (30)	20.8 \pm 1.5 (22)	19.0 \pm 1.6 (22)
	NB		28.4 \pm 8.4 (9)	32.9 \pm 7.3 (22)
Time at sea (%)	S	82.5 \pm 1.3 (15)	84.1 \pm 2.8 (9)	81.5 \pm 2.5 (9)
	U	79.8 \pm 1.5 (30)	68.8 \pm 3.0 (22)	74.3 \pm 2.3 (22)
	NB		77.8 \pm 3.8 (9)	68.5 \pm 1.9 (4)
Duration of stays on shore (days)	S	3.5 \pm 1.5 (15)	3.1 \pm 0.7 (9)	3.19 \pm 0.6 (9)
	U	7.8 \pm 6.0 (30)	10.2 \pm 1.5 (22)	7.0 \pm 1.1 (22)
	NB		6.7 \pm 1.6 (9)	14.4 \pm 2.4 (4)

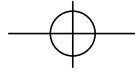


Table 4. Winter breeding parameters of successful male and female king penguins in 1999/2000. Values are means \pm s.e. All durations are in days.

^a Period between chick emancipation and last feed.

^b Period between chick emancipation and the first long foraging trip.

^c Period between the first and last long winter foraging trip.

^d Period between the last long foraging trip and last feed.

		Males (n = 20)	Females (n = 20)	Difference
Crèche period ^a	Duration	321 \pm 5	31 \pm 4	$t_{3,8} = 0.4$, $P = 0.67$
	Total time at sea (days)	255 \pm 6	253 \pm 5	$t_{3,8} = 0.4$, $P = 0.72$
	Number of stays ashore	24 \pm 1	23 \pm 1	$U = 175.0$, $P = 0.50$
First feeding phase ^b	Duration	87 \pm 4	101 \pm 10	$t_{3,8} = 1.4$, $P = 0.19$
	Number of stays ashore	8 \pm 1	10 \pm 1	$U = 221.0$, $P = 0.57$
	Duration of stays ashore	4.0 \pm 0.3	3.3 \pm 0.2	$t_{3,8} = 1.9$, $P = 0.07$
Winter fasting period ^c	Duration	131 \pm 5	122 \pm 10	$t_{3,8} = 0.7$, $P = 0.47$
	Number of stays ashore	4 \pm 1	2 \pm 1	$U = 117$, $P = 0.02$
Last feeding phase ^d	Beginning	Sept-07 \pm 5	Sept-14 \pm 3	$U = 268.0$, $P = 0.07$
	Duration	103 \pm 5	94 \pm 6	$t_{3,8} = 1.1$, $P = 0.27$
	Number of stays ashore	12 \pm 1	11 \pm 1	$U = 175.5$, $P = 0.51$

have an effect on the end of this period (Table 2b; $H = 5.6$, $n = 33$, $P = 0.06$) and on the mean duration of the feeding trips (Table 2b; $F_{2,30} = 3.0$, $P = 0.06$).

Male and female investment in chick rearing

The length of the period between hatching and the end of chick feeding was not significantly different between males and females (Table 4). There was no significant difference between the maximum number of stays ashore (Table 4) and the date of the last stay ashore (17 December \pm 5 d, $n = 20$ for males, 17 December \pm 5 d, $n = 20$ for females, Mann-Whitney $U = 207.5$, $n = 40$, $P = 0.84$). Males and females spent the same amount of time at sea during chick rearing (Table 4). During the first phase of the crèche period, from chick emancipation to the first long winter trip, females tended to make shorter stays ashore (Table 4). During the fasting period (between the first and the last long winter trip), males came ashore more frequently than females (Table 4). After this period, the phase of frequent feeds in spring tended to begin earlier for males (Table 4).

For females, the sum of shifts 2 and 4 of incubation gave the time they spent at sea during incubation and the sum of shifts 3 and 5 the time their male partner spent at sea. Females spent significantly longer at sea than did males (24.9 ± 4.1 d for males, 34.6 ± 5.5 d for females; paired t-test, $t_{13} = 4.4$, $P = 0.001$).

Discussion

The full breeding cycle of undisturbed king penguins is described here for the first time by using an automatic identification system over three breeding seasons. We have established the activities of successful, unsuccessful and non-breeding adults throughout the year and particularly during winter.

We were able to distinguish three different phases during the crèche period for successful birds (Fig. 2): a first feeding phase (of about 2.5 months) with short stays ashore and foraging trips of about one week, a winter period with long stays ashore and long trips at sea (which lasts on average 4.5 months), and a second feeding phase (a little less than 3 months) with the same characteristics as the first. By taking the time complement for the other parent and assuming that parents fed their chick each time they came ashore, we can calculate the number of meals chicks received in each of these three periods. Both parents on average fed the chicks 15 times during the first summer phase of feeding and 20 times during the second summer phase of feeding. During the winter period, the chicks were visited on average six times (four times by the male, twice by the female). Chérel et al. (1987) found that chicks received on average three meals in the period between 1 May and 31 August. Weimerskirch et al. (1992) found for the same period of observation that 48 % of chicks

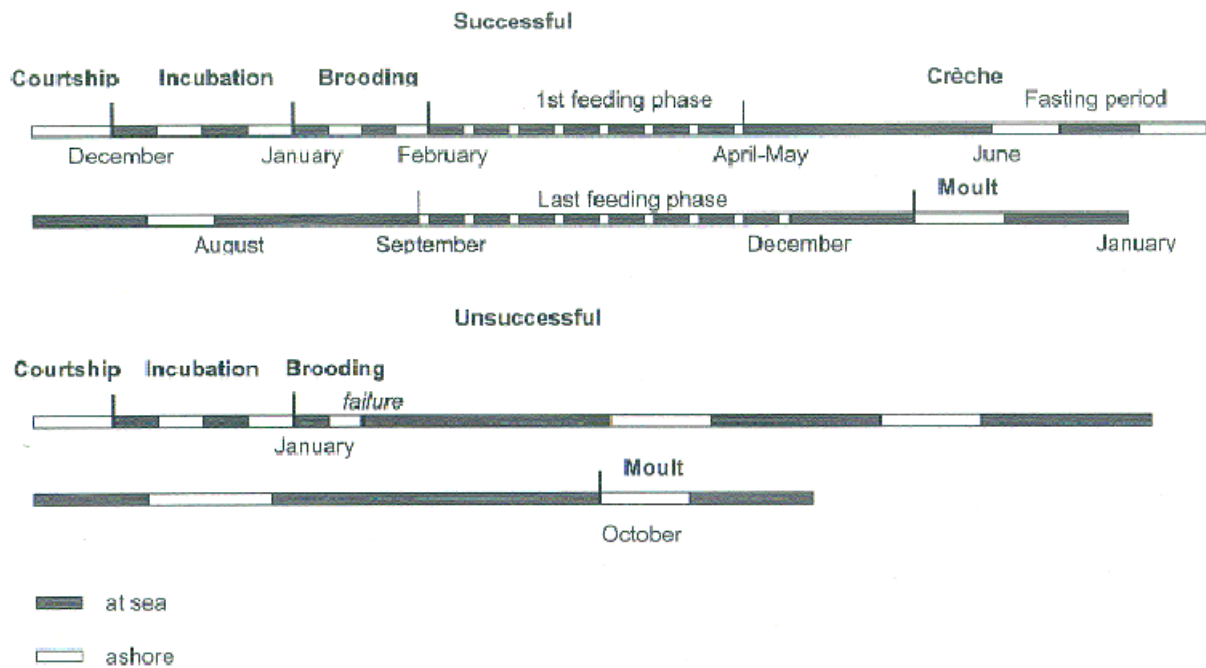
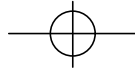


Figure 2. Annual activities of successful and unsuccessful king penguins. Examples are shown of a successful female and a female that failed during brooding.

were never fed, 26 % were fed once and 26 % twice. Importantly, in our study, the transponded parents fed all of the 33 fledging chicks at least once during this period and this parent alone made almost five visits on average.

The longest trip during winter lasted on average 65 ± 3 days (range: 34 – 98 days). Satellite tracking during the winter has shown that during these extended trips, the adult may forage as far as the Antarctic pack-ice region (Jouventin et al. 1994, Moore et al. 1999, Charassin & Bost 2001). Even if the other parent left and returned to the colony at exactly the same dates, which is highly improbable, the maximum chick fast duration was on average 65 days. Between 1 May and 31 August, the mean duration of sea travel, which corresponds to the mean interval between two successive visits of the transponded parent, was about 25 days. The mean interval between two successive feeds was therefore less than 25 days, which differs from the earlier finding of Cherel et al. (1987), who found a mean interval of 39 days. We assumed that every trip longer than 2.5 days corresponded to a sea trip. Nevertheless, even if we had considered only trips longer than 10 days, every chick would have received at least one visit by its

transponded parent in the period 1 May–31 August, and the number of visits during this period, averaged over the three seasons, would have been 2.5. With this method of estimation, each chick would have received a total of about five visits by its two parents. We have most probably underestimated the number of short foraging trips (< 2.5 days) during the winter phase and thus the number of chick feeds. Indeed, an absence of 1–2 days from the colony during the winter period could also correspond to a short foraging trip to bring a meal to the chick, as observed in other seabird species in which the adult alternates short and long foraging trips at sea (Weimerskirch et al. 1994). Our data therefore suggest that the number of meals received by chicks during winter is greater than in previous studies. One explanation could be that previous studies relied on visual observations and some of the adult's visits may have been missed. Furthermore, previous results depended on flipper-banding, which may handicap the birds. Particularly during winter, banded penguins are less often present in the colony and make longer trips than unbanded individuals (Gauthier-Clerc et al., unpubl. data).

Many adults frequent the colony during winter, in-



cluding birds not involved in chick rearing. Between 1 March and 1 September, unsuccessful and non-breeding penguins spent about 25 % of their time ashore and, when ashore, stayed much longer than successful penguins. Nevertheless, their activities throughout the year, even during winter, are not fundamentally different from the activities of successful penguins. We speculate that birds without a chick may come back to the colony during winter once they have accumulated sufficient body reserves. It may be an advantage to be ashore, where they are safe from their main predators, the leopard seal *Hydrurga leptonyx*, the fur seals *Arctocephalus gazella* and *A. tropicalis*, and killer whales *Orcinus orca*.

Stonehouse (1960) supposed that parental investment during the final chick growth stage after the winter differed between male and female, the chick being fed only by the male while the female begins her moult, whereas Olsson (1996) found no difference during the same period. Our results show that males and females visited their chick the same number of times and spent the same time at sea from hatching to fledging. During the winter fast period, however, females came ashore less frequently than males and the number of feeds by females during winter was lower than by males. In addition, during the five incubation shifts, females spent 58 % of their time at sea and assumed a less important role in incubation than males. Thus over the complete cycle, the parental time investment is similar but differences occur during incubation and winter.

The overall breeding success found in our study did not differ from previous findings (28 % in our study; 22 % in Jiguet & Jouventin 1999; 36 % in Jouventin & Lagarde 1995; 31 % in Weimerskirch et al. 1992). Seventy-eight percent of the successful penguins in 1999/2000 had fledged a chick two years before. This result suggests that some birds are better able to rear a chick than others and that the outcome of the breeding attempt two years before has an effect on the probability of success (Olsson 1996, Jiguet & Jouventin 1999).

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Density dependent population limitation in dark-bellied brent geese *Branta b. bernicla*

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The dynamics were investigated of the world population of dark-bellied brent geese *Branta b. bernicla*, which winter in western Europe and reproduce on the Siberian tundra. The world population was fluctuating between approximately 220,000 and 315,000 individuals in the last decade of the 20th century, after recovering from an extremely low level of about 15,000 in 1955. Cyclical fluctuations are related to the population dynamics of lemmings on the Taymyr Peninsula in Siberia and have been present during the whole study period 1955–1998. We investigated whether, apart from these fluctuations, the population size will level off due to density dependence in reproduction or in survival. This being the case, we also aimed at predicting the approximate equilibrium population size.

Data are provided on the world population since 1955, counted every January, giving details on adult survival and reproduction. A simple discrete-time model was formulated where the reproductive season in Siberia and the winter season in Europe are treated separately allowing for density dependence during either season.

The nature of the density dependence for the model was estimated from the data. Density dependence was significant in reproduction, but not in adult survival. We argue that availability of suitable nesting habitat is an important factor influencing reproduction potential, but the possibility of other factors (e.g. competition for food during spring staging) cannot be excluded.

Analysis of the simple model yields a relation between the predicted equilibrium population size and a constant adult death rate estimated at 0.15, which corresponds to a predicted maximum population size of 286,000–332,000 at the time of the January census. Although it is tempting to use such a generic model as a basis to gauge effects of habitat loss on migrating bird species, great care should be taken in formulating rules-of-thumb.

Key words: density dependence, seasonal environment, *Branta b. bernicla*, population modelling, population limitation.

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Detailed data on the entire world population of dark-bellied brent geese *Branta b. bernicla*, which has shown a marked increase from 1955 to the early 1990s, offer an excellent opportunity to study the possible occurrence of density-dependent control in a natural population. A marked change in the rate of increase in

1972 (Fig. 1), which coincided with a hunting ban in Denmark, has often been interpreted as showing that hunting was the key factor reducing the dark-bellied brent goose population level (Prokosch 1984, Ebbinge 1985). Dark-bellied brent geese winter in western Europe, notably along the coasts of western France, Great

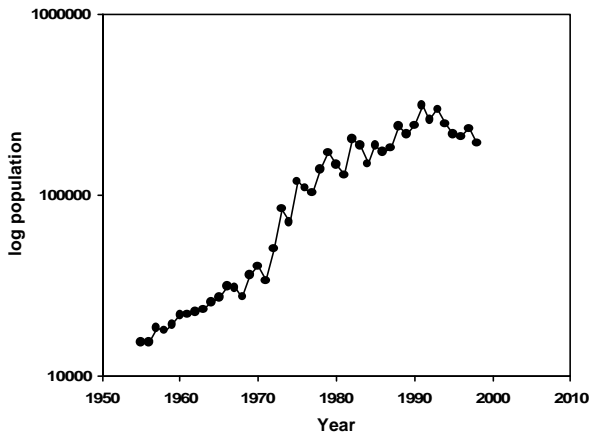


Figure 1. The world population of dark-bellied brent geese from 1955 to 1999 on a logarithmic scale using the data from Table 1.

Britain, and in the Dutch Wadden Sea. Range expansion, by moving further north along sea coasts of Britain and into grassland territory inland, has occurred to accommodate the growing numbers of wintering birds (Ebbinge et al. 1999). With this inland shift, the birds cause an increasing amount of agricultural damage, so that to assess the future impact of this population on agriculture, it is important to understand its dynamics.

The number of birds in the world population has risen from about 15,000 in 1955 to between 220,000 and 315,000 in the last decade of the 20th century. In earlier work, Prokosch (1984) and Ebbinge (1985) suggested that this increase already showed signs of levelling off in the early 1980s. The latter paper based its conclusion on the observed relation between the number of successful breeding pairs and the number of potential breeding pairs in consecutive years, using the data available at the time. However, a sound statistical analysis of the data was not made. Summers and Underhill (1991) later did undertake a statistical analysis and showed that the relation was not significantly different from a straight line, thus arguing against density dependence controlling the number of breeding pairs. At that time data were available only until 1985. Thirteen years of additional data are now available (until 1998) and we re-address the question whether, with more data, a different method and statistical analysis, the population development of dark-bellied brent geese shows signs of density dependence.

Our method involves a simple mathematical model. Animal populations living in a seasonal environment are usually characterised by a season where resources are plentiful, allowing the animals to reproduce, and a season where resources are scarce, during which the animals may experience great difficulty to survive. Though dark-bellied brent geese reduce the effects of seasonality to a considerable extent by their migratory behaviour, they reproduce only during the short summer in the high arctic, and merely try to survive during their 8-month stay along the coasts of western Europe. To our knowledge, Fretwell (1972) was the first to develop a simple population model like the one we use below, characterised by a season of reproduction, followed by a season with no reproduction and much mortality. From a graphical analysis he concluded that the dynamic behaviour of such models could be quite complex, depending on the form of the curves describing density dependence in reproduction or survival and their intersections. Here, we use a simple two-season model where the curves describing reproduction and survival in different seasons are estimated from the data set for the dark-bellied brent goose. The model allows for equilibrium states and remains simple enough to investigate the relationship between equilibrium population sizes and adult death rate.

The dynamics of this population are complicated by the fact that almost invariably a virtually complete breeding failure occurs every three years (Roselaar 1979, Summers & Underhill 1987, Greenwood 1987, Ebbinge 1989). These years follow upon peak years for populations of the lemmings *Lemmus sibiricus* and *Dicrostonyx torquatus* in the breeding area of the geese, the Taimyr peninsula. It has been suggested that numbers of the key lemming-predator, the Arctic fox *Alopex lagopus*, increase markedly in lemming peak years and are forced to switch to alternative prey, notably bird eggs and young geese, in the year after the lemming population has collapsed (Summers & Underhill 1987, Spaans et al. 1998). The various explanations for the lemming cycle still lack critical empirical support (Krebs 1993, Stenseth 1999) but its indirect effect on the dynamics of brent geese and waders is substantial and highly predictable. These fluctuations with a more or less tri-annual cycle have been present throughout the whole time series and an underlying trend in growth rate can clearly be discerned. In this paper we analyse whether the overall population growth over a much lon-

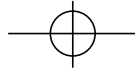


Table 1. Demographic data for dark-bellied brent geese. Breeding success expressed as percentage of first-winter birds in the winter following year x . Population size (number) is estimated in January ($x+1$). Average family size = number of offspring per family in winter. Lemming densities are scaled from 1 (virtually no lemmings) to 5 (extremely high densities), according to Kokorev & Kuksov (1990, unpubl. report). 1: no lemmings caught per 100 trap days. 2: <3 lemmings caught per 100 trap days. 3: 10 lemmings caught per 100 trap days. 4: 30 lemmings caught per 100 trap days. 5: 80 lemmings caught per 100 trap days in the best areas. Scores 4-5 are densities as occurring in lemming peak years.

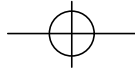
year	number	breeding success	adult survival	average family size	lemming-density Taimyr	year	number	breeding success	adult survival	average family size	lemming-density Taimyr
1955	15500	25,8		?		1977	103400	2,0	0,92	2,8	1
1956	15500	6,5	0,94	?		1978	140000	35,0	0,88	2,8	2
1957	18500	52,8	0,56	?		1979	173000	33,0	0,83	2,4	5
1958	18000	0,4	0,97	?		1980	149000	0,2	0,86	2,8	2
1959	19500	21,6	0,85	?		1981	130000	4,0	0,84	2,8	1
1960	21800	45,0	0,61	?	4	1982	206000	50,0	0,79	3,1	4
1961	22000	5,1	0,96	?	4	1983	190000	3,0	0,89	2,8	3
1962	22800	0,2	1,03	?	1	1984	150000	1,5	0,78	2,8	1
1963	23600	35,0	0,67	?	5	1985	190000	35,0	0,82	2,8	5
1964	25600	34,7	0,71	?	4	1986	174000	0,5	0,91	2,8	1
1965	27300	6,9	0,99	?	2	1987	183000	2,0	1,03	2,6	2
1966	31500	39,7	0,70	?	4	1988	242000	40,0	0,79	3,3	4
1967	31000	5,6	0,93	?	5	1989	219000	0,0	0,90	2,8	1
1968	27600	0,4	0,89	?	1	1990	245000	20,0	0,89	2,8	1
1969	36300	49,7	0,66	2,8	3	1991	314000	35,0	0,83	2,8	4
1970	40800	37,7	0,70	2,8	5	1992	263000	0,0	0,84	2,8	1
1971	34000	0,7	0,83	2,8	2	1993	300000	20,0	0,91	2,8	1
1972	51000	35,5	0,97	2,8	2	1994	250000	7,8	0,77	2,6	4
1973	84500	48,5	0,85	2,8	5	1995	218000	0,4	0,87	2,6	1
1974	71300	0,0	0,84	2,8	1	1996	212000	13,0	0,85	2,3	4
1975	119700	46,3	0,90	2,8	3	1997	235000	14,0	0,95	2,3	2
1976	109900	11,6	0,81	2,5	4	1998	195000	1,0	0,82	2,0	1

ger time span shows any signs of saturation to a constant level.

Data analysis

The full data set on which our analysis is based is given in Table 1. Population censuses are gathered annually under the auspices of the Goose Specialist Group of Wetlands International (Ebbinge et al. 1999, Delany et al. 1999) in the main brent goose wintering area, which stretches from coastal western France in the southwest (44° northern latitude), along the British south and east coasts and south-western Netherlands, to the Dutch, German and Danish Wadden Sea in the north (56° northern latitude). The Goose Specialist Group also

gathers information on annual productivity by assessing the proportion of first-winter birds in late autumn and early winter. Flocks are scanned by telescope to assess the proportion of first-winter birds, which are readily distinguishable by their plumage from adults. This proportion of first-winter birds, multiplied by the total population census in mid-January, yields an estimate of the number of first-winter birds (Prokosch 1984, Ebbinge 1985, Lambeck 1990). Because first-winter birds tend to stay in family groups throughout the winter, family size can be estimated by counting the number of offspring that accompany an adult pair. Family size has been practically constant over the years (Table 1), showing that no reduction in breeding success per successful pair has taken place. Thus, if we are able to find a reduction in overall reproduction, this must mean



that an ever smaller proportion of pairs are able to reproduce at all.

We count years starting just after the breeding season and let k denote the year, such that $k = 0, 1, \dots$, where 0 corresponds to 1955. Annual survival rates in Table 1 were calculated as the number of adult birds in year $k + 1$ divided by the total population size in year k . This requires the assumption that adult survival rate equals survival rate of first-winter birds, at least after January, when these first-winter birds are older than six months. First-winter birds that do not reach that age are not taken into account at all, because they do not live long enough to be included in the mid-January census (Ebbinge et al. 1991). Overestimation of the total population size in one year leads to an underestimation of the death rate, and even impossible negative death rates such as in 1961 and 1986. However, this underestimation in one year is directly compensated for by an overestimation of the death rate in the next year. The population trend of dark-bellied brent geese from 1955 to 1999 is given in Figure 1.

We differentiate between two seasons in the same year and express this in the notation. By N_{2k} we denote the population size of dark-bellied brent geese in August of year k , and ignore all young that are doomed to die before January. By N_{2k+1} we denote the population size in January, after the autumn migration. So, for example, year 0 has the population sizes N_0 just after the breeding season in 1955 and a population size reduced by mortality N_1 at the start of the wintering season in 1955–56). Likewise N_3 denotes the population size just after the breeding season in year 1 (1956) and N_4 the winter population in 1956–57, etc. The data points are interpreted as values for odd indices of the discrete variable N (i.e. as estimates for consecutive values of N_{2k+1} , $k = 0, 1, \dots$).

Counts were analysed by means of a log-linear model with overdispersion (McCullagh & Nelder 1989). The overdispersion parameter was estimated by means of Pearson's statistic. Deviance differences, adjusted for overdispersion, were employed for significance testing.

We did not find a significant density dependence in survival during the non-reproductive season, i.e. the number surviving was found to be directly proportional to the population size. In a log-linear model with only a constant and an offset for $\log(\text{population size})$, the constant represents the proportionality parameter. We indicate this parameter by d , the fraction of the popula-

tion that does not survive the non-reproductive season (which includes mortality during the migration from Siberia to Europe). The estimate of d over the 1955–1997 period equals 0.15 with 95 % confidence interval (0.13, 0.17). The years 1961 and 1986 had to be excluded from the analysis because they showed 'negative mortality'. Though theoretically this leads to an overestimation of the mean mortality rate (d), the amount of this overestimation is negligible. We tested this by setting the mortality rate in 1961 and 1986 at 0 %, and 'adding' the 'negative mortality' rates to the subsequent years 1962 and 1987. This led to a value for $d = 0.14$ (0.12–0.16). Several alternative ways of dealing with the 'negative' years gave the same result to two decimal places. An independent estimate for the adult annual death rate based on re-sightings of individual colour-ringed brent geese over the period 1973–1989 using a Jolly-Seber approach yielded the value of 0.16 (Ebbinge 1992), which falls within the confidence interval above. We also tested whether survival differed in the period before and after the hunting ban in Denmark in 1972. This resulted in the estimates $d = 0.18$ for the period 1955–1972 and $d = 0.15$ for 1973–1997. The variance for 1955–1972 is seven times greater than the variance for 1973–1997. The two estimates are not significantly different.

For the analysis of the data on reproduction a number of choices had to be made, because we were interested only in establishing whether the trend in population development shows density dependence. When Ebbinge (1985) analysed the brent goose data set for the period 1960–1984 there was a clear dichotomy in 'good' and 'bad' years. There were either years with at least 33 % first-winter birds, averaging 40.8 %, or years with less than 12 % first-winter birds, averaging 3.2 %. There were no years with values between 12 % and 33 %. More recently this dichotomy has been less clear, because more intermediate values have occurred, e.g. 20 % in 1990 and 1993, 13 % in 1996 and 14 % in 1997, at the expense of years with high productivity. This in itself can be seen as an indication for density dependence starting to operate. However, we prefer an objective approach, by defining criteria to exclude those years when breeding success was low, because of other reasons than density dependence. In other words, we wish to filter out the years when, on an almost regular basis, complete to almost complete breeding failure occurred. We took two approaches.

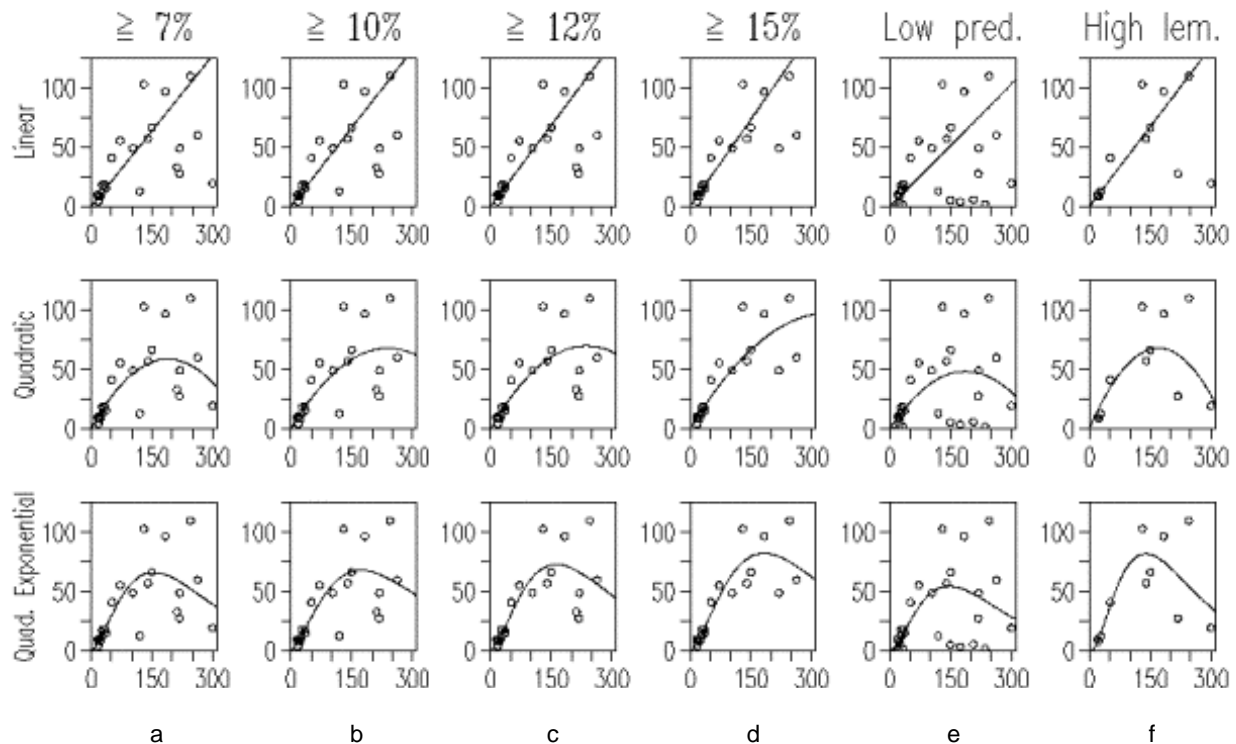
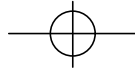


Figure 2. Plot of linear, quadratic and a quadratic \times exponential function $Nf(N)$ describing the number of first-winter birds as a function of total population size when only the years are considered in which (a–d) the proportion of first-winter birds is larger than 7 %, 10 %, 12 % and 15 %, respectively; (e) when years with an inferred high predation pressure (see text) are excluded; and (f) when only years when inferred low predator numbers coincide with a high abundance of lemmings are included.

Because breeding failure is associated with years when predation pressure is high as a result of the three-year lemming cycle, our first approach was to exclude these 'high predation years' from the analysis. For most years we do not have direct observations on predation pressure, which has to be inferred from the available data on lemming density (Table 1). High predation pressure on the geese by arctic foxes and snowy owls *Nyctaea scandiaca* is expected when predator abundance has increased as the result of a lemming peak in the previous year, and when this lemming peak year is followed by a crash in lemming numbers. We would thus exclude years when lemming abundance is scored as 1–2 immediately following upon years with a lemming score of 4–5 (Fig. 2e). A more stringent criterion is to include in the analysis only those years when predator levels are supposed to be low, i.e. when lemming abundance is high (scale 4–5) immediately following a lemming low (1–2; Fig. 2f).

Because we do not know exactly what causes these

perturbations (or indeed the precise lemming cycle), we also adopted a second approach by including only years in which breeding success exceeded a predetermined percentage. We tested several cut-off points: 7 %, 10 %, 12 % and 15 %. In Figure 2a–d we show estimates for the dependence of the number of first-winter birds on the total winter population size for these cut-off points and lemming years.

For the reproduction counts a generalised linear model with both Poisson and gamma distributions was employed. Plots of standardised residuals against fitted values were in favour of the gamma distribution and we therefore chose the gamma distribution for the analysis. We tested a linear relationship through the origin (i.e. no density dependence) against a quadratic relationship, and both of these against a quadratic multiplied by a negative exponential. The differences between these nested models were tested by approximated F-tests. The P-values for these comparisons are given in Table 2. One can see that using supposedly high predator levels

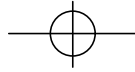


Table 2. P-values for comparison of (1) linear, (2) quadratic and (3) quadratic times exponential for four values of the cut-off point for reproduction and for the cases in which predator peak years are ignored, and when only lemming peak years coinciding with low predator levels are included. P-values less than 0.05 are considered significant.

Including years with	1–2	2–3	1–3
>7 % first-winter birds	0.005	0.153	0.008
>10 % first-winter birds	0.044	0.214	0.063
>12 % first-winter birds	0.028	0.046	0.012
>15 % first-winter birds	0.156	0.024	0.027
predator levels not high	0.072	0.406	0.144
low predator + high lemming	0.035	0.167	0.046

as a selection criterion for excluding years of poor reproduction does not give any insight. There are apparently too many years that also result in a low breeding success for other reasons, e.g. adverse headwinds during spring migration (Ebbinge 1989, Ebbinge 2000). However, using the stricter criterion of including only peak lemming years that coincided with supposedly low predator levels (inferred by also having had low lemming levels the previous year) does yield a significant density dependent effect (Table 2, columns 1–2 and 1–3).

We conclude that there is clear evidence for density dependence. There is also clear evidence that reproduction decreases with increasing population size. For cut-off points at 12 % and 15 % the declining exponential function performed better than the declining quadratic. This is not true, however, for all cut-off points and therefore both the quadratic and the exponential model are used in the subsequent analysis.

Therefore, we denote the estimated curves by $Nf_q(N)$ and $Nf_e(N)$ for the quadratic and exponential function as, respectively

$$Nf_q(N) = aN + bN^2$$

$$Nf_e(N) = (cN + dN^2)e^{-kN}$$

and estimate parameters for a cut-off at 12 %. These are: $a = 0.5897$ (s.e. 0.0783), $b = -0.000001244$ (s.e. 0.000000443), $c = 0.221$ (s.e. 0.199), $d = 0.00001767$ (s.e. 0.00000872), and $k = 0.00001187$ (s.e. 0.00000221).

The model and its analysis

We use a discrete time mathematical model that divides the year into two seasons: a reproductive and a non-reproductive season (akin to models in Fretwell 1972 and Goss-Custard & Sutherland 1997). We assume that in the reproductive season there is no mortality. We had to simplify the real world in order to be able to use the existing population data, which are based on annual censuses in mid-January (see above and Discussion). In the model, therefore, the population size just after reproduction in August is estimated by including only those newly born geese that survive to January. Thus, part of the mortality of young-of-the-year is included in the estimated reproduction. Our reproductive season therefore runs from January to August, and the non-reproductive season from August till January. In the model all mortality occurs only during this non-reproductive season, which includes the period of autumn migration and coincides with the hunting season.

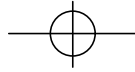
We assume that the number of first-winter birds in year k , is given by

$$N_{2k-1}f(N_{2k-1})$$

where f is a function that describes the possible density dependence in reproductive success (i.e. any density dependence is assumed to arise from the numbers of birds present in the breeding season). Similarly, we assume that the number of birds that do not survive the autumn season in year k is given by

$$N_{2k}h(N_{2k})$$

where $h(N_{2k})$ is the fraction of birds that does not sur-



vive the non-reproductive season, which could possibly also be density dependent.

Our basic model becomes

$$N_{2k} = N_{2k-1}(1 + f(N_{2k-1}))$$

$$N_{2k+1} = N_{2k}(1 - h(N_{2k})).$$

From the data analysis we found that $h(N_{2k}) = \mathbf{d}$ for all k , and for both choices for the reproductive function given in the previous section. The model with the quadratic reproduction function therefore becomes

$$N_{2k} = N_{2k-1}(1 + a + bN_{2k-1})$$

$$N_{2k+1} = N_{2k}(1 - \mathbf{d})$$

with regression parameters a and b given in the previous section, and with the current per capita death rate $\mathbf{d} = 0.15$. In the model with the exponential reproduction function the first equation is replaced by

$$N_{2k} = N_{2k-1}(1 + (c + dN_{2k-1})e^{-kN_{2k-1}})$$

with c , d , and k as above.

The technical details of the analysis of the dynamic behaviour of the model are given in the Appendix, where we also show that the behaviour is generic for a wider class of functions f with similar properties to the forms chosen for best fit in Figure 2. The model allows one or more steady states, depending on reproduction function and the value of \mathbf{d} . The current best estimate for $\mathbf{d} = 0.15$ gives a steady state population size of 332,000 birds in January, using the quadratic reproduction function (see Appendix).

If we use the exponential function for reproduction the situation is more complicated. Because of the exponential term more steady states can exist than in the quadratic case (see Appendix). We find for $\mathbf{d} = 0.15$ that the exponential model predicts a steady state population size of 286,000 birds in January. Because, given our assumptions, the model overestimates various factors (e.g. survival, age at first reproduction), the predicted numbers are probably an overestimate of the maximum population size.

In the model, birds are assumed to reproduce starting in the first breeding season after they were born, whereas in reality brent geese are only capable of reproducing from their second breeding season onwards. The data on the number of first-winter birds in Table 1 have

not been corrected for non-breeding one-year-olds (yearlings) but have been calculated, as is usual, using the total population count and the proportion of first-winter birds in the wintering flocks. A correction for non-breeding yearlings was proposed by Ebbinge (1989), since dark-bellied brent geese do not breed successfully when one year old (B. Ganter in prep.) and the number of yearlings varies strongly between years. However, as most brent geese are born in peak lemming years, which are usually followed by years without any breeding success, the first opportunity to nest does usually not arise before brent geese are at least in their third year. In our 44-year data-set there are only eight exceptions to this rule: 1960, 1964, 1970, 1973, 1976, 1979, 1991 and 1997. For the sake of simplicity, therefore, we do not differentiate between age classes in the model.

Discussion

Density dependence

Density dependence is a widely accepted concept in population ecology (e.g. Sinclair 1989), but data at the level of an entire (closed) population are extremely rare in birds (Newton 1998). Such data exist for bird populations confined to a few small islands, like the Seychelles Warbler *Acrocephalus sechellensis* (Komdeur 1994) and migratory waders and waterfowl which concentrate, often in large numbers, in a few local areas during the non-breeding season. Owen (1984) emphasised density-dependent depression of recruitment rate in the Svalbard population of barnacle geese *Branta leucopsis* as the key factor setting a limit on future population growth. Yet further growth was observed in later years due to the establishment of new colonies, that each went through a cycle of increasing productivity followed by a decline as carrying capacity was reached and the inhabitants became older (Black 1998). Larsson & Forslund (1994; see also Van der Jeugd & Larsson 1998) convincingly demonstrated density dependent effects on reproduction in recently established breeding colonies of barnacle geese on Gotland, Sweden. In dark-bellied brent geese local density-dependent effects on spring staging grounds have been demonstrated (Ebbinge 1992, Ganter & Ebbinge 1997). However, this seemed to have consequences only for the spatial distribution of the geese in spring, and not for the size of



the world population as a whole, because goose numbers still increased on the more recently colonised inland areas, whereas numbers levelled off on the salt marshes that traditionally had been used by brent for many decades.

The present analysis shows that there are now also significant repercussions on the world population level of brent geese, particularly through a reduction in the rate of reproduction. Increasing competition on the spring staging sites in the Wadden Sea or in the White Sea could be a factor responsible for this decline in reproduction. It is well known that the geese must accumulate sufficient body reserves to complete their migration within a limited time and arrive with sufficient reserves to breed successfully (Ebbinge & Spaans 1995). However, up to the year 2000 there has been no detectable decline in spring departure body-mass of birds caught at the end of May in the Wadden Sea (Ebbinge unpubl.).

Effects on the breeding grounds

Several studies on the breeding grounds, from 1990 to 1995, showed that there are different nesting options open to brent geese: on small islands in between gull colonies (Spaans et al. 1993, Ebbinge 2000), on very remote offshore islands, within nesting territories of snowy owls and, although in much lower numbers, scattered over low-lying delta areas (Ebbinge et al. 1999). In general these are areas that are – at least temporarily – inaccessible to Arctic foxes, either because of surrounding water after the ice has melted, or because of fierce defence by snowy owls. The first option (gull colonies) was successfully used during nesting in five out of six years in the Pyasina delta (Spaans et al. 1998), and is probably the most predictable type of nesting habitat for brent. During the same six years two lemming peak years occurred (1991 and 1994) and only in such years were brent geese observed to nest in association with snowy owls elsewhere on the Taymyr Peninsula (Underhill et al. 1993, Summers et al. 1994). We can only speculate about where brent geese mostly nested when the population was still in the increasing phase, but the limited number of gull islands seem to be the most likely candidates. Though documented for black brant *B. bernicla nigricans* on Wrangel Island in the far east of Siberia, nesting within territories of snowy owls is a new phenomenon for dark-bellied brent

on the Taymyr Peninsula. The fact that this occurs at the present population level is probably an indication that nesting habitat is now really a limiting factor. We interpret the observed decline in breeding success mainly as a result of limited safe nesting possibilities. Even within the gull colonies, though still relatively safe during the egg-stage, successful reproduction is extremely difficult for brent geese at the current nesting densities. Only a few brent geese remain on the islands to raise their goslings, and the majority leave these islands with their goslings in the first week after hatching. Despite this, a high proportion of the newly hatched goslings is still taken by gulls (Ebbinge 2000). Therefore we consider crowding on the limited safe nesting sites in Siberia a much more likely explanation for the observed decline in productivity, than competition for food on the spring staging areas. Since there are indications that the total number of juvenile birds is now declining, however, this cannot be the only explanation. If reaching the limitations of the breeding territory were the only factor operating we would expect the yearly total of juveniles to saturate, rather than decline.

The fact that the mean family size has remained virtually constant at about 2.7 offspring per pair (over a period of 25 years in which the population size increased by sevenfold) also indicates that lack of suitable nesting sites is probably the main limiting factor. Those pairs that still have access to those sites are still as productive as at lower population levels.

Adverse headwinds in the Baltic during spring migration that have an impact on reproduction (Ebbinge 1989) cannot explain the observed reduction in breeding success, because in the period 1970 to 1996 adverse wind conditions in spring occurred only in 1971, 1976, 1984, 1987 and 1992. In all other seasons wind conditions were favourable for spring migration. There is thus no discernable trend in the frequency of these adverse conditions.

Hunting

Hunting is usually mentioned as the key factor that reduced brent goose numbers so dramatically in the 20th century (Salomonsen 1958, Prokosch 1984, Ebbinge 1991). In our analysis survival prior to the Danish hunting ban in 1972 is also on average 3 % (= 0.18–0.15) lower than later on, but this difference is not significant. From the published Danish game statistics (Strand-



gaard & Asferg 1980) one can work out that in the period 1955–1971 on average 10 % of the total population was shot annually in Denmark alone. There are large differences between years (varying from 4 % to 18 %) with a particularly high hunting pressure after good breeding seasons with many young birds. Though the estimated 3 % difference is in the right direction, the lack of significance shows that the available census data do not allow very precise estimates. The variance in the data before the hunting ban is seven times greater than the variance after the ban. This does not necessarily mean that the hunting ban in 1972 in Denmark was not the key factor allowing the dark-bellied brent goose population in western Europe to recover. Theoretically one could expect that increased population levels would also lead to increased mortality through increased competition. Among Svalbard barnacle geese mortality during autumn migration increased from 2 % to 8 % when the overall population size increased from 3,000 to 11,000 (Owen & Black 1991). In our case, however, this is probably impossible to ascertain with the available data, because of the simultaneous reduction in hunting pressure. This will have lowered the overall mortality rate, thus masking any increase in natural mortality.

Predicting the effects of habitat loss

It is not the aim of this paper to study the effects of habitat loss for migratory populations as did Fretwell (1972) and Sutherland (1996), based on intersections of curves representing the relationships between population density and, respectively, mortality and reproduction. In the analyses presented in Sutherland (1996) and Goss-Custard & Sutherland (1997), only the steady state population density changed as a result of habitat loss. The reason for this is that the form of the two curves leads to a unique steady state. This corresponds in our case to the quadratic reproduction function, for which a similar intersection study (see Appendix) would result in the intersection of two straight lines. Theoretically, of course, the dynamics can become more complicated if the curves behave differently so as to give rise to multiple steady states. Biologically speaking our model with the exponential reproduction function suggests (see Appendix) that one has to be careful that d is not increased significantly from its present value (e.g. due to renewed hunting). At some point one enters a region where multiple steady states can exist and the following

phenomenon (hysteresis) could occur: in theory the population might collapse completely over a short time period, after which re-establishment is unlikely even if the unfavourable conditions are improved. These more complicated situations can indeed occur in real systems of migrating birds, as when the curves are estimated from our data (see e.g. Sinclair 1989 for a broader ecological context). Consequently the effects of habitat loss can be more dramatic than a gradual shift in expected steady state densities to adapt to new conditions. This makes clear that one has to be careful when deriving rules-of-thumb from postulated curves that do not fully reflect realistic dynamics, as exemplified by the brent geese data. This becomes particularly relevant if one realises that the brent geese data are among the longer and more detailed time series available for any species.

Practical implications

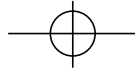
The present conclusion that the world population of dark-bellied brent geese is likely to remain below about 330,000 individuals (and probably below 300,000) has great implications for the management of this subspecies. If correct, it would imply that governments and nature protection societies can now plan for sufficient nature reserves to accommodate this population of high arctic migrants, and that farmers do not have to fear for a further substantial increase in this subspecies and increasing economic loss.

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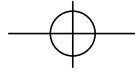
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Appendix

Analysis of the models

We first analyse the more difficult case, i.e. the model with exponential reproduction function (repeated for convenience from the main text).

$$N_{2k} = N_{2k-1} (1 + (c + dN_{2k-1})e^{-kN_{2k-1}})$$

$$N_{2k+1} = N_{2k} (1 - \mathbf{d})$$

Since the time-unit of one year has been divided into two half-year seasons, we look for steady state pairs (N, M) such that

$$N = M (1 + (c + dM)e^{-kM})$$

$$M = N (1 - \mathbf{d})$$

i.e. a steady state is a pair (N, M) such that in each consecutive year there will be N birds in August and M birds at the time of the winter counts in January. Since we only observe the population in January we are interested in the value of M . One can immediately see from the second equation that $M = N(1 - \mathbf{d})$. We can then find N by solving

$$N = N(1 - \mathbf{d}) + (c(1 - \mathbf{d})N + d(1 - \mathbf{d})^2 N^2)e^{-k(1 - \mathbf{d})N}.$$

This leads to $N = 0$, or, for positive N , the possible solution of

$$\frac{\mathbf{d}}{1 - \mathbf{d}} = (c + d(1 - \mathbf{d})N)e^{-kN(1 - \mathbf{d})}.$$

We cannot solve the latter equality for N analytically, but we can analyse it graphically by plotting the right-hand side, which we denote by $g(N) = f(N(1 - \mathbf{d}))$, and the left-hand side, a horizontal line, in one graph as functions of N (see Figure 3a–c). This amounts to plotting re-scaled per capita growth and re-scaled per capita death in one graph. Intersection points are values of population size where, when multiplied by population size, increase over one year equals decrease over one year, i.e. values of $N > 0$ for which the system is in equilibrium. This is also done in Fretwell (1972) and Goss-Custard & Sutherland (1997). As Fretwell points out,

one has to be careful in doing this since the fact that growth and decline happen in different seasons in the model makes it impossible simply to plot the functions f and h directly: the arguments of $Nf(N)$ and $Nh(N)$ are different. The re-scaling takes this into account for f (the re-scaling of h in our case is not strictly necessary since it is a constant function).

The intersection points N^* correspond to positive steady state pairs $(N^*, N^*(1 - \mathbf{d}))$ of our system. We study the various possibilities for intersections of the curves as we vary the only parameter with a clear biological interpretation, i.e. \mathbf{d} , the per capita probability of not surviving the winter season. The other parameters (c, d, k) are set to the values estimated for them from the reproduction data. One can numerically calculate the steady state value for N as a function of the parameter \mathbf{d} . There are three possibilities for increasing values of \mathbf{d} (and one degenerate case between the first and the second), see Figure 3a–c: one positive steady state (stable), two positive steady states (one unstable, one stable), or no positive steady state (and zero is the only equilibrium of the system). For $\mathbf{d} = 0.15$ and the parameters relevant for the cut-off point of 12 % one finds a unique stable positive steady state $N^* \approx 336,000$. This leads to a steady state size at the January of $M^* \approx 286,000$ birds.

One can compute in a straightforward way, by looking at the maximum of g , the values for \mathbf{d} where two steady states exist, and the value of \mathbf{d} above which no positive steady state exists. Because the precise form of the reproduction function is unknown, these details have little merit and we do not carry out this calculation.

For the quadratic reproduction function we obtain (see Figure 3a) with similar reasoning that either $N = 0$ or N is the solution of

$$\frac{\mathbf{d}}{1 - \mathbf{d}} = a + bN$$

We then find a unique positive steady state

$$N^* = \frac{\mathbf{d}}{(1 - \mathbf{d})^2 b} - \frac{a}{(1 - \mathbf{d})b},$$

which exists for all $\mathbf{d} < a/(1 + a) = 0.37$. The parameter values corresponding to the cut-off point of 12 % and $\mathbf{d} = 0.15$ yield $N^* \approx 390,000$. This results in a steady state value $M^* \approx 332,000$ birds at the January census.

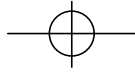
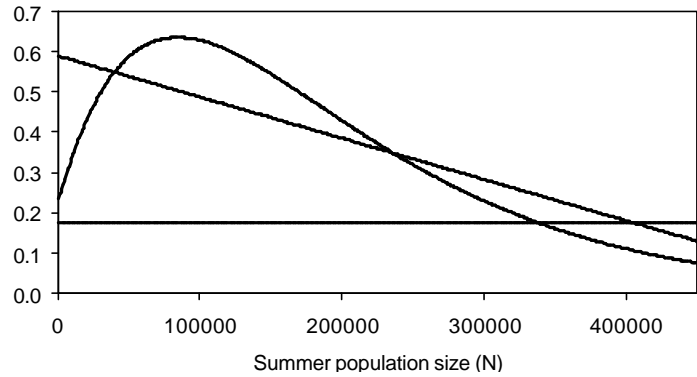
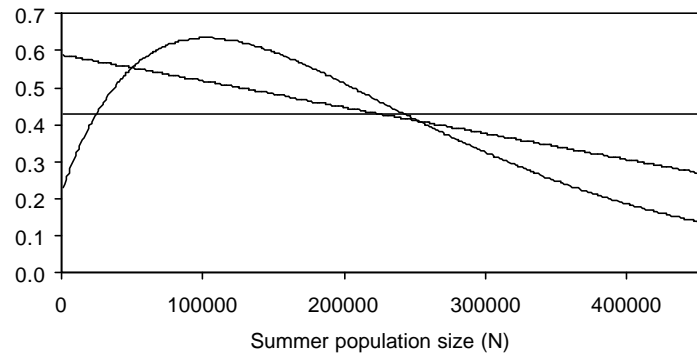
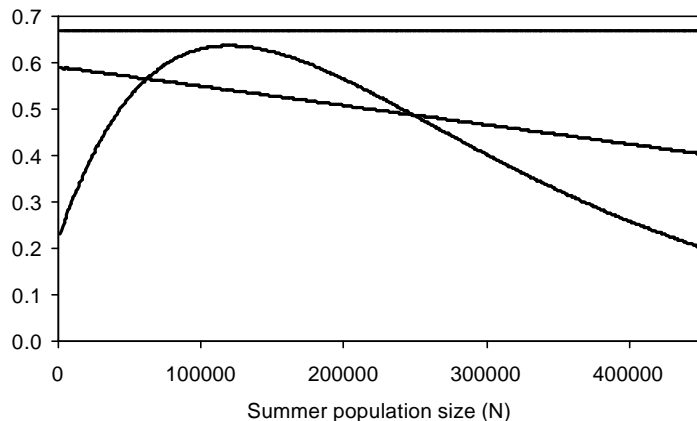
Figure 3a, $d = 0.15$ Figure 3b, $d = 0.30$ Figure 3c, $d = 0.40$ 

Figure 3. Plot of constant scaled mortality $d/(1-d)$ (horizontal line) and the scaled per capita reproduction functions $f(N(1-d))$ against total population size N (in August). Intersections of the horizontal line and each of the two curves correspond to positive steady states of the corresponding models. (a)–(c) are for $d = 0.15, 0.30$ and 0.40 respectively. The scaled per capita quadratic reproduction function is a straight line with negative slope, giving one or no intersection with the scaled mortality. The re-scaled per capita exponential reproduction function is the unimodal curve with one, two or no intersections.

In the case of the quadratic reproduction function we therefore find a unique steady state, whereas the exponential reproduction function leads to more complicated dynamic behaviour. These findings are rather robust to the precise choice of the two functions in the sense that functions having the same qualitative

features as the ones chosen will give the same generic picture. For example, in the case of the exponential reproduction function, behaviour will be the same as long as the curve $Nf(N)$ is S-shaped for small values of N and is unimodal, or monotonically increasing to a level of saturation.



No evidence for tree phenology as a cue for the timing of reproduction in tits *Parus* spp

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There is ample evidence that avian timing of reproduction is under strong natural selection. However, which cues birds use to time their reproduction is largely unknown. This knowledge is essential if we wish to understand the limits of adaptation in the timing of reproduction to large-scale changes in climate and land use. We test whether birds use the phenology of trees that host the main prey species for their offspring in their timing. We carried out three experiments on captive birds in which: (1) pairs of great tits *Parus major* were given branches of oak *Quercus* sp with either early or late bud burst; (2) pairs of blue tits *P. caeruleus* were given an oak branch or not, and (3) male great tits were given a branch of birch *Betula* sp or not. No effect of tree phenology on laying date in the predicted direction was found in experiments 1 or 2. In experiment 3 there was no effect on gonadal growth or testosterone, but there was a faster increase in LH in the exposed group. We conclude that great and blue tit do not use oak phenology as a cue. This conclusion is confirmed by a natural experiment where in one year there was a decoupling of spring temperatures and date of bud burst.

Key words: timing of reproduction, birds, tree phenology, *Parus major*, *Parus caeruleus*, hormones, climate change.

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Only a short period of the year is suitable for reproduction in the temperate zone (Murton & Westwood 1977). The time within a year at which food availability peaks varies between areas and years, and as a consequence the optimal timing of reproduction will also vary. The fitness consequences of timing have been extensively studied (see Nilsson 1999, for a review). However, the proximate factors (cues) used in the timing of reproduction to enhance synchrony between offspring requirements and food availability are much more poorly known (Visser & Lambrechts 1999). As reproduction is initiated much earlier than the time of maximum food requirement of the offspring, individuals should start reproduction in response to cues, available at the time of reproductive decision making,

which predict the moment of maximum food abundance (Wingfield et al. 1992). The process by which internal (condition, etc.) and external cues (photoperiod, temperature, etc.) are translated into a reproductive decision is termed the response mechanism (Visser & Lambrechts 1999).

As there is spatial and temporal variation in the time of maximum food abundance, the response mechanism should track this variation. In other words, the response mechanism should produce adaptive phenotypic plasticity, and selection will act on this reaction norm (i.e. how the decision changes along an environmental axis), rather than on the decision in a particular year or area. Our knowledge of the response mechanism and the cues involved is currently limited but crucial for a



full understanding of intra-specific variation in the timing of reproduction at different temporal and spatial scales.

Insight into the response mechanism leads to a better understanding of the limits of adaptation to large-scale change in climate and land use. Over the past 25 years spring temperatures have increased (Houghton et al. 1996). A wide variety of organisms have responded to this (Wuethrich 2000, Hughes 2000), including species that have advanced their timing of reproduction or growth (Beebee 1995, Winkel & Hudde 1997, Crick et al. 1997, McCleery & Perrins 1998, Crick & Sparks 1999, Brown et al. 1999, Visser & Holleman 2001, Both & Visser 2001). In some cases, however, there has been an insufficient or no advancement (Visser et al. 1998, Both & Visser 2001), leading to increased selection for early reproduction. In the case of Dutch great tits *Parus major*, the peak date of food abundance for their offspring has advanced over the past 20 years but their laying date has not (Visser et al. 1998). One explanation for this lack of advancement is that early spring has not become warmer, while late spring has. The response mechanism underlying timing has evolved given a specific relationship between early and late spring temperatures. Now that this relationship has altered, the response mechanism the birds use may no longer correctly translate the cues in early spring to an optimal laying date, and is thus no longer adaptive. If there is heritable variation in this response mechanism, selection may take place for a mechanism that is better adapted to the changed environment in which the birds need to time their reproduction. This would result in an advancement of laying date (Visser et al. 1998). In order to test this hypothesis, however, we need to identify the cues involved in the response mechanism underlying the timing of reproduction.

A potentially important cue for the timing of reproduction of insectivorous birds, such as great tits and blue tits *Parus caeruleus*, is the time of bud burst of deciduous trees (Lack 1966, van Balen 1973, Blondel et al. 1993). Caterpillars on these trees, like the winter moth *Operophtera brumata*, form the main source of food for the tits' nestlings. These caterpillars can only start their development just after bud burst, as earlier there is no food available and later in the season leaf quality declines rapidly (Feeney 1970, Holliday 1985). Winter moth development is temperature dependent, and for average spring temperatures it takes about 40

days from egg hatching until pupation (Topp & Kirsten 1991), after which they are no longer available to the birds. This period more or less matches the interval from the onset of rapid yolk formation in the tits to having 10-day-old chicks. Thus, bud burst could be a reliable cue for the time of maximum food abundance, although temperatures after laying can advance or delay caterpillar development, resulting in a mismatch between nestlings' requirements and food abundance (van Noordwijk et al. 1995). Indeed, Slagsvold (1976) demonstrated that the laying date of great tits in Norway is well synchronised with the bud burst of the dominant tree species, birch *Betula pubescens*. As laying date was also strongly correlated to temperature, however, it was not possible to distinguish between the roles of tree phenology, the appearance of insects and temperature as cues in the timing of reproduction.

A possible causal pathway by which bud burst may play a role is via a chemical substance 6-methoxybenzoxazolinone (6-MBOA). This chemical, a cyclic carbamate, is formed from its precursor, 2,4-Dihydroxy-7-methoxy-2H-1,4-benzoxazin-3-(4H)-one (DIMBOA), when predators damage plants. DIMBOA is particularly abundant in growing seedlings. In both field and laboratory experiments it has been shown that 6-MBOA is a strong reproductive stimulant for montane voles *Microtus montanus* (Berger et al. 1981, 1987). Although not yet shown, it is possible that buds of trees also contain substantial amounts of DIMBOA. As blue tits and, to a lesser extent, great tits eat buds in early spring (Betts 1955), they can thus potentially come into contact with 6-MBOA which may then affect their reproductive system.

Despite the fact that it is more than 30 years since it was first suggested that birds might use tree phenology as a cue (Lack 1966), no definitive conclusion has been reached. This is due to the difficulty of studying potential cues under field conditions, as potentially important variables co-vary from year to year. In other words, years with high spring temperatures are in general also years in which trees have an early bud burst and in which insects appear earlier. The controlled laboratory conditions needed to assess the role of tree phenology are now available, enabling us to address the issue experimentally for the first time.

To study whether tree phenology is used as a cue for the timing of reproduction in blue and great tits we carried out three studies using birds in captivity. These ex-



periments were conducted at three different laboratories, independently of each other. At the 1998 International Ornithological Congress, MEV, BS and MML discussed the potential role of tree phenology on the timing of avian reproduction, and realised that they all had performed an experiment on this. Rather than publishing these studies separately, we present them here jointly. Work on captive birds has the disadvantage that not all necessary stimuli may be present, or that stress from being captured masks relationships that do occur under natural conditions (Visser & Lambrechts 1999, Lambrechts et al. 1999). Therefore, we also report on a 'natural experiment' where bud burst in the field was delayed due to conditions in the previous year, and the laying date of the birds in response to this delay could be measured.

In experiment 1 we determined the laying date of pairs of great tits in aviaries where half of the pairs were given branches from pedunculate oaks *Quercus robur* with an early bud burst, while the other half were given branches from late oaks. In experiment 2, some blue tit pairs were given branches from another deciduous species, the downy oak *Q. pubescens*, while other pairs served as controls. Again, the effect on laying date was determined. We used oak branches in these two experiments because these are the main host trees for the tits' prey at the time of chick feeding. Lastly, in experiment 3, male great tits were kept in a room with or without branches of birch *Betula pubescens*, the main tree species used by this northern tit population. In this experiment gonadal growth and the concentration of two hormones, testosterone and lutenizing hormone (LH), were determined.

Methods

Experiment 1: great tit pairs

We tested whether the stage of oak leaf phenology affects laying date in an experiment using pairs of great tits in closed aviaries (one pair per aviary of 2 m × 2 m × 2.25 m) under artificial light and at ambient temperatures. The experiment was run for two years (1997 and 1998), starting with 16 pairs per year. Photoperiod was increased twice a week following the natural increase in day length. Birds caught from the wild from a location near Arnhem (The Netherlands) were introduced into the aviaries at the end of January (photoperiod of

less than 9 h), well before the critical photoperiod for the start of the rapid gonadal growth (between 11 and 12 h, Silverin et al. 1993). The birds were given a constant daily amount of food throughout the experiment, consisting of fly pupae, sunflower seeds, fat and commercial softbill food (a mixture of proteins, vitamins, minerals and trace elements), as well as nesting material and a surplus of calcium in the form of egg and snail shells. Three nestboxes were provided per aviary, which were checked three times a week for eggs.

When the photoperiod reached 14 h 15 min large branches of oak trees were introduced into the aviaries. Because the pattern of day length used was not exactly the same in the two years, this was not on the same date. The two treatments differed only in the stage of the buds on the branches. These were recorded on a scale ranging from 0 (winter rest) to 3 (fully unfolded leaves; Merle & Mazet 1983, Visser & Holleman 2001). The difference in developmental stage of the buds corresponded to a period of 7–10 days. Branches were replaced weekly, and bud burst advanced over time. The difference in development of buds was preserved for as long as possible. If bud burst is a cue in the timing of reproduction we would expect laying date to differ by 7–10 days between the two treatments. The branches were collected at a relatively isolated site and on two occasions a sample of the branches were searched for caterpillars. None was found.

Experiment 2: blue tit pairs

Blue tits from two Corsican populations, Muro and Pirió, were kept as pairs (4 Pirió and 4 Muro pairs) in outdoor aviaries in Montpellier, France. Birds from these two populations were used for reasons that fall outside the scope of this paper (see Lambrechts et al. 1999). Relevant to our study is the fact that the Pirió population inhabits evergreen forest, and the Muro population inhabits deciduous woodland. Bud burst of the deciduous trees occurs about 4 weeks earlier than the evergreen trees, which are therefore unlikely to trigger gonadal development. This could explain why under field conditions Muro birds lay about four weeks earlier than the Pirió birds but in aviaries containing an evergreen holm oak *Quercus ilex* Muro birds lay about two weeks later than the Pirió birds (Lambrechts et al. 1997, 1999).

Birds were collected from Corsica in the autumn of 1997. In five of the aviaries a branch from the same in-



dividual deciduous oak tree (*Q. pubescens*) was introduced each week from 3 March to 2 April 1998. The leaf phenology of these branches therefore followed the natural pattern. In the other aviaries, an evergreen *Q. ilex* tree was present. Nestboxes were checked weekly to determine the laying date. If the phenology of *Q. pubescens* acted as a cue for the timing of reproduction, we would expect blue tits presented with a branch to have laid earlier than the control group.

Pairs were exposed to *Q. pubescens* branches in 1998, and in that year four more pairs from Muro, but not Pirio, were kept with an evergreen *Q. ilex*. We therefore tested for the effect of leaf phenology on laying date by comparing the laying dates of the 1998 pairs with the broad leaved deciduous oak branches with those from pairs with an evergreen oak for the whole range of years available (for Pirio (evergreen) 1986–1988, 1992, 1994–1997, for Muro (deciduous) 1994–1999; see Lambrechts et al. 1999).

Due to the unbalanced data set a 3-way ANOVA with treatment, year and origin is somewhat unsatisfactory. We therefore also present a 2-way ANOVA with only treatment and origin, effectively pooling years without taking year differences into account (following Blondel et al. 1990, Lambrechts & Dias 1993). As year was not significant in the 3-way ANOVA ($F_{9,25} = 0.24$, $P = 0.98$, Table 1), this seems appropriate.

The percentage of the oak buds eaten was determined from 1 or 2 twigs after the branches had been in the aviary for a week. In addition, all pairs were observed for 15 min every week, between 09.00 and 12.00 h. Every minute it was noted whether at least one member of the pair was either perching on the branch or eating (or pecking at) the buds. The proportion of the 15 minutes in which these behaviours were noted, as well as the proportion buds eaten, were analysed in relation to week number and origin (Muro or Pirio). We used binominal errors in analysing the proportion of buds eaten, but used arcsine transformed proportions for the time spend eating and the time spend perching, as a binominal error structure is incorrect when analysing proportions of time. As we have repeated measurements on pairs, we corrected for this in the statistical analysis.

Experiment 3: great tit males

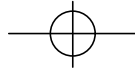
Sixteen male great tits were caught in the first week of February 1995 in a deciduous forest 50 km east of Göteborg, Sweden, and acclimatised to laboratory condi-

tions under a natural photoperiod before the experiment started on 27 February. Birds were housed individually in cages (60 × 30 × 36 cm), to which nest-boxes were attached. Birds were given ad libitum water (with vitamins) and food (sunflower seeds, live mealworms and dried insects). Although only male great tits were used, moss was provided as nest-building material. The cages were set up in two separate rooms (8 cages per room), and there were two treatments. In one room the males were exposed to birch leaves (see below) and the other room served as a control. If birch bud burst is a cue in timing, we would expect the males presented with branches to increase their hormone levels earlier, and have full grown testes earlier.

As there were no natural birch leaves available at the start of the experiment (late winter), small birches (about 1.5–2 m high) were taken indoors and kept at room temperature to obtain branches with leaves of about 10 mm. At the start of the experiment, these branches were placed in the room used for the birch treatment, and smaller branches with leaves were placed in the cages. Small trees were taken indoors regularly and put in water, so that birds were exposed throughout the experiment to fresh birch leaves of about the same size.

At the start of the experiment the light regime was equal to the natural day length (10 h 40 min). After a week day-length was increased by 35 minutes to 11 h 15 min, and the next week by another 30 min to 11 h 45 min. To speed up the increase in day-length and to be closer to natural photoperiods, day-length was then increased by 1 h each week for the next two weeks (= 12 h 45 min and 13 h 45 min respectively). At the end of this last week the experiment was ended. The birds were fully photosensitive at the onset of the experiment but because day-lengths were below the photoperiodic threshold all reproductive variables were still basal.

At the end of each week a blood sample (about 200 µl) was collected from the jugular vein of each individual into a heparinised syringe. Blood samples were kept on ice until centrifuged within an hour. Plasma was stored at –20 °C until analysed. Testosterone was later measured by a single-antibody assay after chromatographic separation and purification on microcolumns of celite: glycol, where steroids can be eluted in order of polarity. Each sample was assayed in duplicate. The samples were assayed in two successive assays. Aliquots from mallards *Anas platyrhynchos*, as well as solvent blanks, were included in triplicate in the assay.



Intra- and interassay coefficients of variation were 6.3 % and 10.6 %. The method has been described in more detail by Röhss & Silverin (1983) and Ball & Wingfield (1987). Plasma samples were assayed for LH using an homologous chicken LH double-antibody radioimmunoassay technique previously described by Röhss & Silverin (1983). All LH samples were measured in duplicate and in one single assay. The intra-assay variation was 6.4 %.

Testicular size (left testis) was measured to the nearest 0.2 mm by laparotomy at 2-weekly intervals. Laparotomies were carried out under methoxyflurane (Metofane Pitman-Moore, Inc.) anaesthesia.

Natural experiment

In 1991 a late frost damaged many of the freshly opened oak buds in the Hoge Veluwe area, The Netherlands. As a consequence, the trees had a second bud burst of their dormant buds. The timing of oak bud burst can be well described with a temperature-based model (Kramer 1994) but defoliation of trees may lead to a delayed bud burst in the next year (Visser & Kramer, unpubl.). When the observed bud burst dates on the Hoge Veluwe are plotted against the predicted values for a 12 year period, it is clear that in 1992, the year after the late frost, the buds opened later than predicted, while for the other years Kramer's model predicts bud burst rather well (Fig. 5a). Thus, in 1992 the date of bud burst and spring temperatures appeared to be uncoupled. If birds use bud burst as a cue we expect them to have laid relatively late in 1992; if they do not use bud burst we expect the difference between mean laying date and bud burst to deviate from the normal range. We calculated the mean laying date of first year female great tits, as older birds may have adjusted their laying dates in 1992 due to the

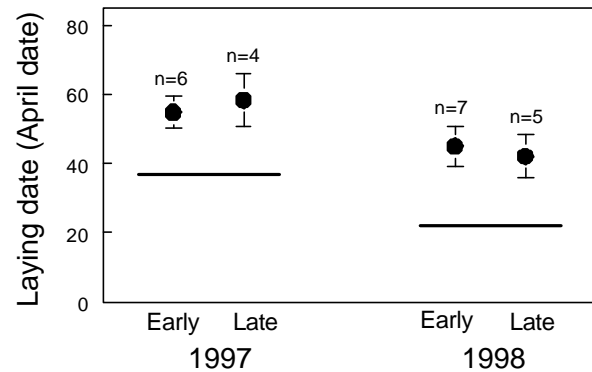


Figure 1. Experiment 1: the effect of exposure to branches of oaks *Quercus robur* that had either an early or a late bud burst on the laying date of great tit pairs from The Netherlands in 2 years. The horizontal lines indicate the date on which the first branches were introduced. Means \pm s.e. and sample sizes (n) are indicated.

1991 events. We then tested in an outlier analysis (Dixon 1950) whether the difference between this laying date and the observed oak bud burst was significantly different from the other 11 years for which bud burst data were available.

Results

Experiment 1: great tit pairs

In both treatments (and in both years) the first pairs started to lay about a week after the first introduction of the branches. However, there was no significant difference in laying date between the two treatments (Figure 1, 2-way ANOVA: treatment $F_{1,19} = 0.07$, $P = 0.80$; year $F_{1,19}$

Table 1. ANOVAs of experiment 2 on the effect of exposure to branches of deciduous downy oak *Quercus pubescens* (treatment) on the laying date of blue tits from two Corsican populations (origin: Muro (deciduous woodland) and Piro (evergreen oak woodland)). The experiment was carried out in 1998, but controls were used from 1994–1999 (Muro) and 1986–1988, 1992, 1994–1997 (Piro).

	Incl. year in model		Excl. year in model	
	F-value	P-value	F-value	P-value
Treatment	$F_{1,25} = 2.92$	0.10	$F_{1,34} = 18.16$	<0.0001
Origin	$F_{1,25} = 5.26$	0.03	$F_{1,34} = 14.65$	0.0005
Year	$F_{9,25} = 0.24$	0.98	n.a.	n.a.

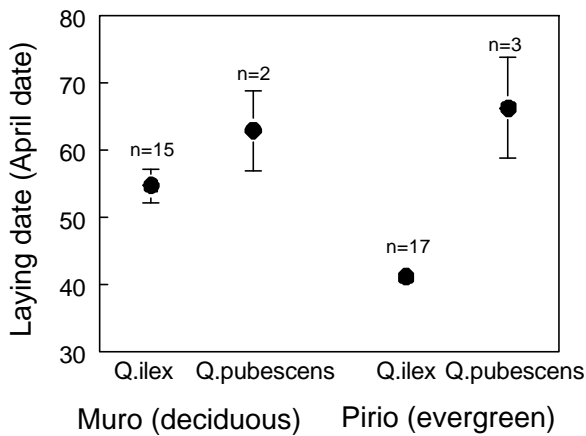
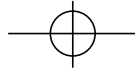


Figure 2. Experiment 2: the effect of exposure to branches of deciduous downy oak *Quercus pubescens* or evergreen holm oak *Q. ilex* on the laying dates of blue tit pairs from two Corsican populations (Muro and Pirió). Means \pm s.e. and sample sizes (n) are indicated.

= 0.91, $P = 0.35$; treatment \times year $F_{1,18} = 0.06$, $P = 0.81$). Thus, it appears that the birds' timing of reproduction was not affected by the stage of bud burst. In most cases, the birds ate all the buds from the branches within a few days. Only fully closed buds and fully unfolded leaves were less attractive.

Experiment 2: blue tit pairs

There was a clear effect of the availability of branches of deciduous oaks on laying date, especially for the Pirió pairs (from the evergreen forest), but in the opposite direction to that expected: the birds laid later in the presence of the branches (Figure 2, Table 1). When the analysis is limited to the 1998 experiment with Muro

birds (the only situation where some animals from the same population were presented with a deciduous oak branch ($n = 2$) and others not ($n = 4$) in the same year) there is no effect of the presence of a branch ($F_{1,5} = 0.22$, $P = 0.66$).

The proportion of buds (partly) eaten increased over the 4-week period (no data for week 5), with the Muro (deciduous) pairs eating a larger proportion of the buds than the Pirió pairs (Table 2, Figure 3). The proportion of time during which blue tits were observed eating buds or perching on the branches also increased over the 5-week period, with an effect of origin for the amount of time spent perching but not for time spent eating (Table 2).

Experiment 3: great tit males

Treatment affected LH levels only, and not testis size or testosterone (Figure 4, Table 3). Thus, gonadal development was not advanced by exposure to birch leaves, but the rise in LH level was (see Discussion).

Natural experiment

It is clear that in 1992 the birds laid much earlier than the actual date of bud burst (Fig. 5b). While the bud burst was the latest in the series of years 1988–2000, laying date was the earliest, and 1992 differed significantly from the other 11 years available (outlier analysis (Dixon 1950) on laying date minus bud burst date: $r_{2,1} (12) = 0.525$, $P = 0.05$).

In this natural experiment, we assume that there has been an uncoupling of spring temperatures and bud burst date for 1992. This is confirmed by Fig. 5a but can also be checked by testing whether the laying date in

Table 2. Statistical analysis of the proportion of buds eaten from branches of *Quercus pubescens* (logistic regression, correcting for overdispersion and for repeated measurements), the number of minutes out of 15 minutes observation time that one or both members of the blue tit pair was observed eating buds or perching on the branch (both analysis: ANOVA on arcsine transformed proportions, correcting for repeated measurements) in experiment 2. The experiment ran for 5 weeks (week number), and pairs from two Corsica populations (Muro and Pirió) were used (origin).

	Proportion of buds eaten		Proportion of time eating		Proportion of time perching	
	Z	P	Z	P	Z	P
Week number	6.96	<0.0001	2.36	0.018	-4.42	<0.0001
Origin	2.62	<0.01	1.70	0.09	-0.98	0.047
Week \times origin	-0.19	0.85	-0.04	0.97	2.30	0.02

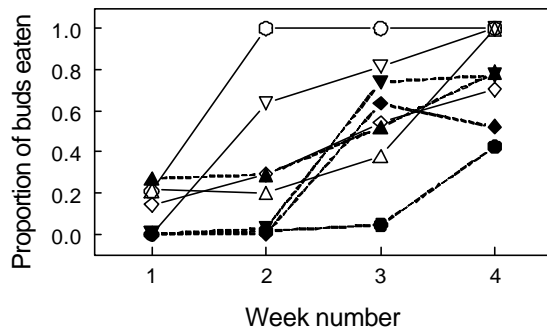
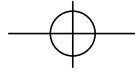


Figure 3. The proportion of buds eaten from branches of *Quercus pubescens* in experiment 2. The experiment ran for 5 weeks, but no data were collected in week 5. Blue tit pairs came from two Corsican populations (4 pairs from Muro – open symbols and solid lines; and 4 pairs from Pirio – closed symbols and broken lines).

1992 was also exceptionally late compared to the predicted bud burst, which is calculated from a descriptive model based on temperature. In this analysis, the interval between observed laying date and predicted bud burst for 1992 is not an outlier (the 1997 interval is more extreme, i.e. shorter). This confirms our assumption.

Discussion

In all three experiments there was no clear effect of tree phenology on the timing of reproduction (or gonadal growth) in the predicted direction. The observations during the natural experiment of 1992 are in agreement with this result: great tits and blue tits appear not to use tree phenology as a cue in their timing of reproduction.

A general problem with experiments that show no effect of treatment is that this could be due to low statistical power. As experiment 1 was the first experiment on laying date in great tits under controlled conditions (artificial light, etc.) we had no estimate for the within-treatment variation in laying date prior to the experiment, and hence were unable to assess the number of replicates needed to obtain sufficient power. In retrospect, the sample sizes of 13 and 9 and observed standard deviations of 13.8 and 16.1 days, gives only a 45 % probability of detecting a 10-day difference (as expected from the differences in bud burst) between the experimental groups. To increase this probability to

80 %, another 35 values are needed. We can obtain 16 data points at most per year (with 12 as a more realistic value), which would mean another 3 years of running the experiment. The results from the two years presented here do not justify such an effort.

We did find an effect of tree phenology in the predicted direction in the experiment in which male great tits were exposed to birch branches: LH, but not testosterone, concentrations were affected. The reason for this discrepancy is unclear. It might be a result of the hypothalamus-pituitary system being more sensitive to changes in the environment than the gonads, i.e. the pituitary responds more rapidly to environmental changes. If birds are exposed to an abrupt change in day length (prolongation) it is well known from studies on several avian species, including the great tit (Silverin 1994), that LH secretion may start to increase up to se-

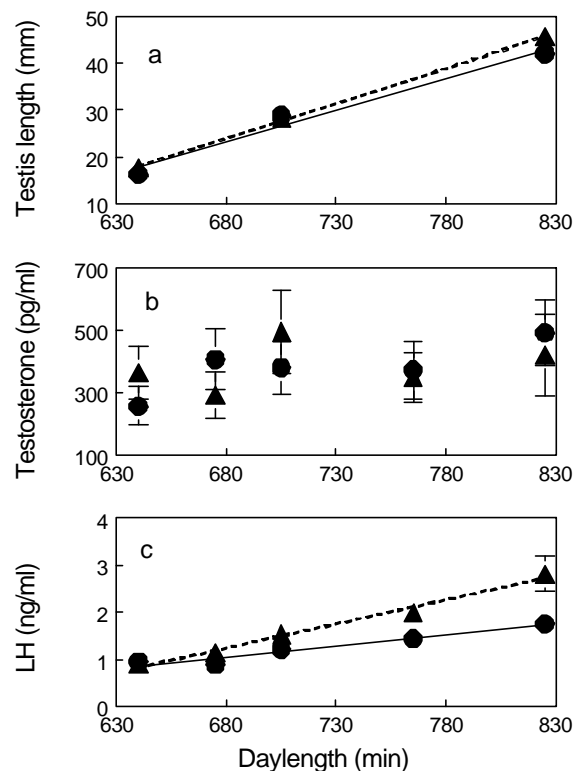


Figure 4. The effect of exposure to branches of birch *Betula pubescens* (circles: no birch, $n = 8$; triangles: exposure to birch, $n = 8$) on (a) gonadal development, (b) testosterone concentration, and (c) LH concentration in blood plasma of male great tits from Sweden. During the experiment, day length was increased from 10 h 40 min to 13 h 45 min.

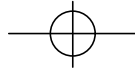


Table 3. ANCOVA of the effect of exposure to branches of birch *Betula pubescens* (treatment) on gonadal development and hormone levels in male great tits from Sweden, correcting for repeated measurements. During the experiment, day length was increased from 10 h 40 min to 13 h 45 min.

	Testes length (mm)		Testosterone (pg/ml)		LH (ng/ml)	
	Z	P	Z	P	Z	P
Treatment	-0.74	0.46	0.65	0.52	-2.36	0.02
Day length	14.98	<0.0001	1.50	0.13	3.03	0.002
Treatment x day length	0.84	0.40	-0.63	0.53	2.52	0.01

veral weeks before the circulating levels of testosterone start to increase.

Among Corsican blue tits there was an unexpected effect of the tree species available in the aviaries, whereby the birds laid *later* when presented with deciduous oak than with evergreen oak. This may be due to captivity related stress. Lambrechts et al. (1999) suggested that the blue tits from Muro were more sensitive to being held in captivity than the Pirio birds. The birds that were given an evergreen tree in the experiment were able to seek cover because these trees had leaves during the entire experiment. The birds with the deciduous branches had no cover at all, especially since the buds were eaten and there was no leaf development. Eventually the birds started to reproduce due to the increasing day lengths, when photoperiod became an overriding cue (Lambrechts & Perret 2000). This could also explain the similar laying dates for the two populations when presented with the deciduous oak: laying dates would then have been triggered by photoperiod only.

Response mechanisms and cues

In general, environmental variables can serve as cues when they have some predictive value for the conditions at the time of selection (in the case of the great tits, the time of highest food demand by the chicks). But in order to serve as a cue these environmental variables should also be apparent at the time the decision (in our case the start of egg laying) has to be taken. So, why did birds not use leaf phenology as a cue in their timing of reproduction? This might be because the bud burst of oaks and laying by great tit have only recently coincided. Van Balen (1973) stated that 'it would be profitable for a great tit to possess a mechanism reacting to the first signs of bud opening ... however, in most years, the mean laying date coincides with the opening of only the earliest trees'. Based on this observation he concluded that it is unlikely that the birds use bud burst as a cue. Van Balen's data are from the late 1950s and 60s. Dates of bud burst and laying have been much more

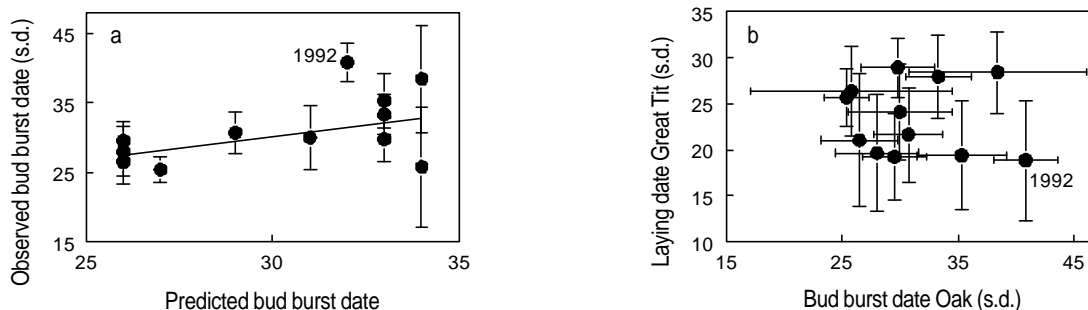


Figure 5. (a) Bud burst date (date on which young leaves protruded partly from the bud (stage = 1) for the crown of the tree) of 103 oaks on the Hoge Veluwe (Netherlands) in 1988–2000 (excluding 1991) versus the predicted date from a descriptive model (Kramer 1994). (b) Mean laying date of first year great tits (number of clutches per year: mean = 52, range = 14–85) against the observed bud burst of oaks (mean of 103 oaks), at the Hoge Veluwe (Netherlands) in 1988–2000 (excluding 1991).



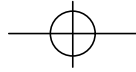
synchronised in recent years (Fig. 5b). This is due to an increase in spring temperatures, which has led to an advancement of bud burst but not of great tit laying date at the Hoge Veluwe (Visser et al. 1998). Thus, although oak bud burst currently seems to be a reliable and available cue, this may not always have been the case. Interestingly, birch bud burst is much less sensitive to spring temperatures and the increase of spring temperatures has been less marked in the north of Europe. It is therefore possible that birch bud burst is, and has been, early enough to be used as a cue by the birds (Slagsvold 1976). Given the significant effect of birch buds on LH levels in male great tits, we cannot exclude the possibility that birch bud burst has some effect on the timing of reproduction in northern populations of great tits.

Many bird species have advanced their laying date due to the increase in spring temperatures over the past 25 years (Crick et al. 1997). In some populations, however, this increase has been absent or insufficient to maintain the synchrony between food availability and the needs of offspring (Visser et al. 1998). This may have caused selection on the response mechanism. It seems however more likely that this will involve a change in the importance of the different cues than in the incorporation of novel cues. In order to estimate how the response mechanisms could respond to selection we need to identify which cues play a role, and estimate the heritability of the response mechanism itself. Investigating the response mechanism is therefore crucial to understanding the limitations of adaptation to large-scale changes in climate and land-use.

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Observation of free-flying nocturnal migrants at Falsterbo: occurrence of reverse flight directions in autumn

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Reverse migration, i.e. movements of birds opposite to the seasonally appropriate flight direction, has been reported from many different sites, for both diurnal and nocturnal migrants, in spring as well as in autumn. We investigated the occurrence of nocturnal flights of migrating birds in reverse directions as observed with an infrared device during the autumn migration season 1998 at Falsterbo, a coastal site in southwest Sweden. The mean proportion of reverse movements of 12 % was similar to that at various other sites in Europe and did not differ from inland observation sites. No night was recorded where birds flew mainly in reverse directions. The two nights with the most intense movements in reverse directions showed multimodal distributions skewed to one side. The proportion of reverse tracks increased with decreasing air pressure, low visibility and high temperature, indicating the approach of a low pressure system. However, in most nights directional distributions were similar to a wrapped normal distribution. Axial distributions were rare. Hence, the small but regularly occurring proportion of birds flying in seasonally inappropriate directions may partly be attributed to a limitation in orientation accuracy of the birds. In addition, reverse movements may be increased by inclement weather, leading either to a general increase in scatter, to skewed or multimodal distributions or, as a special case, to axial distributions.

Key words: autumn bird migration, reverse migration, nocturnal migration, infrared, Sweden.

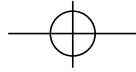
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Flights of birds on migration opposite to the seasonally appropriate direction have puzzled many scientists. Such flights were reported as exceptional events or in response to particular circumstances (e.g. Koch 1934, Lewis 1939, von Haartman 1945, von Haartman et al. 1946) and termed 'reversed migration' (Baird & Nisbet 1960, Rabøl 1969), 'retromigration' (Lewis 1939, Lack & Williamson 1959), or 'retreat migration' (Lindström & Alerstam 1986). Many of these events were explained as retreat from cold or snow in early spring, or reactions of birds with low fat reserves to barriers ahead (e.g. Alerstam 1990). With the increase of radar observations, it became clear that movements in seasonally inappropriate directions were more common

than previously assumed, occurring anywhere along the migratory routes and at any seasonal stage of migration (review in Richardson 1978; directional distributions for various regions in Bruderer 1975, Bruderer & Liechti 1990, Liechti 1993, Liechti & Bruderer 1995, Bruderer & Liechti 1998a,b, Williams et al. 2001, Zehnder et al. in press). Such distributions were in many cases similar to wrapped normal distributions (Batschelet 1981). Some distributions are skewed to one side or even multimodal, often entailing increased scatter into the sector opposite to forward migration. The pattern often implicitly understood as true reverse migration, is a bimodal axial distribution. Axial distributions are mostly found under particular weather con-



ditions (e.g. Alerstam 1990, Bloch et al. 1981) and in front of ecological barriers (Alerstam 1978, Williams 1985, Åkesson 1995, Åkesson et al. 1996), but also frequently in orientation cage experiments (e.g. Sandberg et al. 1988, Able & Able 1995, Åkesson et al. 1995, Bäckman et al. 1997, Thorup 1998).

Visual observations and ringing of day migrating finches in southern Sweden show that reverse migration regularly occurs in this area, and that birds with low fat reserves are engaged in these movements (Lindström & Alerstam 1986, see also Bäckman et al. 1997). Similarly, radar observations on an island in the western Mediterranean Sea showed increasing proportions of reverse migration during the course of the night (Bruderer & Liechti 1998b). Birds returning from the sea at low altitudes and low speeds were interpreted as the result of a declining motivation to migrate according to their normal diurnal schedule of migration and/or declining fat reserves, such that they now preferred to return instead of undertaking a risky sea-crossing over an unknown distance. Analyses of ringing data from Fal-

sterbo have been used to elucidate the widespread occurrence of this behaviour among different types of migrants. Recoveries of birds ringed at Falsterbo resulted in a very high proportion (64 %) of reverse flights within the first 10 days after capture (Åkesson et al. 1996).

In this study we observed nocturnal autumn migratory passage on the Falsterbo Peninsula, Sweden, by means of a passive infrared device. High concentrations of diurnally migrating birds are observed regularly in autumn at Falsterbo (e.g. Rudebeck 1950, Ulfstrand et al. 1974, Karlsson 1993), where the Baltic Sea forms a relatively small but obvious barrier for some migratory birds (e.g. Alerstam 1978, Sandberg et al. 1988, Åkesson et al. 1996, Åkesson & Sandberg 1999). Our aim was to investigate whether the patterns of nocturnal migration at Falsterbo are consistent with any of the three types of reverse movements suggested above: (a) scatter within circular normal distributions, (b) skewed or multimodal distributions, or (c) axial distributions; and to analyse the influence of the weather on the proportion of reverse movements.

Methods

Study site, passive infrared observations and data processing

The study was carried out at a coastal site on the Falsterbo Peninsula in southwest Sweden ($55^{\circ}23' N$, $12^{\circ}50' E$; Fig. 1). The distances of over-sea flights from Falsterbo in the autumn migratory directions are 24–47 km towards southwest before the birds reach Sjælland or Møn (Denmark) and 87 km towards south or southeast to Rügen (Germany).

The study period lasted from 7 August until 28 October 1998 and covered the main passage of autumn nocturnal passerine migration at Falsterbo, which starts in July and continues until November (Karlsson 1993). The observations started one hour before sunset and ended one hour after sunrise, unless prevented by rain.

Bird passage was recorded by a passive infrared device (Long-Range-Infrared System LORIS, IRTV-445L, Inframetrics Massachusetts, USA). The camera was placed in a vertical position on the ground (approx. 5 m above sea level) inside the lighthouse garden surrounded by an open field. The camera detected thermal



Figure 1. Location of the observation site at the Falsterbo peninsula in south-west Sweden. The lines delimit the sectors of forward (FM), and of reverse movements (RM), each of 120° . The square in the overview map (below) marks the limits of the upper map.



radiation differences of ≥ 0.06 °C. Under optimal conditions, songbirds are registered against the cloudless sky up to about 3000 m above ground level. This has been demonstrated through direct comparisons with pencil-beam radar (Bruderer & Liechti 1994, Liechti et al. 1995). The signals were stored on videotapes and later analysed on a monitor. The surveyed space corresponded to a cone with an opening angle of 1.45° . Flight directions were determined according to the clock face method suggested by Lowery and Newman (1955) for the moon-watching technique. This resulted in 24 flight classes of 15° each. Flight altitudes were estimated from the size of the silhouette on the screen. We distinguished seven categories, which were calibrated by comparison with a pencil-beam radar (Liechti et al. 1995); the smaller the silhouette the higher the flight altitude (see Zehnder et al. 2001). According to the number of observed birds per flight altitude and time interval, we calculated migratory intensities expressed as Migration Traffic Rate (MTR). The MTR is defined as the number of birds crossing a line of one kilometre perpendicular to the flight direction during one hour ($\text{birds km}^{-1}\text{h}^{-1}$; adjusted to the metric system from Lowery 1951). Identification of species by this method is not possible.

The overall nightly pattern showed two clear minima of mean MTR, the first near the end of the civil twilight period at dusk and the second near the beginning of civil twilight at dawn. To exclude day migration, which showed a marked increase about one hour before sunrise, we used the twilight phases to define the period of nocturnal migration (Zehnder et al. 2001).

Analyses of weather conditions at Falsterbo are based on weather data collected by the Swedish Meteorological and Hydrological Institute (measurements every 3 hours of surface wind direction and speed, temperature, dew point temperature, altitude of cloud ceiling, degree of cloud cover, air pressure, visibility). Means based on the 21, 00 and 03 UTC (United Time Coordinated) measurements were used for all analyses. Additionally, we calculated 24 hour changes in temperature and air pressure as differences between the measurements at 00 UTC of two consecutive nights. Data for wind speed at higher altitudes were derived from the 23 UTC radiosonde at Kastrup (25 km north of Falsterbo). The European Meteorological Bulletin, published by the German Weather Service (Deutscher Wetterdienst) provided general information about front passages.

Statistics

We used vector addition to calculate the mean track direction a , based on individual flight directions weighted by their contribution to the migratory intensity (Batschelet 1981). The mean vector length r , which ranges from 0 to 1, gives a measure of concentration of the circular distribution. To test for axially distributed track directions, we calculated the mean vector length based on doubled angles, r_2 . If $r_2 > r$ and significantly different from random, the distribution of flight direction was classified as axial. We used the Rayleigh test, based on the original number of birds, to calculate the significance levels of the circular distributions (Batschelet 1981). Circular statistics are according to Batschelet (1981). Statistical analyses (linear regressions, multiple regressions in stepwise forward procedures and chi-square tests) were done with the STATISTICA 5.0 software program (Stat Soft 1995). For the multiple regression analysis we originally included all weather variables from Falsterbo as well as the 24 hour changes in air pressure and temperature. Additionally, we included the tailwind component, which is a measurement of wind support in the basic migratory direction (see further below).

Definition of forward and reverse movements

Migratory directions at a specific site are a mixture of individual directions, reflecting the location of the birds' breeding, resting and wintering grounds. Furthermore, the flight directions are influenced by ecological factors such as large scale and regional topography (e.g. location of stop-over sites or ecological barriers) and shifted to a certain extent according to local topography (e.g. mountain ridges, coast lines), and to weather conditions such as wind and visibility (Bruderer 1997a, b). The observed track distribution may also partially be due to pseudodrift, i.e. populations initiating migration under winds favourable for their preferred direction (Alerstam 1978). Fortunately, at Falsterbo, pseudodrift towards the southeast is usually negligible, because only few birds arrive from the northwest due to the distribution of land and sea. Forward as well as reverse directions may differ from site to site; therefore, we based our definition of normal migration on the locally measured basic direction. This was derived from birds flying on nights with low wind speeds ($v_w \leq 5 \text{ m s}^{-1}$)

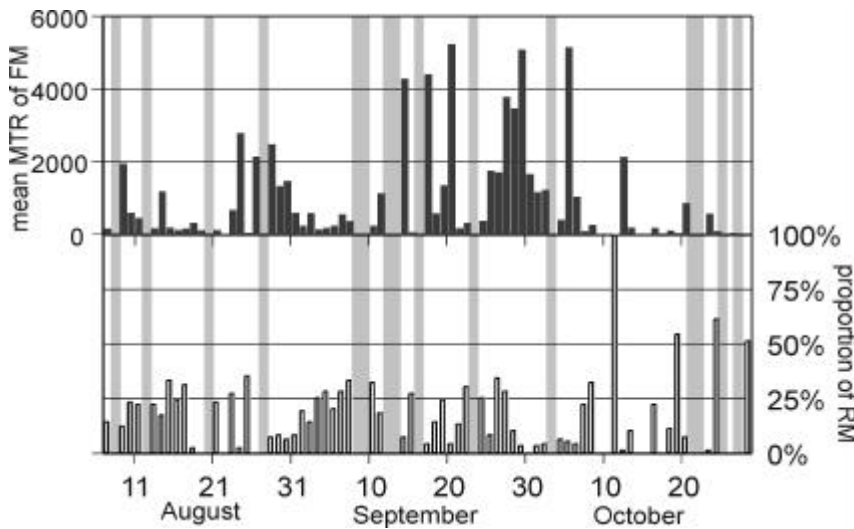
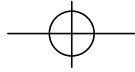


Figure 2. Seasonal pattern of mean Migration Traffic Rate (MTR, birds km⁻¹h⁻¹) in forward directions (FM, filled columns, above) and of the proportion of movements in reverse directions (RM, open columns, below). Nights without observations due to precipitation are marked with grey bars.

where birds can be expected to compensate fully for the relatively small lateral wind drift (Bruderer et al. 1989, Bruderer & Liechti 1990). The 120° sector centred on this basic direction comprised the forward movements (FM), while the 120° sector exactly opposite delimited reverse movements (RM).

In autumn 1998 the basic nocturnal migratory direction at Falsterbo was 225° ($n = 9654$, $r = 0.60$, $P < 0.001$, Rayleigh test; Fig. 1) based on 22 nights with surface wind speeds ≤ 5 m s⁻¹. Hence, the forward sector comprised directions from 165° to 284° and the reverse sector from 345° to 104° (0° = N, 180° = S, clockwise; Fig. 1). According to the determination of flight direction by the infrared method, the FM and RM sectors included eight 15°-classes of flight directions each, while the intermediate 60°-sectors towards SE and NW included four each. The proportions of migration in the reverse, SE and NW sectors are calculated as MTRs of RM divided by the total MTR, and analogously for the SE and NW sectors. For the comparison of FM and RM the proportions of RM were calculated as $RM/(FM + RM)$.

Results

Seasonal and nocturnal pattern

The observation period comprised 51 nights with full coverage (from the end of civil twilight at dusk to the beginning of civil twilight at dawn); 17 nights were

interrupted by precipitation and 15 nights were without observations due to rain (see Appendix 1). In total we observed 17,411 birds in 623.3 hours of observation. The seasonal MTR of the time intervals with observations was 1319 birds km⁻¹h⁻¹ (median 566 birds km⁻¹h⁻¹). A detailed description of the seasonal and daily patterns is given in Zehnder et al. (2001).

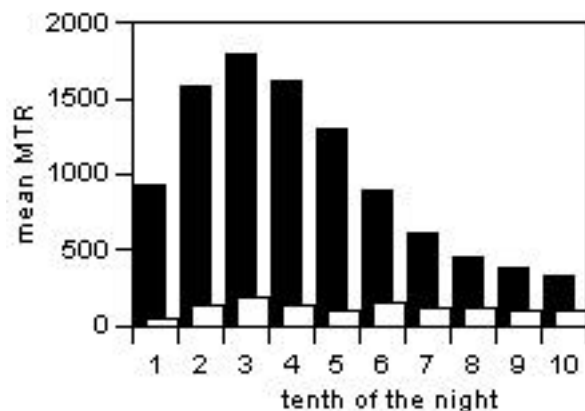


Figure 3. Nocturnal pattern of forward and reverse movements represented as mean Migration Traffic Rate (MTR, birds km⁻¹h⁻¹), as pooled from data collected throughout the entire season. Time intervals of the night are expressed as tenths of the time between the end of the civil twilight period at dusk and the beginning of the civil twilight period at dawn. Filled columns show migratory intensities in forward and open columns in reverse directions.

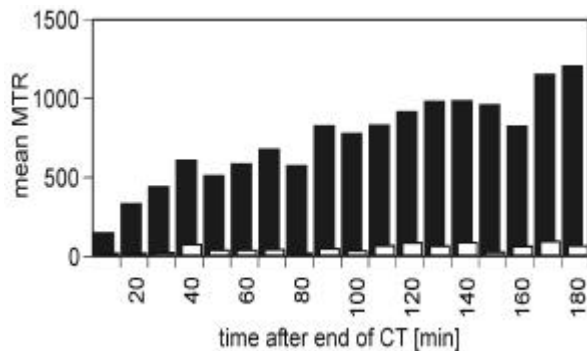
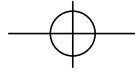


Figure 4. Migratory intensities in 10-min intervals of the first three hours after the end of the civil twilight (CT), i.e. on average 44 minutes after sunset. All data were pooled. Filled columns represent mean Migration Traffic Rate (MTR, birds $\text{km}^{-1}\text{h}^{-1}$) in forward directions and open columns represent mean MTR in reverse directions.

The intensity of forward (FM) and reverse movements (RM) showed large variation from night to night (Fig. 2). Migratory intensity increased during August, reached its peak in September and declined in October. The median MTR of FM was $380 \text{ birds km}^{-1}\text{h}^{-1}$ and that of RM $68 \text{ birds km}^{-1}\text{h}^{-1}$. In absolute numbers, the highest nightly MTRs of RM were observed on the nights of 26 and 27 September with mean values of 871 and $1451 \text{ birds km}^{-1}\text{h}^{-1}$, respectively. The mean proportion of RM, calculated as the mean of the nightly proportions weighted by mean MTR, was 11.7 % (median = 13.3 %; interquartile range = 3.8% – 25.4 %). Since the proportion of RM fluctuated widely due to stochasticity in observations with very low total migration intensities, we excluded nine nights with mean MTR $< 100 \text{ birds km}^{-1}\text{h}^{-1}$ from further linear and multiple regression analyses. There was a significant negative correlation between the proportion of RM and the nightly mean MTR ($n = 59$, $R = -0.38$, $P < 0.003$).

The peak of nocturnal migration occurred in the third tenth of the night (on average 3 h after dusk), for both FM (mean MTR = $1786 \text{ birds km}^{-1}\text{h}^{-1}$) and RM (mean MTR = $196 \text{ birds km}^{-1}\text{h}^{-1}$; Fig. 3). The proportion of RM increased towards the morning (5 % in the first tenth to 24 % in the last tenth).

The MTRs in 10-min intervals of the first three hours after the end of civil twilight at dusk show that RM began as night fell (Fig. 4). After 30 minutes the mean MTR for RM fluctuated around $52 \text{ birds km}^{-1}\text{h}^{-1}$ (6%),

whereas MTR for FM increased steadily during the first 180 minutes from 147 to $1205 \text{ birds km}^{-1}\text{h}^{-1}$. The proportion of RM in the period between 0 and 30 minutes after the end of civil twilight was 3 %, and increased to 6 % between 30 and 180 minutes.

Flight directions

The pooled data of all nocturnal movements showed a mean track direction of $\alpha = 219^\circ$ ($n = 17,411$, $r = 0.62$, $P < 0.001$, Rayleigh-test), very close to the centre of the sector defining forward migration (Fig. 5, cf. Fig. 1). The theoretical von Mises distribution (Batschelet 1981) with $r = 0.62$ implies a frequency of reverse tracks of 7 %. The distribution of flight directions had a clear peak in forward direction, whereas there was no obvious peak in the reverse sector. The percentage of movements in the NW sector correlates positively with the percentage in the reverse sector ($n = 57$, $R^2 = 0.38$, $P = 0.003$, $b = 0.92$; geometric mean regression, Sokal & Rohlf 1981). Therefore, the migratory intensity in the NW sector was approximately twice as large as in the reverse sector considering the sizes of the compared sectors. The percentage of movements SE was about 30 % lower than those towards NW and was not correlated with the proportions of RM. Hence, the distribution of tracks was skewed to the NW.

We calculated a possible orientation accuracy based on the proportion of RM for the take-off phase (0 – 180

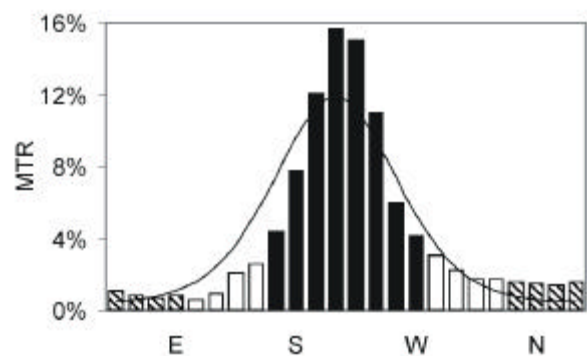


Figure 5. Relative distribution of flight directions of all nocturnal migrants registered. The black columns correspond to directions in the forward sector, the hatched columns to the reverse sector, and white columns to the SE and NW sectors. The line corresponds to a theoretical von Mises distribution (Batschelet 1981) around the mode of 225° with $r = 0.62$.

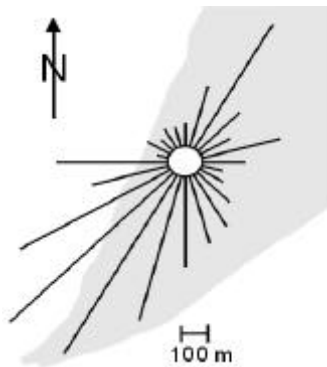
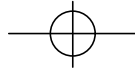


Figure 6. Distribution of flight directions on the six nights with an axial distribution (mean Migration Traffic Rate = $426 \text{ birds km}^{-1}\text{h}^{-1}$; $\alpha_2 = 38^\circ/218^\circ$, $n = 376$, $r_2 = 0.39$, $P = 0.001$, Rayleigh test). Bimodality was indicated by a larger mean vector length r_2 calculated from doubled angles (see Appendix 2). The length of the lines indicates the relative migratory intensity in each 15° sector, the longest towards 210° corresponding to $50 \text{ birds km}^{-1}\text{h}^{-1}$ mean MTR. The shaded area shows the southwestern tip of Falsterbo peninsula.

min after end of civil twilight) under the most favourable migratory conditions, thus including only the five peak migratory nights with more than $4000 \text{ birds km}^{-1}\text{h}^{-1}$ in the FM-sector ($\alpha = 220^\circ$; $n = 2684$; $r = 0.84$; cf. Fig. 2). If we adapt a theoretical von Mises distribution to the 3 % of RM observed in this time interval we obtain a theoretical mean vector length of 0.71.

To test for axial distributions we calculated mean vector lengths per night based on doubled angles (r_2 ; Batschelet 1981). In six nights out of 68 the r_2 value was larger than the unimodal mean vector length r (see Appendix 2). The pooled flight directions of these six nights showed a clear bimodality along the NE–SW axis (Fig. 6). These six nights represent 9 % of the observation time, but only 3 % of the total migratory intensity.

The two exceptional nights of 26/27 and 27/28 September with particularly high mean MTR (2.5 times and 5 times above the mean) and substantial numbers of birds migrating in reverse directions, were not among the six nights with higher r_2 than r values. Both nights presented multimodal distributions, including many flight directions towards the NW and SE (Fig. 7, for circular statistics see Appendix 1).

Weather factors

A multiple regression analysis showed that 36 % of the variability in the proportion of reverse movements can be explained by decreasing air pressure, high temperature and low visibility (Table 1). No other weather components explained a significant proportion of the variation.

On the two exceptional nights with intense migration and a high proportion of RM (Fig. 7), the synoptic surface weather maps showed a very peculiar front movement. While front passages at these latitudes commonly occur from W to E, during 26 and 27 September a front approached steadily from the south. Over the whole period of these two days there was mist (possibly fog) over the Baltic Sea south of Falsterbo and finally it started to rain at 03:15 h on the morning of 28 September (Fig. 7b).

Discussion

The seasonal pattern of nocturnal bird migration observed at Falsterbo showed the typical variations and seasonal trends that have earlier been recorded at other sites in Europe (Bruderer 1971, Baumgartner 1997). The proportion of 12 % reverse migration at Falsterbo is similar to those observed in southern Germany (Nuremberg 10 %), southern Spain (Malaga 10 %) and the

Table 1. Result of a multiple regression analysis relating the proportion of reverse movements to weather variables ($R^2 = 0.36$, $F_{3,55} = 11.75$, $P \ll 0.001$; s.e. of estimate: 10.05).

	B	(s.e.)	t 53	P
Intercept	9.58	(7.13)	1.34	0.184
24-hour change of air pressure	−0.56	(0.17)	−3.33	0.002
Visibility	−0.28	(0.09)	−3.27	0.002
Temperature	1.16	(0.52)	2.19	0.032

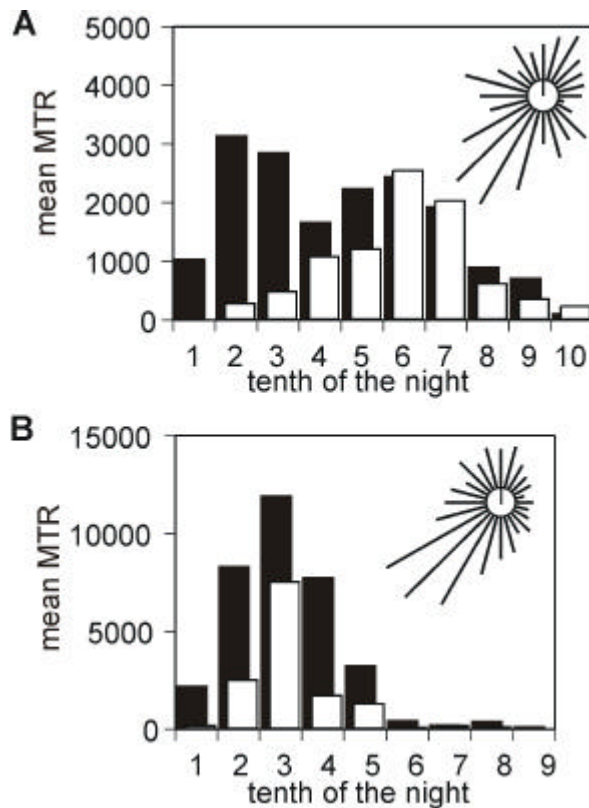
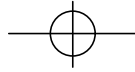


Figure 7. Nocturnal pattern of mean Migration Traffic Rate (MTR, birds $\text{km}^{-1} \text{h}^{-1}$) in tenths of the night and distribution of flight directions based on data of 26/27 September (A) and 27/28 September (B). Filled columns denote migrants observed in the forward direction, open columns denote reverse migration. The insets show the relative distribution of flight directions for the 15° sectors, the longest line in A (210°) representing 345 mean MTR, and in B (225°) 749 mean MTR. Geographic north is indicated within the circles.

Balearic Islands (Mallorca 14 %) (Liechti 1993, Bruderer & Liechti 1998b). Yet Åkesson et al. (1996) found a much higher proportion of reverse migration (64 %) in birds ringed at Falsterbo and recaptured within 10 days. The high proportion of recoveries reported in reverse directions (north to east of Falsterbo) might partly be explained by the higher probability of birds being recovered at short distances in reverse directions (land) compared to the expected migratory direction towards south-west (sea). On the other hand, it is plausible to assume that passerine migrants move away from the coast when grounded (Lindström & Alerstam 1986, Åkesson

et al. 1996). In contrast to grounded individuals trapped and later recaptured to the north, most actively migrating birds seem to continue their migration during large parts of the night in spite of the water ahead (e. g. Bruderer & Liechti 1998b). Åkesson (1999) could demonstrate that many fewer reverse recaptures were observed at an inland site. Therefore, many birds captured at Falsterbo bird observatory return to stopover sites further inland, either to refuel or to wait for better weather conditions (Alerstam 1978, Lindström & Alerstam 1986, Åkesson et al. 1996). Such reverse flights were also observed in a study on visible morning flights at a coastal site in North America (Wiedner et al. 1992). Probably the birds fly further inland some time after sunrise and were therefore not detected by our infrared observations.

The distribution of nocturnal flight directions at our study site, i.e. mean track direction and concentration, is similar to those reported for other places in western Europe and Israel, and is not different from inland sites (Liechti & Bruderer 1995, Bruderer & Liechti 1998b and references therein). Differences between observation sites can be partly explained by the local topography (Liechti 1993). The selection of a flight direction is the result of an adaptive behaviour, but its accuracy is limited. Inappropriate flight directions are possibly due to an omnipresent initial error in orientation as proposed by Kendall (1974) based on his simulation of initial bearings of released birds. Similarly, Mouritsen (1998) introduced a model for clock-and-compass orientation, based on a circular normal-like distribution. He proposed that the mechanism for the selection of the actual flight direction might be based on such a probability function, and that the repeated selection results in a vector summation sufficiently accurate for successful migration. Such a scatter is likely to result in a proportion of birds oriented towards other than seasonally appropriate directions, depending on the individual or species-specific capability for accurate orientation. The scatter of directions of all flights that we observed during the entire season was close to the value calculated by Mouritsen (1998) for a single species based on ringing recoveries ($r = 0.66$). We assume that the observed concentration in orientation behaviour would easily be sufficient to reach the winter quarters successfully. Even under almost optimal circumstances at departure we detected 3 % of tracks in reverse directions.



Alerstam (1978) postulated a temporary retreat as an adaptive behaviour in front of an ecological barrier that would lead to flight directions directly opposite to the initial migratory courses. The axial distribution of flight directions reported by Williams (1985) from an oceanic site is in accordance with this hypothesis. However, axial distributions of flight directions were very rare at Falsterbo. It seems likely that the increase in reverse migration 30 min after the initial take-off of forward migration (Fig. 4) is caused by birds coming in from southern Sjælland (Denmark), which is about the time it takes a small passerine to cross the sea (25 km). These reverse flights cannot be assigned to reverse movements caused by low fat reserves before taking off on flights across an ecological barrier. Furthermore, at an inland site in Israel a small fraction of reverse migration was also detected during all nights of spring and autumn observations (Zehnder et al. in press). Hence, this small but regular proportion of reverse movements may be explained by a limitation in orientation accuracy.

The proportion of reverse migration was low on nights with high migratory intensity. Correspondingly, increasing reverse migration was related to deteriorating weather as indicated by weather variables that are characteristic of an approaching low pressure system. Bad weather conditions are known to increase reverse migration in autumn (Richardson 1978), but also generally increase the directional scatter (Liechti & Bruderer 1986, Åkesson 1994, Åkesson & Bäckman 1999). The increase in the proportion of reverse migration throughout the night indicates that there was also a barrier effect, as more and more birds reaching Falsterbo after several hours flight with probably reduced fat loads returned to land. Åkesson et al. (1996, see also Åkesson 1999) showed that birds with smaller fat loads are more prone to undertake reverse inland flights.

Interestingly, movements to the northwest were relatively more frequent than reverse migration (cf. Fig. 5), but showed a similar temporal pattern as reverse migration. At Falsterbo the distribution of land and water caused the nocturnal migrants to cross the Baltic either towards WSW or NW where the sea crossing is shortest, or to fly northeast back to the Swedish mainland. Possibly the glow of the city of Copenhagen in the NW served as a particular point of attraction (cf. Sandberg et al. 1988).

The unusual situation during the nights of 26/27 and 27/28 September, with a warm front system moving

from south to north, demonstrates the variability in adaptation of flight direction due to deteriorating weather conditions. In recruiting areas north of Falsterbo migrants apparently still found good departure conditions. As they approached the coast at Falsterbo they were flying under a low cloud cover and encountered low visibility and even mist (or fog) over the Baltic Sea. Under those conditions the coast lines of Denmark were no longer visible and the sea became an ecological barrier of undefined width for the migrants en route.

In conclusion, we suggest that the occurrence of reverse migration for free-flying birds migrating above Falsterbo in autumn might partly be related to a natural scatter of orientation and not a response to the ecological barrier alone. The distribution of flight directions very much resembles a wrapped normal distribution. We suggest that adverse weather conditions may either impair orientation accuracy or influence the birds' motivation for forward migration, or both. The time effect is probably associated with the normal diurnal schedule of migratory activity and the influence of the ecological barrier ahead.

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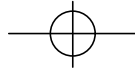
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Appendix 1. Daily means of Migration Traffic Rate (birds $\text{km}^{-1}\text{h}^{-1}$) from nights with observations. Between 7 August and 28 October observations were not possible on 15 nights due to rain. Percentages (in brackets) are given for nights where the observations did not cover the total time interval between civil twilight due to interruptions by precipitation. α is the mean track direction. P gives the significance level according to the Rayleigh test based on the mean vector length r (Batschelet 1981).

Date	N of birds	mean MTR	α	r	P
7.8	40	277	200°	0.45	0.001
9.8	515	2626	224°	0.59	0.001
10.8	176	909	245°	0.48	0.001
11.8	118	669	239°	0.47	0.001
13.8	30	232	231°	0.44	0.01
14.8	259	1835	242° (94%)	0.52	0.001
15.8	47	386	247°	0.33	0.01
16.8	29	191	194°	0.38	0.0
17.8	22	279	212°	0.32	0.104
18.8	41	338	188°	0.90	0.001
19.8	11	121	231°	0.81	0.001
21.8	21	192	175°	0.49	0.01
22.8	12	54	142°	0.94	0.001
23.8	191	1207	218°	0.32	0.001
24.8	926	2943	190°	0.91	0.001
25.8	25	106	137°	0.78	0.001
26.8	611	2280	200°	0.89	0.001
28.8	727	2811	210°	0.76	0.001
29.8	393	1616	216° (97%)	0.68	0.001
30.8	482	1703	212° (99%)	0.74	0.001
31.8	138	724	225°	0.74	0.001
1.9	60	319	245°	0.60	0.001
2.9	115	803	240°	0.62	0.001
3.9	31	244	280°	0.65	0.001
4.9	26	275	271°	0.47	0.01
5.9	68	337	225°	0.50	0.001
6.9	154	840	204°	0.38	0.001
7.9	90	592	212°	0.33	0.001
10.9	33	414	195° (88%)	0.22	0.208
11.9	160	1646	238° (98%)	0.50	0.001
14.9	1112	5163	215°	0.73	0.001
15.9	28	137	154°	0.59	0.001
17.9	1900	4927	201°	0.81	0.001
18.9	152	821	243°	0.60	0.001
19.9	407	2556	239°	0.36	0.001
20.9	1760	5901	221°	0.82	0.001
21.9	37	303	233°	0.39	0.01
22.9	93	589	260°	0.40	0.001
24.9	72	543	238°	0.42	0.001
25.9	297	2196	229°	0.70	0.001
26.9	454	3396	233°	0.25	0.001

Date	N of birds	mean MTR	α	r	P
27.9	775	6618	240° (91%)	0.36	0.001
28.9	621	4901	228°	0.59	0.001
29.9	885	5966	233°	0.79	0.001
30.9	270	1959	241°	0.82	0.001
1.10	175	1395	233°	0.77	0.001
2.10	162	1354	226°	0.84	0.001
4.10	46	461	226° (96%)	0.75	0.001
5.10	965	5938	222°	0.78	0.001
6.10	144	1128	236°	0.83	0.001
7.10	15	126	268°	0.67	0.001
8.10	52	459	246°	0.29	0.01
9.10	1	12	12° (92%)		
10.10	6	63	138° (27%)	0.98	0.001
11.10	6	57	111° (45%)	0.97	0.001
12.10	834	2439	182°	0.90	0.001
13.10	35	317	219° (56%)	0.56	0.001
14.10	8	37	138°	0.96	0.001
15.10	13	70	146°	0.99	0.001
16.10	10	248	262° (33%)	0.65	0.05
17.10	1	6	173° (73%)		
18.10	65	214	156°	0.87	0.001
19.10	9	81	347° (93%)	0.13	0.321
20.10	237	1087	172°	0.83	0.001
23.10	121	616	233° (87%)	0.85	0.001
24.10	17	327	319° (47%)	0.74	0.001
26.10	57	244	141° (93%)	0.97	0.001
28.10	18	89	133°	0.64	0.001

Appendix 2. Circular statistics for the six nights with an axial distribution of flight directions based on doubled angles. α_2 is the mean axis, r_2 the mean vector length and P_2 the significance level according to the Rayleigh test (Batschelet 1981). Bimodality is indicated if $r_2 > r$ (for r see Appendix 1).

Date	α_2	r_2	P_2
6.9	29° / 209°	0.54	0.001
7.9	43° / 223°	0.47	0.001
10.9	33° / 213°	0.27	0.164
24.9	57° / 237°	0.50	0.001
19.10	24° / 204°	0.37	0.300
28.10	160° / 340°	0.65	0.001

