

Spatially explicit, individual-based, behavioural models of the annual cycle of two migratory goose populations

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Summary

1. Behaviour-based models of animal population dynamics provide ecologists with a powerful tool for predicting the response of such populations to both natural and human-induced environmental changes.
2. We developed this approach by addressing two outstanding issues in the application of such models: the need to adopt a large-scale spatially explicit approach, and the need to consider the year-round dynamics of animal populations.
3. Spatially explicit, year-round, behaviour-based models of two populations of arctic-breeding geese, the Svalbard population of the barnacle goose *Branta leucopsis* and the dark-bellied race of the brent goose *Branta bernicla*, were developed. Both populations have been the subject of serious conservation concern and are currently a source of increasing conflict with agricultural interests.
4. There was generally good agreement between empirically derived and model-generated density-dependent functions, and of seasonal patterns of the distribution and movement of populations within and between sites, and of energy reserve levels within a population.
5. Sensitivity analyses, however, highlighted the importance of accurate parameter estimation with respect to the predictions of such models, and the potential flaws in the predictions of existing models that have not adopted a spatially explicit approach when dealing with wide-ranging migratory populations.
6. The effect of the removal of a given area of habitat on both populations was predicted to vary depending upon the spatial configuration of the change. This further emphasizes the need for a spatially explicit approach.
7. Both barnacle goose and brent goose populations were predicted to decline following habitat loss in their winter or spring-staging sites. Simulations suggested that barnacle geese might be less vulnerable to winter habitat loss than brent geese. This reflected the relative strengths of the density-dependence of productivity and winter mortality in the two models and provided a clear illustration of the need for a year-round approach to animal population dynamics.
8. We believe that these models, and this approach to understanding the population dynamics of long-distance migrants, will be beneficial in attempting to answer the increasingly urgent and frequent requests to predict the response of such populations to environmental change.

Key-words: *Branta bernicla*, *Branta leucopsis*, habitat loss, migration, modelling population dynamics.

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Introduction

In recent years there has been an increasing awareness of the threats posed to populations of animals by natural or, more often, human-induced changes to the environment. This has resulted in increasing demands on ecologists to inform management and conservation policy decisions by forecasting the likely response of populations to new circumstances (Caldow & Racey 2000; Ormerod & Watkinson 2000). In this paper we present models of the dynamics of two populations of arctic-breeding geese with a view to making such predictions and simultaneously developing current modelling approaches.

Attempts by biologists to capture the essence of the dynamics of populations have a long history (Verhulst 1838; Pearl & Reed 1920). The concepts of the logistic equation and of carrying capacity are still in use today, even when dealing with populations of free-ranging vertebrates (Bayliss 1989). However, an increasing number of studies have not fitted the expected pattern (reviewed in Varley, Gradwell & Hassell 1973). In addition, May (1975, 1976) showed that the logistic and similar 'simple' models could result in complex population dynamics ranging from monotonic damping through to chaotic behaviour.

Most predictive models used by conservation biologists fall into the category that can be termed population-based (Pettifor, Norris & Rowcliffe 1999). A wide range of model structures have been used, depending on the specific questions addressed and the availability and quality of the data (Duncan 1978; Ginzburg *et al.* 1982; Bayliss 1989; Fogarty, Sissenwine & Cohen 1991; Burgman, Ferson & Akçakaya 1993; Wanless *et al.* 1996; Cowley *et al.* 2000; Gaston *et al.* 2000; Petty *et al.* 2000; Sherratt *et al.* 2000). Development of the Leslie matrix model has been particularly prominent in conservation biology, allowing species- or population-specific models to be written consonant with the ecological detail available for any given study (Houllier & Lebreton 1986; Crouse, Crowder & Caswell 1987; Caswell 1989; Price & Kelly 1994). These matrix models allow spatially explicit modelling of populations, either using a patch-occupancy metapopulation approach (Levins 1969; Hanski 1991; Hanski & Thomas 1994; Hanski & Gilpin 1997) or through a more complex model structure of differential migration within a landscape of varying habitat quality (Lande 1988; Akçakaya, McCarthy & Pearce 1995). The problem with all such models, however, is the robustness of their predictions to novel circumstances.

First, as pointed out by Baillie *et al.* (2000), it is often difficult to obtain the necessary data for demographic correlations, especially density dependence. This is true even of long-term individual-based stu-

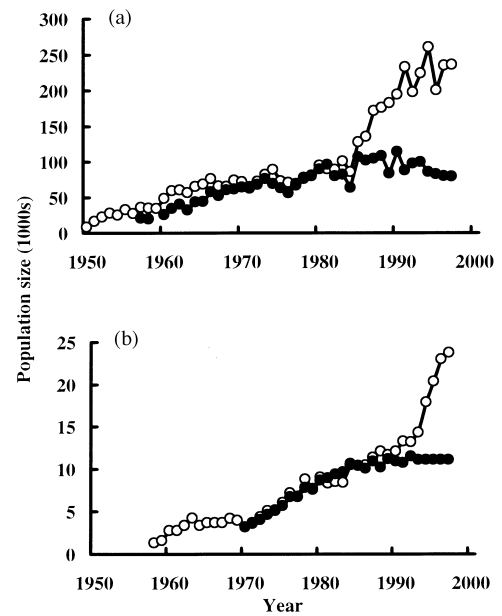


Fig. 1. (a) Annual overwintering population sizes of the Icelandic/Greenlandic pink-footed goose *Anser brachyrhynchus* (Baillon) (○) and the Icelandic greylag goose *A. anser* (L.) (●). There would have been no basis for predicting the rapid divergence of these two populations post-1980 had a 'population-based model' been constructed using the demographic data available for the period 1950–80 (Pettifor, Rowcliffe & Mudge 1997). (b) The observed (○) and predicted (●) growth of the Svalbard barnacle goose population. The pattern of predicted growth is derived from a stochastic matrix model based on analysis of the reproductive success and survival probabilities of known individuals between 1960 and 1990. The subsequent mismatch between the predicted population sizes and those observed is due to a number of factors including (i) undercounting of the population in the late 1980s/early 1990s that resulted in overestimation of the strength of the density-dependent relationships, and (ii) the recent expansion of breeding birds to new colonies (see the discussion in Pettifor *et al.* 1998).

dies (cf. Fig. 1; Pettifor, Norris & Rowcliffe 1999). Secondly, such correlations incorporate an unknown degree of estimation error, and it is therefore difficult or impossible to assess the true level of variability in the population (Bayliss 1989). Thirdly, correlational effects in population size between successive years make parameterization and statistical inferences difficult (Royama 1992). Fourthly, population correlations rarely cover a sufficiently broad range of environmental or population variables, and where these strongly regulate a population such that density is stable over time, then population behaviour at more extreme sizes will rarely be known (Goss-Custard 1993; Goss-Custard *et al.* 1995a). Finally, the necessary assumption, that the conditions under which correlational data were collected will apply to the situation for which predictions are required, is unlikely to apply (Goss-Custard *et al.*

1995a; Pettifor, Norris & Rowcliffe 1999; Fig. 1). Thus, empirical demographic relationships established in the current environment may not apply in the new circumstances for which predictions are required. In their attempt to predict the likely consequences of changes to agricultural habitats for populations of a small passerine bird, Baillie *et al.* (2000) address this issue by generating new density-dependent parameters that might be appropriate under the new circumstances. However, much ecological prediction fails precisely because it is not possible to foresee how these critically important demographic relationships will change under the new circumstances for which predictions are required. For all of these reasons, the utility of 'population-based' models as predictive tools is highly restricted.

Lomnicki (1978, 1980) is credited with first formulating an individual-based approach in order to understand the dynamics of populations. An increasing number of researchers are exploring this approach, see chapters in DeAngelis & Gross (1992). The development of behavioural ecology (Krebs & Davies 1978) provided evolutionary biology with a 'currency' with which to work, namely the maximization of fitness (or some correlated measure such as rate of energy gain), allowing economic optimization paradigms to be adapted as an aid to understanding the behaviour of 'ideal' animals (e.g. optimal foraging; Charnov 1976; Stephens & Krebs 1986). One of the most important paradigms to be adopted as a modelling aid was the concept of evolutionarily stable strategies (Maynard-Smith 1982) and the ideal free and despotic distributions (Fretwell & Lucas 1970). Subsequent developments included state-dependent dynamic models (McNamara & Houston 1986; Mangel & Clark 1988; McNamara & Houston 1996). These make it possible to consider optimal strategies, where a strategy is a rule that specifies how behaviour depends on state.

Such behavioural-based models can potentially avoid the problems discussed above (Pettifor, Norris & Rowcliffe 1999). Goss-Custard *et al.* (1995a,b,c,d,e, 1996a) have made major advances in building and testing models that generate quantitative predictions of a population's response to environmental change from the behaviour of its heterogeneous, but fitness-maximizing, constituents. The original model was individual-based game-theoretic and physiologically structured. Because of these three characteristics, Goss-Custard *et al.* (1995a,b,c,d,e) argued that it was better able to predict the behaviour of populations forced to experience novel circumstances, such as anthropogenic change, than any other approach. Indeed the model has been validated successfully (Goss-Custard *et al.* 1995a,b,c, 1996a,b) and predictions made of local carrying capacity and the population consequences

of the loss of habitat of above or below average quality (Goss-Custard *et al.* 1995a,c,d,e, 1996a,b).

However, being based on the ideal-free theory of animal distribution, the models of Goss-Custard *et al.* (1995a,b,c) have been constrained by their underlying assumptions, namely that all individuals are ideal in their knowledge of the relative suitability of all available patches of resource and, at least potentially, able to occupy any patch at any point in time. These assumptions are valid when a small spatial scale is considered but are violated if the patches of resource are widely scattered relative to the ability of the animals to move between them. Thus, in the model of the response of a population of oystercatchers *Haematopus ostralegus* L. to loss of beds of mussels *Mytilus edulis* L. (Goss-Custard *et al.* 1995a,b,c, 1996b) only a single estuary has in effect been modelled. Yet, the size of a local population on such a site depends heavily on the quality, extent and proximity of alternative habitats as well as the overall number of birds, or the greater population, competing for them (Goss-Custard 1993). The results of Baillie *et al.* (2000) provide another illustration of this point. Moreover, processes that occur at a local and relatively easily studied scale do not necessarily translate directly to larger scales. In migratory birds such as the oystercatcher, for example, predicting the effect of removing habitat in one wintering site on local numbers may provide only limited information about the wider consequences for the whole population (Goss-Custard & Durell 1990; Goss-Custard 1993).

Density-dependent overwinter mortality functions generated by habitat removal from one site can be extrapolated to apply to the whole population. This assumes, however, that the single site on which the model is based is representative of all winter sites within the entire winter range of the population, so that when habitat is removed, whether it be of poor, average or good quality, the loss applies equally to all individuals in the population. In reality, anthropogenic change (e.g. habitat loss) tends to occur at specific times and places, and environmental change (e.g. global warming), although of a more global nature, is likely to have effects of differing magnitude in different places. Accordingly, habitat loss is likely to influence some parts of a global population directly and affect other sections of the population either indirectly or not at all. These considerations suggest that models which seek to predict the response of populations that have large ranges and occupy a number of spatially discrete sites need to be large-scale and spatially explicit.

For sound practical reasons, the aim of many studies of bird populations has been to understand how the local number of birds is determined (Goss-Custard 1993). Due to numerous advantages of studying breeding birds, there has historically been a considerable emphasis on what determines the size

of local breeding populations (Goss-Custard 1993). However, the concepts and questions appropriate at this scale cannot be simply transferred to the study of the greater population of which local breeding and wintering groups are a part (Goss-Custard 1993). There has been a growing understanding that, at the scale of the greater population, the equilibrium population size is determined by the relative strengths of density-dependent functions in both the summer and the winter and by the magnitude of density-independent factors (Horn 1968; Fretwell & Lucas 1970; Williamson 1972; Goss-Custard 1980, 1981; Goss-Custard & Durell 1984, 1990). Goss-Custard *et al.* (1995e, 1996a) carried out a detailed exploration of the dependence of a population's response to habitat loss by varying the density-dependent productivity and mortality functions. Sutherland (1996a) has recently provided an elegant theoretical demonstration of this point. All of these studies highlight the need for the development of behaviour-based models that adopt a year-round approach to the dynamics of animal populations.

Many field studies have illustrated a link between an individual's energy reserves (condition) at the time of breeding and its subsequent reproductive success (Drent & Daan 1980); state-dependent models support these observations and their interpretation (McNamara & Houston 1992, 1996; Rowe, Ludwig & Schluter 1994). In migratory populations, the time and condition at which birds start to breed, and hence their success, may be determined by preceding events in places far removed from the breeding grounds (MacLean 1969). Studies of geese have shown that an individual's body condition measured at the end of spring on the wintering grounds is a good predictor of their probability of breeding successfully on the breeding grounds over 4000 km away (Spaans *et al.* 1993). Thus, the effects of density-dependent competition for food resources on the wintering grounds may only be expressed demographically through reduced breeding success rather than direct overwinter mortality (or alternatively, both may be operative). Such a scenario provides a further argument in support of adopting a year-round approach to the dynamics of animal populations, particularly those of long-distance migrants.

In this paper we develop the behaviour-based modelling approach to deal explicitly with two outstanding issues (Goss-Custard & Durell 1990; Goss-Custard 1993): the need for models that seek to predict the response of migratory populations to environmental change to (i) be large-scale and spatially explicit, and (ii) encompass the complete annual cycle of the population over generations. The work adds to other ornithological conservation studies carried out during the NERC/SERAD special topic reported here (Baillie *et al.* 2000; Paradis *et al.* 2000).

Methods

THE TWO STUDY POPULATIONS

Below, we present large-scale, spatially explicit, year-round models of two populations of long-distance migrants. The first is one of the three geographically distinct populations of barnacle goose *Branta leucopsis* (Bechstein) that breeds on Svalbard, Norway (78°N 15°E) and winters on the Solway estuary in Britain (55°N 3°W). The second is the dark-bellied brent goose *Branta bernicla bernicla* (L.) (hereafter simply referred to as the 'brent goose') that breeds on the Taimyr Peninsula of northern Russia (75°N 100°E) and winters along the coasts of western Europe.

The Svalbard barnacle goose population (hereafter the 'barnacle goose') currently numbers in excess of 23 000 birds (Pettifor *et al.* 1998), having recovered from around 300 in the late 1940s (Owen & Norderhaug 1977). These geese breed predominantly in colonies on cliffs and islands along the western, southern and south-eastern coasts of Svalbard. Although it is physiologically possible for the barnacle geese to make a non-stop flight between Svalbard and their wintering grounds (Butler & Woakes 1998), a variable number of birds stop off on Bear Island (74°N 19°E) and Helgeland (66°N 13°E) on their way to the Solway. The birds begin to arrive on their wintering grounds in late September, with the bulk of the population having arrived by mid-October. During the winter the entire population spends most of its time on grazed pasture fields and salt-marsh (merse) with only occasional forays onto adjoining arable fields. Departure to their spring-staging areas on Helgeland is variable, but generally most birds leave in late-April/early May. The current state of knowledge concerning various aspects of barnacle geese demography, behaviour and conservation status is given in several chapters in Mehlum, Black & Madsen (1998).

Three races of brent goose are recognized (Owen, Atkinson-Willes & Salmon 1986). The dark-bellied race breeds in western Siberia between 85°E and 115°E (Ogilvie 1978). Autumn migration is thought to begin as early as mid-August, with birds reaching the Baltic from mid-September and numbers building up on their wintering grounds from late September onwards. This population overwinters along the western European seaboard between Germany and south-western France, and along the southern and south-eastern coasts of England (Ogilvie 1978; Ebbinge & St Joseph 1992). Brent geese begin their spring migration earlier than barnacle geese, with movements back to continental Europe recorded from February onwards. Over 90% of the entire population congregates on the Wadden Sea (53°N 5°E) in April and May, prior to their return to the high Arctic via the White Sea (65°N 37°E) (Spaans *et al.* 1993). The brent goose is considered the most

maritime of European geese, with eelgrass *Zostera* spp. being one of its traditional staple foods (Ranwell & Downing 1959; Burton 1961; Charman 1979). Because of an increase in hunting mortality and/or a widespread disease-related die-off of *Zostera marina* (L.) in the 1930s, a major decline in the population of brent geese (to c. 16 500) was recorded by the mid-20th century (Ranwell & Downing 1959). However, since then there has been a marked recovery of the population (Van Nugteren 1997). This has been helped considerably by the implementation of hunting bans throughout Europe, and the population is now between 250 000 and 300 000 (Ganter 1998). This increasing population size has been accompanied by an increasing tendency of brent geese to feed on pastures and arable land, resulting in increasing conflict with farmers. The most recent summary of their demography, distribution and status is given in the first draft of the brent goose flyway management plan (Van Nugteren 1997).

Because both populations winter in western Europe, have high latitude late spring-staging areas and breed in the high Arctic, they follow broadly similar annual cycles of movements. In addition, they both have a common social structure, especially in winter, when they feed in large flocks (Teunissen, Spaans & Drent 1985; Black *et al.* 1992). However, a number of fundamental differences between the biology of the two populations, as well as differences in the extent of existing data, meant that it was necessary to construct separate models for each population.

REASONS FOR BUILDING SEPARATE MODELS

There are two principal reasons for building separate models for the two populations. First, although both barnacle geese and brent geese migrate thousands of kilometres between their breeding and wintering grounds they differ considerably in their winter distribution. The barnacle geese occupy a small, localized, winter range, their movements between October and April being restricted almost entirely to the Solway estuary and its immediate surroundings in Scotland and England (Ogilvie 1978). In contrast, the winter range of the brent goose extends from Germany to south-western France (Ogilvie 1978; Ebbsing & St Joseph 1992). Moreover, individual brent geese are known to move routinely within winters between many sites within this range (Ebbsing & St Joseph 1992; Ganter 1998). This large winter range and the regular occurrence of long-distance within-winter movements by individuals suggested that spatially explicit modelling of these movements was essential to capture the within-winter dynamics of the brent goose population. The restricted winter range of the barnacle geese suggested that this aspect of the model devel-

opment was unnecessary for this population. The long-term data resulting from intensive studies on the winter flock dynamics of barnacle geese on the Solway (Black 1998) permitted a more detailed model of the flock structure, behaviour, dynamics and within-site movements of the barnacle goose population compared with the brent goose.

The second major reason for developing separate models for the two populations was the difference in knowledge concerning events outside western Europe. The population of barnacle geese has been the subject of an ongoing, long-term, individual-based study, covering a range of behavioural, demographic, physiological and ecological research across all phases of the annual cycle (Owen *et al.* 1978; Black 1998). The data collected on their high latitude spring-staging sites in Helgeland and on different breeding colonies on Svalbard have enabled us to construct a year-round model. For example, through collaboration with J. Prop and colleagues, and reference to their published work (Gullestad, Owen & Nugent 1984; Black, Deerenberg & Owen 1991; Prop *et al.* 1998; Prop & Black 1998), we have developed a spring-staging model permitting the consequences of changes in the extent and management of the four habitats that the geese utilize on Helgeland to be examined. Similarly, detailed work conducted on the breeding grounds (Prop, van Eerden & Drent 1984; Prop & de Vries 1993; Loonen, Oosterbeek & Drent 1997; Loonen, Tombre & Mehlum 1998) has allowed development of analytic models of the decision rules that determine departure dates and energy reserves of the geese attempting to reach the breeding grounds. These rules are based on expected rewards, namely offspring successfully reared, and future survival probabilities (Lang 2000). In contrast, it was not until the last decade that it was deduced that brent geese must, like barnacle geese, have a high latitude staging site *en route* to their breeding grounds (Ebbsing & Spaans 1995). Moreover, it is only in recent years that expeditions have been made to the Taimyr Peninsula to map the breeding grounds of the brent goose and conduct detailed research into their breeding biology (Ebbsing 1992a; Ganter 1998). This comparative lack of knowledge about brent geese made it unfeasible to construct detailed models of the late spring-staging and breeding phases of their annual cycle. Instead it was necessary to employ empirical relationships derived from observations of brent geese in western Europe in early spring and autumn (Ebbsing 1992a) to encapsulate events outside western Europe.

In spite of these differences, both models are based on the same fundamental principles of modelling the behavioural responses of populations of heterogeneous fitness-maximizing individuals to their environmental and social circumstances. Both are spatially explicit, game-theoretic, behaviour-based

and physiologically structured. The essence of both models is described in the following section.

BASIC MODEL STRUCTURE

A model world is created in which there are a certain number of discrete sites. These may represent a mixture of breeding, staging and wintering sites, or differing geographical areas within each. A model population of birds is created, comprising a number of discrete individuals each with its own unique set of characteristics that influence its success as a forager. Birds forage only on sites. The models use a game-theoretic approach to determine where each bird should choose to forage from among alternatives that are close together. Birds move over long distances between widely separated sites according to simple empirically derived rules. The models follow the foraging and movements of the birds between the sites throughout their annual cycle. When foraging, the rates of food intake of individuals are calculated from empirically derived functions and parameters, and are dependent upon the characteristics of each individual, the characteristics of the site on which it is foraging, and on the number and characteristics of the other competitors present. Birds acquire energy through foraging, assimilating and storing energy from their food intake with empirically derived efficiencies. Birds expend energy while foraging and while moving between sites at empirically derived rates. The balance between rates of energy acquisition and expenditure determine each bird's energy reserves. If intake exceeds expenditure, birds accumulate energy reserves but deplete them if the opposite is the case. The energy reserve of each individual is tracked every day as it feeds on and moves between sites during the annual cycle. The energy reserves of each bird determine its probability of survival and its reproductive success. Individuals die when their energy reserves fall to zero, i.e. their total body mass falls to an empirically derived starvation mass. On the basis of empirically derived functions, individuals achieve greater reproductive success when their energy reserves are large. Thus, the principal independent outputs of both models are the day-to-day distribution of the population across its resources (i.e. flock sizes, use of different habitats and different sites), the food intake rate achieved by the birds and ultimately the resultant body condition of all the individuals in the population. This determines the mortality and reproductive rates of the population and hence influences the population size that can be sustained under whatever environmental circumstances are simulated.

THE BARNACLE GOOSE MODEL

The values of all the parameters used in this model are presented in Appendix 1.

The model population

The population is divided into classes: age, family size, foraging habitat, and a generic vector that allows us to explore various individual behaviours or quality differences (e.g. foraging efficiency) or define different patch types and foraging preferences ('tradition') within a habitat. Age classes run from 1 to 20 years (despite initial ringing in the 1960s, and more intensive ringing from 1970, few birds reach the age of 20, the oldest bird of known age being a male that died aged 22 years; Wildfowl and Wetlands Trust, unpublished data). Family size categories include single birds and pairs with between zero and five goslings. We assume that each family group behaves as a single indivisible unit, and the term 'individual' is used hereafter to indicate families and pairs, as well as singletons. Energy reserve classes are based on the abdominal profile index scale of zero to eight (Owen 1981; Black, Deerenberg & Owen 1991).

In winter and spring, individuals are assigned a unique dominance rank in a linear hierarchy. In winter, dominance is determined by family size, with larger units dominant over smaller ones (Black & Owen 1984, 1987; Black *et al.* 1992). In spring, local linear hierarchies are established on each habitat, dependent on age and whether or not the individual used that habitat in the previous year (Black, Deerenberg & Owen 1991). Dominance ranks are used to determine the feeding conditions achieved, using methods appropriate to each habitat type (see the section Movement within sites).

In both winter and spring, if the daily intake exceeds the daily energetic requirements, the excess is stored. If the intake is below the daily energetic requirement, then stored reserves are used to make up the difference. The physiological process of converting food into fat reserves and vice versa is not fully efficient, and energy added to or removed from storage is therefore reduced by empirically derived factors (Bromley & Jarvis 1993). If the stored reserves fall to zero, the individual dies. The geese also have a maximum daily intake rate determined by their food-processing capacity.

The model world

In winter, we assume that three areas are available (Caerlaverock, 54°59'N 3°32'W; Mersehead, 54°52'N 3°41'W; Rockcliffe, 54°57'N 3°3'W), representing the main foraging areas used by barnacle geese on the Solway Firth (Wildfowl and Wetlands Trust, unpublished data). Within an area, we assume that the available plant biomass is spatially constant. We further assume that travel between areas within the Solway Firth bears no cost. Individuals are free to move to an area only if there is sufficient space to do so, where the area required to

accommodate a given number of geese for a given period is calculated from the empirically derived rate of flock expansion.

The preferred spring habitat of an individual goose is one of four available (see below), which the geese use in a 'traditional' manner. This means that individuals inherit their spring habitat preference from their parents, and this preference is only changed if the energy reserves achieved on departure from the staging grounds in any year fall below a threshold level. Flexibility in spring feeding habitat is seen only in younger birds (Gullestad, Owen & Nugent 1984; Prop *et al.* 1998) and it is therefore assumed that only individuals below an age threshold can change their tradition. Individuals that abandon their traditional habitat are assigned low 'quality' in the subsequent year, but are otherwise high 'quality', and this category is used in the calculation of dominance rank in spring (see below).

The traditional habitats of the geese in spring are small archipelagos in the Helgeland region of Norway. Some of these archipelagos have been managed for livestock while others are unmanaged. Around the rocky shores of all archipelagos is a zone of salt-tolerant *Festuca rubra* (L.) and inland are herb meadows that consist of several herb and some *Poa* species. On the managed islands there are also hay meadows with *F. rubra* and several *Poa* species. The vegetation is sparse on these archipelagos and the geese typically forage in pairs within small, loose flocks (Black, Deerenberg & Owen 1991).

The fields of the agricultural holdings on these inland archipelagos have been reseeded using a predominantly *Phleum* spp. grass mixture and are cut for hay (Black, Deerenberg & Owen 1991). These fields provide a more homogeneous sward than the traditional meadows and the geese forage in flocks of 150–250 birds for most of the day. There are also similar areas of improved meadow on the mainland adjacent to the islands.

Each type of archipelago is modelled separately, with geese free to move within but not between archipelago types within a year. For traditional habitats, the total area of each archipelago type is subdivided by vegetation and each vegetation area is split into many patches of a given area. The shoot density of each patch is drawn from an approximated Poisson distribution and the initial shoot size is taken from a normal distribution.

In both spring and winter, the biomass of each patch is reduced according to the amount of depletion that has occurred, while biomass is increased according to empirically derived relationships describing the influence of temperature and standing biomass on the rate of plant growth (Holmes 1989). Temperature is assumed to be constant during spring staging, but modelled as a sine wave over winter.

Because the geese are diurnal, we use a sine wave to describe the seasonal variation in the daily time available for feeding during the winter. In spring, the length of stay is short and the change in daylight hours thus relatively negligible, and we therefore assume a constant day length for this period.

Movement within sites

Three types of foraging model are used for different habitats – on winter habitats, on agricultural habitats in spring, and on traditional habitats in spring.

Winter habitats. In winter, foraging behaviour is characterized by large flocks of several thousand birds, requiring a specific modelling approach to simulate the distribution and foraging performance of individuals (Rowcliffe, Pettifor & Black 1998). This approach is driven by a combination of depletion, predation risk and competitive exclusion, three fundamental processes that are known to occur, and can be quantified, in barnacle goose flocks. First, depletion means that individuals in the centre or at the back of flocks fare less well than those at the leading edge (Prop & Loonen 1989; Black *et al.* 1992). Secondly, rates of vigilance decrease with increasing flock size (Inglis & Lazarus 1981) and larger flocks are therefore more attractive in terms of the proportion of time that can be spent feeding. Thirdly, dominant individuals are able to displace those less dominant (Black *et al.* 1992; Mulder, Williams & Cooke 1995), and the position of a given individual within a flock can thus be modelled as a despotic distribution. Individuals must therefore decide where to feed on the basis of a trade-off between depletion and time available for feeding.

On this basis, we use a rate-maximizing, game-theoretic process to distribute the population in winter. Each individual in turn assesses the intake rate it could achieve, either in one of the existing flocks or by initiating a new one, processing the entire population in a random order. This process is repeated for the entire population until there is no change in the number and size of flocks. Intake rate is calculated according to empirically derived relationships between feeding parameters, flock size and food availability. We used digitized flock data to map the accumulation of grazing time on the ground for flocks of various sizes. Assuming that individuals maintain their position within flocks over time, we could then describe the distribution of depletion times experienced by all individuals within a flock. From this, we derived a relationship to predict the prior grazing time per unit area experienced by an individual of any given local dominance in a flock of any given size. This relationship is summarized by a skew parameter, which determines the degree of asymmetry in intake rates between individuals in a flock. The biomass encountered by an

individual is given by the initial biomass before the arrival of the flock, reduced by an amount given by the asymptotic functional response integrated over the prior grazing time. The instantaneous intake rate achieved is then given by the functional response for this reduced biomass. Finally, the proportion of time spent feeding is predicted by the size of the flock from an empirically derived capped-linear relationship, and the product of this and the instantaneous intake rate gives the predicted intake for any given flock and patch (for further details see Rowcliffe, Pettifor & Black 1998).

Although individuals choose the patch and flock where they can achieve the highest overall intake rate, they do not necessarily spend all the available time feeding. If the expected daily energy intake exceeds an empirically derived maximum, time spent feeding is reduced to match total intake to this maximum. When this occurs, the flock skew parameter is decreased proportionally to the total reduction in feeding time in the flock in order to reduce the intensity of competition in the flock.

Agricultural habitats in spring. In agricultural habitats on their spring-staging grounds, the flocks are small in comparison to the large winter flocks (no more than a few hundred), presumably reflecting the smaller field size of 0.5 ha or less in Helgeland, compared with about 15 ha in Scotland. Thus, we assume that dominance-related differences in the intake rates of individuals foraging in spring flocks are negligible, and therefore variation in individual intake rates is assumed to be due solely to individual differences in foraging efficiency and the quality of the individual patch the birds arrive on. A simple depletion model is therefore used to predict individual intake rates. The average intake of the population on the habitat is calculated from the average shoot size, and individual intake rates are assigned from a normal distribution around this mean value. The results presented below assume that the intake function and shoot density of *Phleum* meadows are the same as those of *Festuca* meadows.

Traditional archipelagos in spring. The basis of the traditional archipelago model is that a patch of vegetation can be defended by a single pair of geese, and that the geese that are good competitors feed in the patches that provide the highest daily intake. That is, we assume there is a despotic distribution of pairs (Fretwell & Lucas 1970; Sutherland 1996b). Each day the pairs present are allocated to patches in rank order based on intake rate achievable in each.

Movement between sites

Three periods of migration are included: from winter sites to spring, from spring to summer, and from

summer back to winter. Migration assumes an equal loss of fat reserves across all classes, of an amount proportional to the distance flown (Butler & Woakes 1998). The simulations presented here assume that all migration occurs on the same date, which is known not to be the case (Tombre *et al.* 1996). However, our model structure allows for the incorporation of differing departure rules, such that migration may occur over an extended period, with individuals choosing their date of departure on the basis of current energy reserve levels, and an expected optimum date of arrival. An analytic model of departure rules has now been written (Lang 2000), and will be included in future versions of the annual model, but will not be considered further here.

Reproduction

For the summer portion of the annual cycle, the population is treated as class-structured, rather than fully individual-based. Pairs of sufficient age and with sufficient fat reserves may attempt to breed, subject to an upper limit to the number of nest sites available (Prestrud, Black & Owen 1989). When more pairs qualify to breed than the number of nest sites available, the youngest are excluded first. Pairs that are excluded from breeding then fatten independently of breeding pairs (Prop & de Vries 1993). Fattening is density dependent in both groups, with an assumed area available to non-breeders five times larger than that available to breeders. Breeders undergo two periods of fattening, with an intervening period of loss of energy reserves during incubation (Prop, van Eerden & Drent 1984), while non-breeders undergo a single period of fattening. All breeders achieving a threshold level of energy reserves at the onset of incubation are ascribed a brood size drawn from a Poisson distribution (Lang 2000). There is no evidence of density-related variation in brood size in the population as a whole (Pettifor *et al.* 1998), and the mean of this distribution is therefore assumed to be density independent.

THE BRENT GOOSE MODEL

The values of all the parameters used in this model are presented in Appendix 2.

The model population

The foraging behaviour of individual brent geese varies with their age, sex and family size (Teunissen, Spaans & Drent 1985; present study). To capture this variation the model contains a population of discrete individuals, each of which is ascribed to a sex and age (adult, yearling, juvenile) class. In accord with goose biology (Ogilvie 1978), individuals classified as adult males and females are

paired in the model and then individuals classified as juveniles are allocated to pairs to form family units that can contain up to six juveniles. Yearlings are assumed to be unpaired (Ogilvie 1978). The model further assumes that birds in a pair or in a family behave as an indivisible unit that forages together and moves between sites in unison throughout the modelled overwintering period between 15 September and 31 May (Ogilvie 1978). The model also assumes that the day-to-day movements of family units within and between sites serve to maximize the immediate probability of survival of whichever family member has the least energy reserves at that point in time.

Within age and sex classes, individuals in the model also differ in two respects that, in the light of empirical observations (Teunissen, Spaans & Drent 1985; present study), influence their food intake rate: their dominance, i.e. the proportion of non-related birds that they can defeat in competitive encounters; and their efficiency as foragers.

In geese, the dominance of a pair or family is most dependent upon the dominance status of the gander and is positively related to family size. All members of a family share the same dominance status (Raveling 1970; Black & Owen 1989). Accordingly, the dominance scores of non-juvenile individuals are drawn at random from a series of non-overlapping uniform distributions that ensure a continuous hierarchy among unpaired birds from yearling females at the bottom to adult males at the top (Raveling 1970). To mimic the empirically observed positive relationship between dominance and family size, the dominance of individuals in pairs or families is calculated by adding a fixed increment for each additional family member to the basic dominance of the adult male within the family unit. All members of a family unit are given this family score. This results in a hierarchy of 'global' dominance scores that is positively related to family size across the entire range of classes of individuals. The least dominant yearling female has a 'global' dominance score of zero whereas all of the family members of the most dominant gander with a mate and six juveniles have a 'global' dominance score of one. Empirical measurements of dominance scores used to estimate the influence of social status on a bird's intake rate are in effect 'local' to the flocks in which birds choose to forage, i.e. the proportion of hostile encounters with other birds in that flock won by the focal bird. In the model, an individual's 'local' dominance is taken to be the proportion of other non-relatives in a flock that have a lower 'global' score than itself. To accord with the empirically derived equations used to calculate food intake rate it is this 'local' dominance that is used in these calculations (see below).

The current study revealed that a significant proportion of the residual variation in the proportion

of each minute that brent geese spent pecking, which was not accounted for by any characteristics of the individual (age, sex, family size or dominance) or the situation in which it was foraging, could be explained by the ring code of the individual (R. W. G. Caldow, unpublished data). Some individuals spent consistently longer pecking per minute than predicted whereas others showed the opposite tendency. This variation between individuals was used to generate an empirically derived distribution of individual variation in foraging efficiency. Individuals were ascribed a value at random from within this distribution. This was used as a modifier (added or subtracted) to the proportion of each minute spent ingesting food that was calculated from the empirically derived equations (see below) on the basis of the characteristics of the individual, those of the patch and the number and characteristics of other flock members. Thus, within age, sex and family size classes, individuals in the model vary in their dominance and independently in their efficiency as foragers. Thus, the model population contains all of the empirically identified sources of variation between individuals that influence their intake rate.

The model world

Number, location and size of sites and patches. At its simplest, the western European wintering range of brent geese can be characterized as 10 discrete areas, e.g. the south coast of England, or the south-western Delta area of the Netherlands (Ebbinge & St Joseph 1992). Thus, the model contains 10 sites each of which represents one of the principal wintering regions of the brent goose population. For simplicity, these sites are assumed to lie in a straight line, equidistant from one another. The distance between sites approximates the average distance between neighbouring real-world wintering areas.

Unlike most other species of geese, brent geese make extensive use of both intertidal and supra-tidal food resources (Ogilvie 1978). Thus, the model assumes that each site contains two patches on which the birds feed. One of these represents intertidal food resources, e.g. beds of *Zostera* spp., and the other represents terrestrial resources, e.g. managed grasslands. Given the difficulty in estimating the areas of intertidal and particularly of terrestrial habitats that are used, or could be used, by brent geese, the areas of the patches in the model are rather speculative. The area of intertidal *Zostera* spp. beds and terrestrial habitat that supported the population of c. 1500 brent geese on the Exe estuary, England, between 1995 and 1998 was measured accurately (R. W. G. Caldow, unpublished data). These areas were then extrapolated to yield estimates for the total area of habitat that would support the entire world population of brent geese (c.

250 000) (Ganter 1998). This total area was then divided between the 10 sites on the assumption that all wintering sites are of the same area with the exception of the one corresponding to the early spring-staging areas in the Wadden Sea. Because the Wadden Sea supports virtually the entire population in spring (St Joseph 1982) it is assumed that patches on this site are 10 times larger than in the other wintering sites.

Food resources. A review of the literature revealed a measurement of the mean daily proportionate (i.e. biomass dependent) rate of non-grazing loss of live biomass of *Zostera* spp. between September and February (Percival, Sutherland & Evans 1996). Wyer & Waters (1975) noted that *Zostera* spp. begin to grow in March and April and reach the maximum daily growth rate in June/July. For simplicity, therefore, the model assumes a sine wave of productivity throughout the year with *c.* 180 days of net gain and *c.* 180 days of net loss of live biomass, the maximum rate of growth being achieved on 1 June. The maximum and minimum biomass-dependent daily rates of growth were derived in order to generate the observed mean daily rate of non-grazing loss observed between September and February by Percival, Sutherland & Evans (1996). Using this productivity function, the biomass density on intertidal patches on the first day of each year (15 September) was calculated in order to yield the biomass density of live material recorded in mid-October on the Exe estuary in 1995 (R. W. G. Caldow, unpublished data).

A review of the literature also yielded a regression equation describing the productivity of grassland swards between January and March as a function of a constant rate of productivity and temperature and biomass-dependent components (Sutherland & Allport 1994). In view of this, the model assumes that the biomass-dependent (i.e. proportionate) component of productivity is constant throughout the year, the annual cycle in productivity of grass swards being driven by the temperature-dependent component and an annual cycle in mean daily temperature that follows a sine wave with the maximum on 1 July. With this fixed cycle of daily temperature, the initial biomass density of live material on the terrestrial patches on 15 September was calculated so as to generate the value recorded on the Exe estuary in mid-October 1996 (R. W. G. Caldow, unpublished data). For each patch type, the model assumes a constant starting biomass density across all 10 sites.

Values for the digestibility and energy content of *Zostera* spp. (Wyer & Waters 1975; Charman 1979; Drent, Ebbinge & Weijand 1980; Percival & Evans 1997) and of *Lolium perenne* (L.)/*Poa* spp. (Ebbinge, Canters & Drent 1975; Wyer & Waters 1975; Drent, Ebbinge & Weijand 1980) were derived from the lit-

erature. In the case of *Zostera* spp. both of these parameters were assumed, in the light of the empirical data, to vary cyclically throughout the year on the basis of a sine wave, with the maximum digestibility and energy content being attained on 1 June and the minimum, due to natural senescence of the vegetation in the autumn and early winter, being reached on 1 December.

Foraging within sites

The way in which the foraging decisions made by individual brent geese are modelled is similar to the methods described by Goss-Custard *et al.* (1995b,c). As in the single-site model of Goss-Custard *et al.* (1995a,b,c, 1996a), the model assumes that within a site there are no travel costs associated with moving between patches. Individuals choose in an iterative game-theoretical and ideal-free way where to feed every day from among the patches on their current site.

Each day, the model calculates the daily energy acquisition of each bird if it were to feed for the entire time available on each of the patches on its current site. This depends upon two factors, the amount of time for which each patch is available per day and the instantaneous intake that can be achieved when a patch is available.

The time for which intertidal patches are available to geese in the model varies on a daily basis according to a 14-day tidal cycle, being greater on neap tides than on spring tides. The proportion of the total daily availability that occurs during daylight and darkness varies through the year as a consequence of the annual cycle of day length. The availability of non-tidal terrestrial patches is also determined by the annual day length cycle. It is assumed that brent geese do not feed on terrestrial patches at night (Summers & Critchley 1990; R. W. G. Caldow, personal observation).

Calculation of the instantaneous intake rate of each bird on each patch is achieved using empirical regression models derived from analysis of the foraging behaviour of individually ringed brent geese on the beds of *Zostera* spp. and on the managed grasslands of the Exe estuary. The empirical observations were made in such a way as to allow separate analyses of each of the component parts of birds' instantaneous intake rates (mg dry mass ingested per minute active in a foraging habitat). This allowed the varying influence of various independent variables that characterized the birds themselves and the patch in which they foraged on each component of intake rate to be evaluated (see Appendix 2). The putative instantaneous intake rate achieved by each individual in each patch was calculated by multiplication of the empirically derived bite size, ingestion rate and proportion of each minute spent attempting

to ingest food (modified by its own particular foraging efficiency; see above).

The model assumes that if an individual can meet its daily energy expenditure (see below) on both patches on its current site, it should act as a time-minimizer and forage on the patch where it attains the greatest instantaneous intake rate. This is subject to the condition that when instantaneous intake rates differ between the two patches by less than 3% they will choose at random between them due to a limited discriminatory power (Goss-Custard *et al.* 1995b). If an individual can only meet its daily energy expenditure on one patch, or on neither, the model assumes that it should act as an energy maximizer. In this case it will forage on the patch where it can attain the greatest total daily energy intake, even if this requires feeding for a large proportion of the day at a lower instantaneous rate than is achievable on the other patch.

The main point of this decision-making process is that the choices made by one competing individual as to where to feed are contingent upon those made by all the others. Accordingly, the model attempts to find the stable distribution of foraging birds between patches by carrying out an iterative procedure (three iterations were used because the model did not stabilize any more with further iterations), processing birds in a different random order during each iteration. The model calculates the final daily intake rate of each bird each day once each has chosen a patch on the third successive iteration.

At the end of each day, the total biomass eaten by all the birds on each patch is summed and removed, resulting in grazing-induced depletion of the resources on a day-to-day basis. This, in combination with the non-grazing induced daily change in biomass density, calculated as described above, results in day-to-day variation in the biomass density on each patch throughout the annual cycle.

Energetics. To calculate the daily energy expenditure of each individual the model assumes that each bird is active and inactive for 12 h per day. Basal metabolic rate (BMR) while active is calculated from equation 5.5 of Kendeigh, Dol'nik & Gavrillov (1977), whereas when inactive the BMR has an additional thermoregulatory component. This component increases by a constant amount per degree Celsius that the daily temperature is below the lower critical temperature of brent geese. The latter is derived from equation 5.12 of Kendeigh, Dol'nik & Gavrillov (1977) and the increment in expenditure per degree below this value is calculated from equation 5.9 of Kendeigh, Dol'nik & Gavrillov (1977). The model assumes that the daily energy expenditure of a free-ranging goose is twice that calculated in this way (Drent, Ebbinge & Weijand 1980).

Individuals that acquire more energy than they require to match their maintenance expenditure,

convert the excess into energy reserves with an empirically derived efficiency and increase in mass by an amount that depends upon the empirically derived energy density of the reserves. Storage of energy reserves is constrained by two limits, a maximum rate of daily mass increase, derived from the rate of fattening achieved by brent geese in early spring, and an upper limit to total body mass. For birds in the 'facultative' migratory state (see below) this upper target mass is constant throughout the winter and based on empirical data. For birds fattening in an 'obligate' migratory state this target mass is determined by the amount of energy reserves required to fuel their next migratory flight (see below). If either of these two limits constrains a bird's daily storage of energy reserves, it will not feed for all the time that is available to it. In contrast, a bird that cannot meet its maintenance requirements from its daily energy intake will feed for all the time available to it and then mobilize its existing reserves to make up the shortfall. The empirically derived efficiency with which such reserves are mobilized, and their energy density, determine the amount of mass that such birds will lose each day. Birds die when they run out of reserves and their body mass reaches an empirically derived starvation mass.

Movements between sites

The decision rules that are used in this model to control the movements of birds between sites are based on an extensive review of the numerous studies that have addressed the relative importance of endogenous and exogenous factors in controlling bird migration (Berthold 1993). On the basis of empirical information the model assumes that, throughout the autumn, winter and spring, birds can be in one of two migratory states; 'obligate' or 'facultative' (Terrill 1986).

Because brent geese, like most other birds, often use the same wintering, staging and breeding sites each year (Ganter 1998), it is assumed that when on autumn and spring migration each bird has a specific goal site to which it is trying to return. During the autumn, this goal is taken to be one of the 10 wintering sites. During a preliminary series of iterations in each run of the model, each individual is allowed to choose, in an ideal-free game-theoretical way, the best place to forage from amongst all 20 of the available winter foraging patches. The location of each individual at the end of this iterative procedure is taken to be its chosen goal. The model also records the identity of each of the patches on which each individual chooses to forage at the end of each of the preceding iterations. This information serves as a memory of available options to which an individual can try to move during the main model run in the face of unfavourable conditions occurring on its

chosen goal. All individuals within a family unit are assumed to have the same goal and the same knowledge of alternative sites.

The model begins on 15 September with all birds on a notional eleventh site, 2300 km distant from the 'northern' end of the chain of wintering sites. This distance corresponds to that between the White Sea and the Wadden Sea (Ebbinge & Spaans 1995). At this stage all individuals are in the so-called 'obligate' migratory phase (Terrill 1986) because they have not yet reached their wintering goal. While in this state, it is assumed that birds will leave a site only when they have accumulated sufficient energy reserves to enable them to fly to their target, which at this initial stage is assumed, for all geese, to be the nearest wintering site. To avoid the need to model birds' foraging behaviour at this high latitude site, of which comparatively little is known as yet, their initial masses are set so as to enable them to depart immediately for western Europe (see below). On arrival on the 'northernmost' wintering site some individuals reach their goal and switch to the so-called 'facultative' migratory state for the remainder of the winter (Terrill 1986). In this state individuals will only leave a site if conditions become unfavourable for themselves or one of their family members. Empirical studies indicate that animals faced with unfavourable conditions which cause them to lose mass often exhibit pronounced changes in their behaviour only once their reserves reach some lower critical threshold (Piersma & Poot 1993). Accordingly, individuals that gradually lose mass during the winter leave their chosen goal site (and any subsequent site that they visit) only once their reserves reach an empirically derived threshold value (Hulscher 1989, 1990; Piersma & Poot 1993). At this point, all members of a family unit will try to fly to the nearest alternative site of which they have predetermined knowledge. Birds can make such 'facultative' moves between sites throughout the winter as often as necessary but may eventually run out of reserves *en route* between sites and die.

Birds that do not reach their wintering goal on arrival at the 'northernmost' wintering site remain in the 'obligate' state. In this state they will forage until they have accumulated sufficient energy reserves to enable them to fly directly to this goal. They will only leave their current site once they and all their family members have reached this condition. This threshold proportion of body mass, which must consist of expendable energy reserves before individuals in the 'obligate' migratory state can move to their next target, is determined on the basis of the distance between the sites involved and the energetic cost of flight. The latter is calculated following the theory of flight mechanics synthesized in Pennycuick (1989). These calculations require the input of a value for the wing span of a brent goose and a variety of other parameters presented in

Appendix 2, all of which have been ascribed standard values derived from Pennycuick's theory.

The onset of the migratory disposition in birds is believed to be controlled largely by 'a fundamental endogenous system – the circannual rhythms – which operates as an internal "calendar" by initiating and concluding migratory events in conjunction with such synchronizing factors as photoperiod' (Berthold 1984, 1993). To mimic this, the onset of spring migration in the model is constrained until 31 March. At this point, birds switch back from the 'facultative' mode to the 'obligate' mode and begin their preparations to fly to the 'northernmost' site within the wintering region where they stage in preparation for migration to the White Sea, 2300 km distant (Ebbinge & Spaans 1995). This serves to simulate the congregation of the entire brent goose population in the Wadden Sea in spring (St Joseph 1982; Ebbinge & St Joseph 1992). Once again, individuals in the 'obligate' state will leave their current site only when they and their family members have accumulated sufficient reserves to do so. Once birds have reached the 'northernmost' site, they feed in an attempt to accumulate sufficient reserves to enable them to fly the required distance. Once all individuals within a family unit achieve this condition they leave western Europe, and are no longer considered in the day-to-day phase of the model. The day-to-day phase of the model ends on 31 May.

The breeding season

In general, the breeding success of brent geese has been cyclical over the last 40 years. Having bred well in one year, they have subsequently failed completely and then bred with variable and unpredictable success in the next year before breeding well once again in the year after that (Summers & Underhill 1987, 1990; Ebbinge 1989, 1990). In successful years there is a close relationship between the average body mass of females at spring departure from the Wadden Sea and the subsequent breeding success of the population, expressed as the percentage of juveniles in the autumn population (Spaans *et al.* 1993; Ebbinge & Spaans 1995). The model calculates the average mass of all potentially breeding females (surviving adults and yearlings that will recruit to the adult age class) on the last day of the run. To do so, it uses the current mass of individuals still fattening on the 'northernmost' wintering site and the mass at departure from this site for those individuals that have already departed. The model then uses the empirical relationship (see Appendix 2) to determine the potential breeding success of the population from the average body mass of these females in each year. The cycle of breeding success in brent geese is modelled by setting the percentage of juveniles in successive years to be 100%, 0% and then a random percentage of the calculated percentage.

Resightings of colour ringed brent geese over the last 25 years have yielded good estimates of the average annual survival rate of brent geese (Ebbinge 1992b). B. Ebbinge (personal communication) considered that, in the absence of winter hunting, most of the annual mortality of adult brent geese occurs during the breeding season in Siberia and during the lengthy spring and autumn migration between Siberia and the western European wintering grounds, i.e. outwith the overwintering period considered in the model. Accordingly, the model applies a density-independent oversummer mortality to the numbers of each age and sex class at the end of each spring to yield the numbers of each that return in the autumn. The number of surviving juveniles determines the number of yearlings in the subsequent autumn, while surviving yearlings recruit to the adult population. These new numbers, and the predicted percentage of juveniles in the population in the following autumn, are used to calculate the numbers of juveniles that will be present in the next model year. It is assumed that juveniles are born with an equal sex ratio.

MODEL INPUTS, OUTPUTS AND VALIDATION

As described above, and detailed in Appendices 1 and 2, both models were parameterized with the best empirical estimates available, either established from our own fieldwork, or from the literature. As a result of this procedure both models contain empirically derived demographic functions, namely a density-independent oversummer mortality in the brent goose model and an empirically derived upper limit to the number of available nest sites in the barnacle goose model. The inclusion of these functions does not, however, compromise the validation of the models' key outputs. The former has no influence on the two principal outputs of the brent goose model presented here, namely the density-dependence of the starvation-driven overwinter mortality rate and the mass-dependent reproductive rate. The latter has no influence on one of the three principal outputs of the barnacle goose model presented here, namely the density-dependence of the starvation-driven annual mortality rate. Moreover, it is not the sole determinant of the other two outputs of the barnacle goose model, namely the breeding ratio and number of young produced per adult, both of which are also driven at least partly by the birds' masses, which are generated independently by the individual-based model.

No attempt was made to alter any parameter value in order to improve the fit between model predictions of the density-dependence of the key demographic parameters and those patterns currently observed. The first prediction that we make and test is that both models, parameterized to simulate cur-

rent circumstances, generate density-dependent demographic functions that closely match those observed under given circumstances. However, it might be that, by virtue of their complexity, our models reproduce these key functions but do so for the wrong reasons. We examine this possibility by predicting that the models should generate a number of observed seasonal patterns in the way in which geese distribute themselves across their resources and accumulate energy reserves, both crucial determinants of the masses that they achieve and hence their survival and reproductive success. We test these predictions by comparing our models' outputs with independent empirical data.

Discrepancies between model predictions and observations provide a stimulus to investigate further the reasons underlying any lack of congruence. However, a reasonable match between model-generated output and observations should inspire confidence that any match between predicted and observed demographic functions is more likely to be for the right rather than the wrong reasons. Such validation is essential to provide a measure of confidence in the predictions made by such models when, as we illustrate here, they are used to simulate completely novel scenarios.

Results

MODEL VALIDATION

Test of main outputs: the shape of density-dependent functions

A critical test of a model whose purpose is to generate quantitative predictions of population size under novel circumstances is whether it can reproduce faithfully the observed density-dependence of the key demographic functions under current circumstances.

Between 1960 and 1990 there was a roughly four-fold increase in the population of barnacle geese, together with a decline in *per capita* productivity (Pettifor *et al.* 1998). This drop in productivity occurred largely in the first phase of the population increase, with both the number of young produced per adult and the breeding ratio declining from about 0.4 to 0.15. In contrast, the annual survival rate has remained roughly constant at around 0.9. Comparing these observed patterns with those predicted by the model, for populations up to and including the current population size, i.e. where the proportional change in population size is < 1 in Fig. 2a, suggests a reasonably close match.

In the case of the brent goose, there is no statistical evidence for density-dependent effects on either reproductive success or adult mortality at current population levels (Summers & Underhill 1991), and virtually all adult mortality that does occur is outside of the wintering period (B. Ebbinge, personal

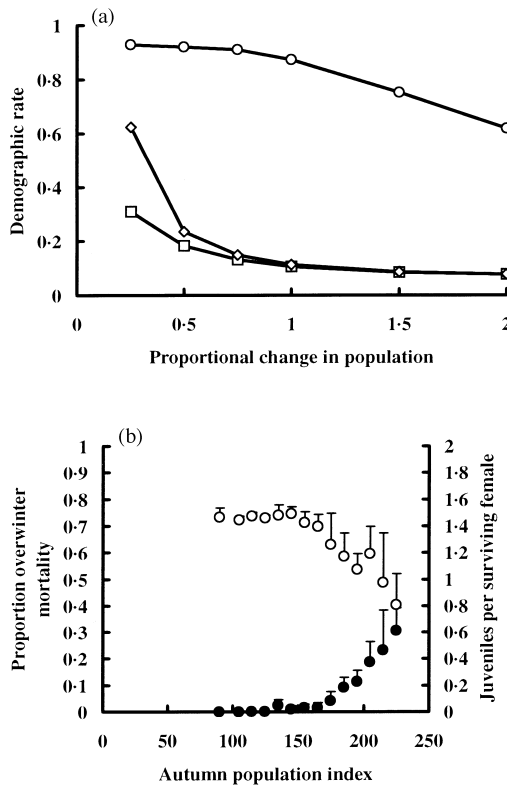


Fig. 2. Density-dependent survival and productivity functions generated by models of (a) barnacle geese and (b) brent geese. (a) The survival rate (○), breeding ratio (□) and productivity rate (◇) as the initial population is varied. A value of 1 on the x-axis corresponds to the population size that equates with the current estimate of the Svalbard barnacle goose population. (b) The proportion of the autumn brent goose population dying overwinter (●) and the productivity (juveniles/surviving female) in summer (○) as a function of the preceding autumn population index. A value of 100 corresponds to the current estimate of the brent goose population. Five replicate runs each of 30 years duration were conducted. Each point depicts the average mortality/productivity (+2 SE) across years grouped by the starting autumn population size.

communication). In accord with these empirical observations, the brent goose model does not predict any overwinter mortality until the autumn population index is well in excess of current population densities (Fig. 2b). The model also predicts no density-dependent reduction in reproductive success until approximately the same autumn population index is reached (Fig. 2b).

All of these density-dependent demographic functions generated by the two models are shaped either entirely or partly by the mass-dependent starvation and reproduction of model birds. Because the mass of individual birds is generated independently by the models, on the basis of their rates of energy intake and expenditure, these comparisons between model-generated and observed demographic functions provide a valid test of the models' principal outputs.

Tests of component predictions

While it is encouraging that the models' outputs matched observed demographic functions well, they may, due to their complexity, have done so for the wrong reasons. Confidence in the validity of these key tests can be improved by a further series of comparisons between model-generated predictions of the way in which geese distribute themselves across their resources and their rates of energy acquisition, and independent empirical data.

Patterns of resource acquisition. A key test of the models is whether they can simulate the observed temporal patterns of fat deposition accurately, because the critical determinant of the output of the whole model process is the rate of energy gain or loss experienced by individuals, which in turn determines their survival probabilities and reproductive output. Predicted energetic gain or loss can be tested against empirically determined measures of the abdominal profile index of individuals in the population collected in the field, because this correlates well with the mass of fat reserves in geese (Owen 1981). Statistical analyses of empirical observations of abdominal profile indices, using generalized additive models, show an increase in reserve levels in autumn, a mid-winter levelling-off or actual decline (dependent on the reproductive class of bird, i.e. its dominance), and a rapid increase from late-winter until departure (Owen, Wells & Black 1992; R. A. Pettifor & J. M. Black, unpublished data). This pattern is reproduced well by the barnacle goose model (Fig. 3), although predicted values tend to over-

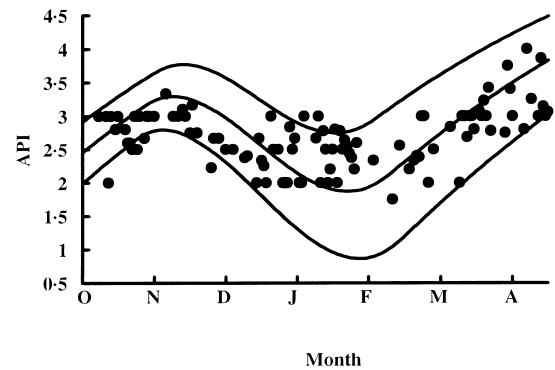


Fig. 3. Seasonal changes in the observed (points) and predicted (lines) abdominal profile index (API) of barnacle geese. The observed data represent APIs collected in the 1997/98 winter season ($n = 588$, with each point representing between 1 and 16 individuals with the same API on the same day). The upper, middle and lower lines depict the seasonal change in the predicted population maximum, median and minimum API. Monthly mean observed and predicted values were significantly correlated ($r^2 = 0.7$, $n = 7$, $P < 0.05$), with slope and intercept parameters not significantly different from the line of equality (slope = 1, $P > 0.1$, intercept = 0, $P > 0.2$).

emphasize the mid-winter decline in condition. Figure 3 also demonstrates the outcome of competition, whereby less dominant individuals suffer a more pronounced loss of reserves that is initiated earlier in the season than amongst dominants, and from which the subsequent recovery in late winter and early spring is later and less complete.

Barnacle geese on their spring-staging grounds in Helgeland acquire fat reserves extremely rapidly, with an increase of between two and four abdominal profile index (API) points during their brief stay on the staging areas (R. A. Pettifor & J. M. Black, unpublished data), and this rate of fattening is closely matched by the model. Empirical data show that on the traditional sites, individuals feeding in managed areas achieve higher energetic intake rates than those on unmanaged areas. The performance of individuals on agricultural areas is higher still (Prop & Black 1998; Prop *et al.* 1998). In the model, the pattern of relative performance of individuals feeding in these various areas is dependent not only upon the initial quality assigned to the areas, but also upon the way in which the model predicts the population, and hence the intensity of competition and depletion is distributed across the areas. The observed pattern of relative performance generated by the model matches that observed (Fig. 4).

Patterns of within-winter population distribution: flock-sizes. A further test of whether the models capture the essence of the way in which geese utilize their resources is to compare observed and predicted flock sizes. In barnacle geese, the predicted flock sizes in early winter are generally between 500 and 5000, becoming smaller as the season progresses. This matches well the observed flock sizes in winter

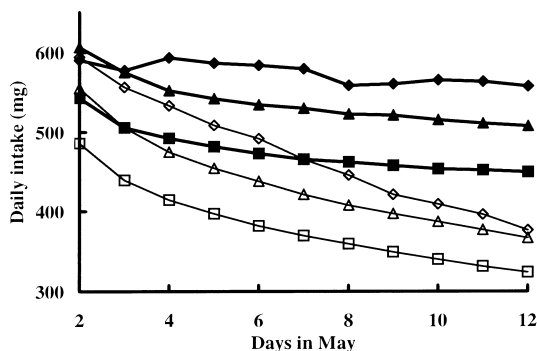


Fig. 4. Predicted daily intake rates (mg) of barnacle geese feeding, over a 10-day period, on the different alternative habitats (◆, ◇ agricultural areas; ▲, △ managed areas; ■, □ unmanaged areas) utilized during their brief stay on the spring-staging grounds in Helgeland. Solid symbols depict intake rates when the population size is small whereas open symbols depict intake rates when the population size is large.

[median (interquartile range) in early and mid-winter, respectively, 800 (500–2250) and 600 (317–1213); J. M. Rowcliffe & R. A. Pettifor, unpublished data].

Patterns of within-winter population distribution: movements between habitats within sites. Systematic counts of brent geese on and around the Exe estuary in two successive winters revealed a pronounced switch in their usage of the two principal alternative habitats, namely intertidal and terrestrial. Initially the entire population fed on intertidal beds of *Zostera* spp. (Fig. 5). In November, however, this habitat was largely abandoned as the population began to feed on pastures and other managed grasslands surrounding the estuary (Fig. 5). The brent goose model also generated this habitat switch, and its predicted timing coincides closely with that observed (Fig. 5).

Patterns of within-winter population distribution: movements between sites. Regular censuses of the proportion of juvenile brent geese within the population on the Exe estuary in both 1996–97 and 1997–98 revealed a distinctive seasonal pattern (Fig. 6). Early arrivals contained no juveniles at all, and not until the second half of November and the first half of December did the proportion of juveniles within the local population level off. Between early and mid-February the proportion of juveniles increased markedly again in both years. With the exception of the increase in early spring, the brent goose model faithfully reproduces this seasonal pattern (Fig. 6).

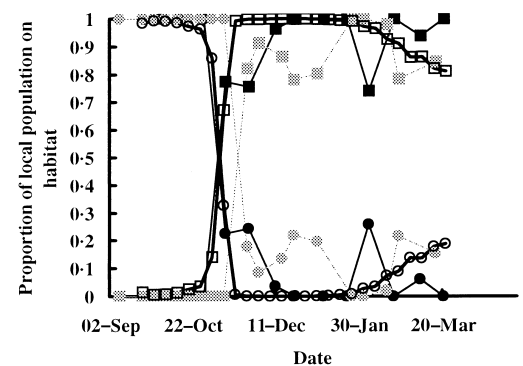


Fig. 5. The observed and predicted distribution of a local population of brent geese between two alternative wintering habitats. Circles depict the seasonal change in the proportion of the population on intertidal beds of *Zostera* spp. whereas squares depict the seasonal change in the proportion on pastures. Solid symbols represent the observed distribution on the Exe estuary in 1995–96 (pale) and 1996–97 (dark). The corresponding open symbols are weekly averages predicted by the model over a run of 30 consecutive years.

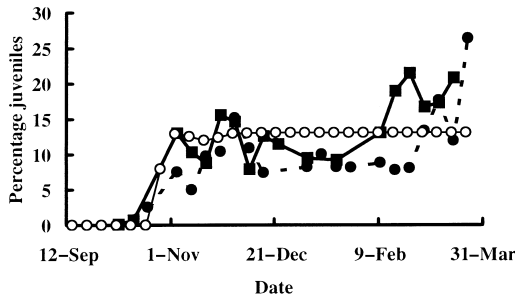


Fig. 6. The observed and predicted proportion of a local population of brent geese comprising juvenile birds. Solid symbols represent the observed data from the Exe estuary in 1996–97 (■) and 1997–98 (●). Each point is a weighted weekly average. Open circles depict the weekly averages predicted by the model, averaged only over those years ($n = 6$) within a 30-year run in which breeding success of the model population was between 5% and 20% juveniles and hence similar to that observed on the Exe estuary in 1996–97 and 1997–98.

SENSITIVITY TO MODEL PARAMETERS

The proportional change in equilibrium population size caused by fixed proportional increases or decreases in single model parameters was used to assess the sensitivity of the predictions of the models to the values of the parameter estimates. Figure 7 shows that, in the barnacle goose, the initial biomass has relatively little effect on the equilibrium population size, but that variation in intake rates and the energy content of the food has major implications. The latter two parameters show asymmetric effects; low intake rates and energy density [metabolizable energy (kJ) per gram biomass] result in large reductions in equilibrium population size, whereas increases in these two parameters have relatively little effect. Furthermore, this pattern was evident for both spring and winter in the case of energy density of the vegetation, but was relatively weak for intake rate in the spring. Further single factor sensitivity analyses for spring parameters (in this case using final reserves at the end of the staging period as the measure of sensitivity) showed the model to be sensitive primarily to parameter values for the time available in a day for feeding, the proportion of time spent on vigilance, and daily energetic expenditure.

For the brent goose, we examined the sensitivity of the model to various parameters involved in the calculation of intake rates, namely: bite sizes, peck rates and the proportion of each minute spent feeding. Analysis of empirical data gathered on the Exe yielded estimates of the average bite sizes achieved by brent geese feeding on grassland of 4.75 mg dry mass peck⁻¹. When brent geese feed on *Zostera* spp. it is not possible to discern individual bites. However, the amount of time that birds spend with their

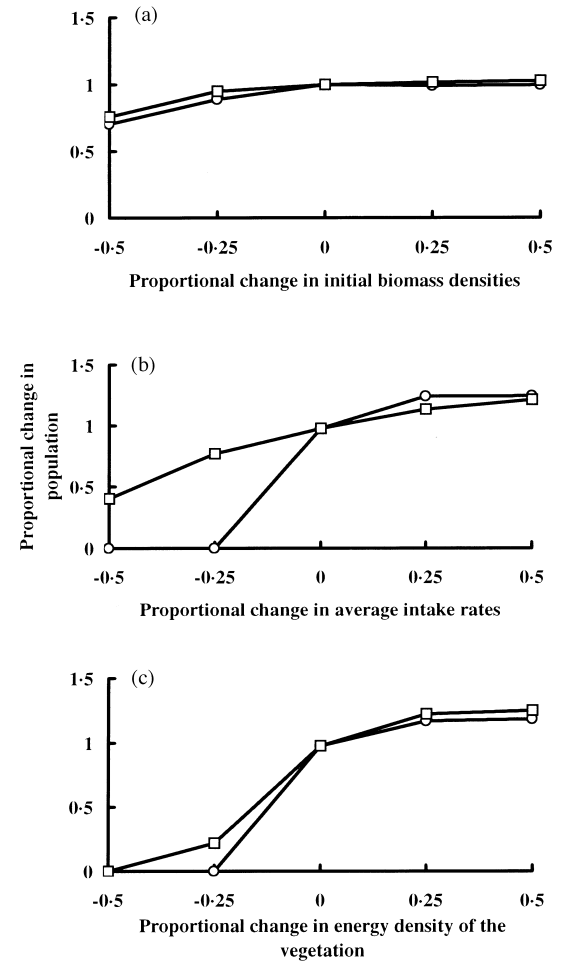


Fig. 7. The sensitivity of the predicted equilibrium population size of barnacle geese to variation in (a) initial biomass densities, (b) average intake rates and (c) energy density of the vegetation, in either winter (○) or in spring (□). Predicted autumn population sizes are expressed as a proportion of that under default conditions (i.e. no change to parameter value).

bill in contact with the vegetation can be measured easily. The average ‘bite’ size when feeding on *Zostera* spp. was, thus, estimated as 10.28 mg dry mass second⁻¹ with the bill in contact with the vegetation.

In neither habitat did the estimated bite sizes of brent geese vary with the biomass density of live vegetation on which the birds were feeding. Thus, combining our data with other empirical studies (Rowcliffe 1994) we fitted negative exponential relationships between bite sizes in the two habitats and biomass density. Increasing the asymptotic bite sizes in the two habitats by 25% or even 50% over the default values has virtually no effect on the average autumn population that can be sustained (Fig. 8a). A reduction of 25% in the asymptotic bite sizes had a similarly negligible effect. However, a decrease by a further 10% resulted in extinction of the population (Fig. 8a).

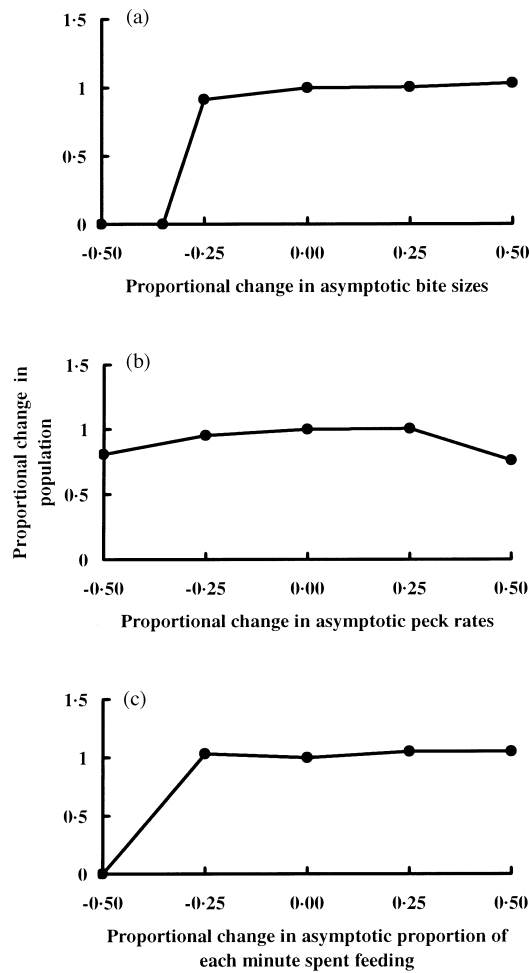


Fig. 8. The sensitivity of the predicted autumn population size of brent geese to variation in asymptotic (a) bite sizes, (b) peck rates and (c) proportion of each minute spent feeding. Predicted autumn population sizes are expressed as a proportion of that under default conditions (i.e. no change to parameter value). Each point is an average derived from the autumn populations over the last 15 years of a 30-year run.

The peck rate of brent geese feeding on grassland declined with increasing biomass density to reach a stable lower asymptote across the majority of the range of biomass densities (R. W. G. Caldow, unpublished data). Increasing or decreasing this value by 25% had virtually no effect on the average size of the autumn population (Fig. 8b). However, both an increase and a decrease of 50% in peck rates (Fig. 8b) produced a reduction in the average population. Reduction of the asymptotic peck rates by 50% did not cause population extinction.

When feeding on *Zostera* spp. during the first 6 weeks after arrival on the Exe estuary, the proportion of each minute spent by geese with their head below their shoulder in a feeding posture showed a negative exponential relationship with biomass density (R. W. G. Caldow, unpublished data). When

feeding on grassland during the remaining 16 weeks of the winter the proportion of each minute spent by geese with their head below their shoulder showed a negative exponential relationship with date (R. W. G. Caldow, unpublished data). The response of the population to variation in these asymptotic values was very similar to that shown to variation in bite sizes (Fig. 8c). Although a 25% reduction in the asymptotic proportion of each minute spent feeding had no effect on the population, a 50% reduction resulted in its extinction.

SENSITIVITY TO MODEL ASSUMPTIONS

One of the key assumptions of our models is that prediction of the dynamics of wide-ranging long-distance migrant populations like the brent goose depends upon modelling long-distance between-site movements by individuals faced with unfavourable conditions. The sensitivity of the model output to this assumption was tested by comparison of outputs under this assumption and under the alternative assumption that such movements are not possible.

The average autumn population of the brent goose was reduced by over 40% when birds were not able to move between sites. This difference arises because of changes to the shape of the density-dependent overwinter mortality function (Fig. 9a). The average density of competitors at which overwinter mortality was first observed, decreased when winter mobility was prevented. Indeed, winter mortality then occurred at population indices below that which corresponds to the current size of the brent goose population. Under the default assumption that birds can move between sites in winter, the model predicted a density-dependent reduction in the breeding success of the surviving females (Fig. 9b). The prevention of within-winter movements, by increasing overwinter mortality, tended to reduce the strength of this density-dependence (Fig. 9b).

PREDICTING THE EFFECTS OF HABITAT CHANGE

Application of the model

The models that we have developed are capable of simulating an almost limitless number of potential scenarios to mimic habitat changes that might occur due to natural or human-induced changes at either the global or at a very local scale. A number of such scenarios and the circumstances in which they might arise are presented in Table 1. Here, however, we present only a few example outputs. These illustrate both the necessity of adopting a large-scale spatially explicit and year-round approach to predicting the effects of habitat change on wide-ranging migratory

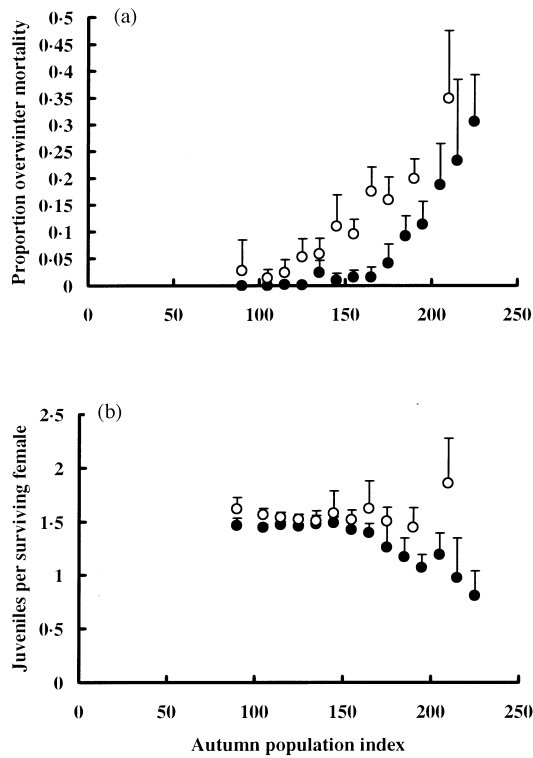


Fig. 9. Density-dependent (a) overwinter mortality and (b) productivity of brent geese when they are allowed to move between winter sites (●) and when they are not allowed to do so (○). In the latter case, the assumption that birds will not move to alternative sites in an attempt to survive was introduced simply by setting the threshold of reserves at which model birds opt to leave their current site to zero. Five replicate runs each of 30 years duration were conducted for both scenarios. Each point depicts the average mortality/productivity (+2 SE) across years grouped by the starting autumn population size. A value of 100 on the x-axis corresponds to the current estimate of the brent goose population.

populations, and the ability of the models to address applied management questions.

Variation in the spatial configuration of habitat loss

The predicted responses of the goose populations to various forms of habitat loss are illustrated in Figs 10 and 11. In the brent goose model we explored the effect of removing a fixed area of winter habitat, either by the removal of an identical area from every patch on every winter site or by the removal of entire sites. Up to five entire sites were removed sequentially starting either (i) with the one furthest from the site in which the population congregates in spring or (ii) with the one closest to that site. Removal of habitat equally from all wintering sites resulted in a virtually proportionate reduction in the average autumn population. In contrast the sequential loss of distant sites resulted in a subproportional reduction in the population. However, the sequential loss of the sites closest to the early spring-staging site always led to a supra-proportional reduction in the average autumn population that could be supported. The response of this population to winter habitat loss clearly depends upon the precise spatial configuration of the habitat removal (Fig. 10a).

We also explored the effect of habitat loss in the barnacle goose, removing a proportion of the habitat from either winter or spring areas and examining the resultant equilibrium population size (Fig. 10b). In both cases, and for any amount of habitat loss, the effect is subproportional, that is, for any given proportion of habitat lost, a smaller proportion of the equilibrium population is lost. The effect of removing a given proportion of the spring habitat is less severe than the equivalent loss in winter (Fig. 10b).

An example of a more explicitly applied nature is presented in Fig. 11. Here we show the predicted effect that changed socio-political or economic circumstances in Helgeland, resulting in the loss of one of the four spring habitats used by the barnacle geese, would have on the population. In all cases, changes to agricultural practices are predicted to

Table 1. List of some of the potential habitat change scenarios to which models could predict the population response

Habitat change	Causative agent
Global changes	
Removal of intertidal patches of <i>Zostera</i> spp.	Recurrence of <i>Zostera</i> spp. wasting disease
Reduced availability of intertidal habitats	Sea-level rise
Altered areas of managed grasslands	Changes to Common Agricultural Policy
Altered timing of vegetative growth	Climate change
Loss of specific habitat (e.g. currently managed pasture reverting to rough grassland when grazing livestock removed)	Socio-economic factors
Local changes	
Removal of intertidal habitats	Reclamation, development, tidal barrages
Reduced area of managed grassland	Local development
Increased area of managed grassland	Creation of reserves
Increased nutritive quality of grassland	Fertilization of pasture

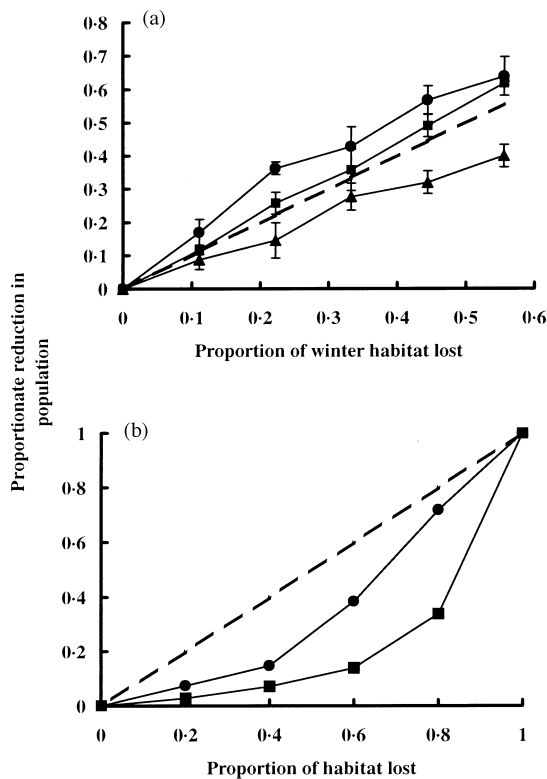


Fig. 10. The proportionate reduction in the equilibrium population of (a) brent geese and (b) barnacle geese, following the removal of habitat. (a) The effect of removal of winter habitat from all sites equally (■) is compared with the effect of the removal of consecutive sites most distant from the early spring-staging grounds (▲) and the removal of consecutive sites closest to the early spring-staging sites (●). Each point is derived from the average autumn populations over the last 15 years of five 30-year runs and shows the mean proportionate reduction in the population (± 2 SE). (b) The effects of removing habitat from only the wintering sites (●) or spring-staging sites (■). The dashed line is the line of proportionality in both plots.

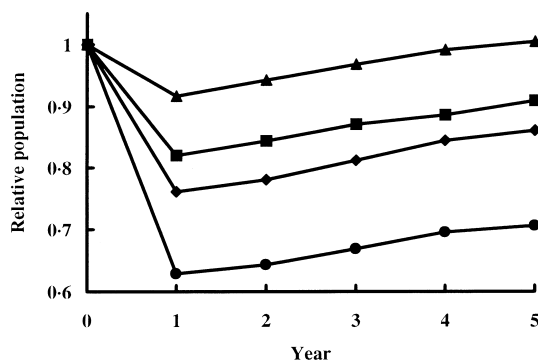


Fig. 11. The predicted population trajectory of the Svalbard barnacle goose population over 5 years following removal of each of the four alternative spring-staging habitats; managed traditional (◆), unmanaged traditional (■), agricultural island (▲), and agricultural mainland (●).

lead to an immediate decline in the population, because individuals that formally fed in the affected habitat find their traditional resource missing. This is, in all cases, followed by a gradual recovery of the population, in some scenarios to a size close to or even above the original size, as the birds redistribute themselves between the remaining habitats. The magnitude of the immediate population crash and the population's ability to recover is predicted to vary depending upon precisely which habitat is affected. The removal of agricultural islands would seem likely to be the least threatening habitat change for the barnacle goose population. The population is predicted to be most severely affected if the agricultural mainland is no longer available, because this provides the only alternative to the limited area of islands if conditions on the islands deteriorate.

Discussion

MODEL STRUCTURE

A frequent criticism of models that attempt to incorporate the biological complexity of real organisms is that their resultant intricate structure and the interactions between parameters makes their interpretation all but impossible. From the outset of this project, we consciously developed our annual model in such a manner that: (i) it was extremely flexible in terms of the detail that needed to be provided, for example the age vector could be either interval (0, 1, 2 ... 20) or categorical (juvenile, subadult, adult); (ii) it was composed of a number of submodels, allowing these to be explored on their own or within the annual model iterated over generations but with all other model parameters held constant; and (iii) decision rules could be entered into the model – some of these might be physiological or behavioural constraints based on empirical data (e.g. gut-processing time, or only younger birds being able to switch habitats on Helgeland) or could be based on optimality criteria (e.g. decision rules governing the trade-off between fat reserves, time of departure and reproductive success and survival). Tightening or relaxing these 'rules' provides an insight into the significance of empirically determined constraints and the validity of the assumptions behind our optimality criteria.

Another aspect of our approach that needs stressing at this stage is the unique role that our models can play in determining which areas of field research need more attention. For example, our winter flock models in the barnacle goose, even prior to incorporation into the annual model, clearly sign-posted the need for us to collect more detailed information on the role that quality of forage plays in the intake rates of geese as opposed to simple energetic gain. Both the brent and the barnacle goose models high-

lighted the requirement to obtain detailed measures of bite size in these geese (see Discussion below). Similarly, more detail is required on the breeding grounds. Even for the barnacle goose, where there is a history of intensive fieldwork at the breeding colonies, there is an urgent need to understand the formation of new breeding colonies and their subsequent contribution to the demography and dynamics of the population. The list could be continued. However, it is hoped that our results, and the discussion below, indicate the uniqueness of our modelling approach to understanding population processes through the formulation of our models on sound evolutionary principles, and also the utility of our approach in the management of populations.

MODEL VALIDATION

Density-dependent functions

In common with many population models, the predictions of a population's response to habitat change generated by the model of Baillie *et al.* (2000) are dependent upon the specification of the empirically derived density-dependence of key demographic parameters, e.g. over-winter survival. In contrast, one of the most powerful tests of a behaviour-based model that aims to predict density-dependent functions under novel circumstances is its ability to generate such functions in close agreement to ones that have been derived empirically. That behaviour-based models of the type presented here can do so has been illustrated successfully in the case of a model of oystercatchers foraging on beds of mussels (Durell *et al.* 2000; Stillman *et al.* 2000). The model for the barnacle goose presented here also predicts demographic trends that match the observed historical patterns of density dependence well (Pettifor *et al.* 1998). Reducing the model population from current levels was predicted to result in an accelerating increase in productivity. This arose partly because the empirically derived upper limit to the number of nest sites resulted in a higher proportion of the population gaining access to a breeding site, but also because the model predicted that those which attempted to breed were, due to reduced competition, in better condition. In contrast, the model predicted that survival would increase only marginally as population size declined. This qualitative pattern matches that recorded for the population once hunting and disturbance had been banned or minimized (Owen & Norderhaug 1977; Owen 1984; Pettifor *et al.* 1998). Overall, the good fit of the model-generated functions to observed data gives us some confidence that the underlying mechanisms are accurately represented in the model.

The lack of any significant overwinter mortality in brent geese reduces this model test to the more simple question of whether or not the model pre-

dicts any overwinter mortality at all. The fact that the model does not do so, at least until the index of autumn population density is in excess of that which corresponds to current densities, is at least encouraging. Similarly the model correctly predicts that up to current population sizes there is no density-dependent effect apparent in brent goose reproductive success (Summers & Underhill 1991). Nonetheless, the model predicts that, at sufficiently large population sizes, overwinter mortality will become density-dependent and reproductive success will decline as a consequence of increased competition for resources in spring and a consequent reduction in female body condition.

Population distribution within and between sites, energy intake rates and reserve levels

Our observations of habitat switching by brent geese on the Exe estuary are consistent with the findings of many other studies (Charman 1979; Tubbs & Tubbs 1982; Summers & Critchley 1990; Vickery *et al.* 1995). Thus, the simulated within-site movements between habitats are consistent with the behaviour of brent geese. At the larger spatial scale of movements throughout Europe, it is well established that the first birds to arrive in western Europe in autumn are generally failed or non-breeders, with families containing birds of the year arriving sometime later (Summers *et al.* 1996; Ganter 1998). Summers *et al.* (1996) also showed that the proportion of juvenile geese in Norfolk increased in early spring because juveniles lagged behind the rest of the population in their move back to the Netherlands. Our observations on the Exe were consistent with these established patterns and the model was successful in generating the observed pattern, at least until early spring. Given the rather inconclusive evidence of the brent goose model's ability to generate realistic density-dependent functions, it is encouraging that both tests of the model's ability to mimic the observed patterns of movements of brent geese within and between sites proved largely successful.

In the barnacle goose winter foraging model, the population splits into flocks because individuals must make a trade-off between the increasing depletion experienced in large flocks and the increasing necessity for vigilance in small flocks. In mid-winter, depletion with little regrowth leads to lower food availability, and because the functional response is asymptotic, the relative importance of depletion within flocks increases, resulting in smaller predicted flock sizes. In contrast, renewed growth in the spring allows partial recovery of the food stock, leading to a small up-turn in predicted flock size. This predicted seasonal pattern matches the observed data well, and the range of predicted flock sizes is also close to that observed. The good fit between the predicted and observed seasonal trends in fat loads of

barnacle geese under current conditions provides further confidence in the structure of our models of winter foraging.

All of these component predictions relating to how populations of geese distribute themselves in space and time and acquire resources are generated independently by the models, and arise from the choices made by the optimizing individuals as to where and when to feed. Because these foraging choices determine the body condition of individuals which in turn drives, either entirely or at least in part, the density-dependent demographic functions generated by the models, the generally good fit between the component predictions generated by the models and independently observed empirical data is encouraging. While this by no means rules out a case of 'the right result for the wrong reason', the validations carried out so far certainly support further investigation of the models' properties and implications.

SENSITIVITY ANALYSES

Sensitivity to parameter estimates

The crux of both of our models lies in the calculation of the energy intake rates achieved by foraging individuals and the variation in individual performance within the population. This requires empirical measurements of many parameters, all of which are in themselves subject to error in their measurement. Our results indicate that in some cases a 25–50% reduction in a parameter value (e.g. the energy density of the vegetation in winter or the bite sizes) was sufficient to cause population extinction. R. Van der Wal (personal communication) noted that estimates of the bite sizes taken by captive brent geese can vary by up to twofold. Our sensitivity analyses make clear the impact that such errors could have on model predictions. However, an iterative procedure of validating model outputs against independent empirical data, such as we have illustrated, and the refinement of the estimates of crucial parameters, identified by means of sensitivity analyses, represents a productive route to the construction of progressively more powerful predictive models.

Sensitivity to model assumptions

The ideal free theory of the distribution of competitors in a patchy environment (Fretwell & Lucas 1970; Fretwell 1972) makes two key assumptions: (i) that individuals have perfect knowledge about resource profitabilities, and (ii) that travel costs between patches have a negligible effect on the distribution of organisms (Kennedy & Gray 1993). Models developed to predict the response of animal populations to habitat loss based on this theory (Goss-Custard *et al.* 1995a,b,c, 1996a) have, to

satisfy these assumptions, effectively ignored any spatial component and adopted a single-site approach. Sutherland & Dolman (1994) developed a model of a long-distance migratory population in which the costs of migration from breeding grounds to wintering grounds were considered. However, even this model did not allow for the fact that individuals may move between alternative winter sites in response to habitat change. The cold-weather movements of birds in winter provide many examples of such plasticity in individual behaviour in response to, albeit temporary, habitat loss (Townshend 1982; Hulscher, Exo & Clark 1996). Models that do not allow such emigration during adverse circumstances effectively assume that the costs of travelling between sites are infinite, so that continued residency is always the optimal strategy no matter how unfavourable the local conditions become.

Our comparison of the output of the brent goose model when birds either were or were not allowed to move between sites highlights the difference that this assumption makes to the predictions of the model. This leads to the conclusion, that can also be drawn from many of the other papers in this volume (e.g. Baillie *et al.* 2000; Sherratt *et al.* 2000), namely that dispersal movements whether over small or large spatial scales, are of fundamental importance to population dynamics in a heterogeneous landscape. When birds are denied the possibility of moving over long distances between alternative sites, the density-dependent overwinter mortality curve is markedly altered. This is in accord with the results of Turner *et al.* (1993). The same is also true of the density-dependent productivity function. This suggests that predictions of the response of a population to environmental change derived from models based on the assumption that residency is always the optimal strategy may either be seriously in error or else fortuitously correct only because of the interplay between density-dependent functions in different seasons.

THE NEED FOR A YEAR-ROUND SPATIALLY EXPLICIT APPROACH

Many models have already illustrated that the effect of habitat loss on a population depends on the quality of the habitat removed (Sutherland & Dolman 1994; Goss-Custard *et al.* 1996a,b). Our model of barnacle geese also demonstrates this. In this case, in accord with empirical observations (Gullestad, Owen & Nugent 1984; Black, Deerenberg & Owen 1991), the scope for individual movement between alternative spring habitats is limited. Therefore, the differential effect of the loss of different spring-staging habitats arises purely as a result of differential profitability between the habitats (Prop *et al.* 1998; Prop & Black 1998). Hay meadows and agricultural pastures are the most profitable habitats, and loss of

the agricultural mainland, composed entirely of pastures, thus has the greatest effect on the population. Managed traditional islands hold hay meadows, but also less profitable *Festuca* and herb swards, and the loss of these areas has a less severe effect. Unmanaged traditional islands hold only herb and *Festuca* swards, giving a lower overall profitability, and accordingly a lower impact of habitat loss. The low impact of losing agricultural islands, despite their high profitability per unit area, can be explained by the relatively small total area of this habitat type (see also Lang *et al.* 1998).

Our models also illustrate that the response of a global population to habitat change depends crucially on the precise spatial configuration of such changes. Although removal of winter habitat from all sites equally resulted in a proportional reduction in the size of the population of brent geese, this was not the case if the same area of habitat was removed by the loss of entire sites. Sub- or supra-proportional responses were elicited depending on which sites were affected. The most probable explanation for these differences lies in the effects of the various habitat loss scenarios on the distance that the average bird has to fly to and from its winter goal. This does not change with habitat loss from all sites equally. This is, however, decreased by the sequential removal of sites that were effectively furthest south in the wintering range, presumably easing overwinter survival and preparation for spring migration, and increased by the sequential removal of those sites closest to the early spring-staging site (the 'northernmost' wintering site) due to the creation of an increasingly large gap between the staging site and the rest of the wintering grounds.

The importance of adopting a spatially explicit year-round approach is also illustrated in the barnacle goose model by the apparently more severe effect of habitat loss in winter than in spring. This appears to run counter to empirical observations that reserves gained in spring are crucial for successful breeding (Black, Deerenberg & Owen 1991). However, the exact positions of the spring and winter habitat loss curves relative to one another should be treated with some caution. First, the simulations used empirical data indicating that spring-staging lasted for only 10 days, compared with 210 days for the winter period. In this context, the effect of spring habitat loss is disproportionate to the amount of time the geese spend there. A second caveat is that all of these predicted responses to habitat loss are likely to be sensitive to the exact area that is assumed to be the default available before habitat loss. As noted in the methods, the definition of available area is somewhat speculative, because there are no clear boundaries between what can, and what definitely cannot, be used by the geese for foraging, and starting with a notional and very large habitat availability will clearly lead to a considerable

reduction in the apparent importance of habitat loss. However, whatever assumptions are made regarding initial habitat availability, the results clearly emphasize the point that the loss of habitat in any part of the range is likely to affect equilibrium population size significantly, and thus no single stage has an overriding influence on the long-term dynamics of the population. Again this is perhaps intuitively obvious, but our models provide us with a tool with which we can explore, in a quantitative way, the different effects of habitat change in different places.

The sensitivity of equilibrium population size to the parameter values of density-dependent functions in both the summer and winter, and to the values of density-independent mortalities of different age classes, has been appreciated for many years (Fretwell 1972; Goss-Custard 1980, 1981, 1993; Goss-Custard & Durell 1984, 1990). In recent years, the quantitative dependence of population size on the relative strengths of these demographic functions has been illustrated extensively, as have the consequences of such dependence for population responses to habitat loss in one season or the other (Goss-Custard 1993; Goss-Custard *et al.* 1995d, 1996b; Sutherland 1996a). The models of Goss-Custard *et al.* (1995d, 1996b) that have explored this issue have relied on empirically derived best-estimates of mortality and reproductive parameters, rather than using a year-round behaviour-based model of the entire population to generate the density-dependent functions. The relationship between spring body condition and reproductive success in the brent goose model goes some way to achieving this year-round approach. Our model of the barnacle goose population, in which the high latitude staging period in Helgeland and reproduction in Svalbard are, in addition to the wintering period, modelled in some detail, approaches even more closely the ideal of a fully developed year-round model.

The predicted overwinter mortality of brent geese when within-winter movements were constrained resulted in a slight weakening of the density-dependent reduction in breeding success for those surviving females. This arises because of the increased density-dependent overwinter mortality, the resultant reduced competition between surviving individuals in spring, and the positive relationship between the spring-body condition of female brent geese and their reproductive success. Had this relationship been more marked, it is possible that the slackening or even reversal of the dependence of reproductive output on autumn population density would have compensated for the increased winter mortality. This could have led to no discernible effect of the assumption of winter movements on the average population size, even though the density dependence of reproductive output and winter-mortality would have been quite different. This high-

lights the point that, because of the interdependence of demographic functions in different seasons, a model might produce realistic estimates of population size without necessarily accurately matching real-world density-dependent functions. This further emphasizes the considerable value of being able to test a model's prediction of the density-dependence of key demographic parameters (Durell *et al.* 2000; Stillman *et al.* 2000; this study).

Simulations of the effect of winter habitat loss on the populations revealed rather different responses between the two species. Comparisons of the model outputs suggest that brent geese may be more vulnerable to winter habitat loss than barnacle geese. Given the relative simplicity with which we modelled the breeding biology of brent geese we do not suggest that this conclusion is necessarily true. However, the difference between the two predictions almost certainly arises because of the relative strengths of density dependence of mortality and reproduction generated by the two models. In the case of the brent goose model, high autumn densities are predicted to lead to increasing overwinter mortality. In spite of the resultant reduction in the number of competitors in spring, high autumn densities are also predicted, under default movement rules, to lead to a reduction in the average body condition of surviving females and hence their breeding success at high initial population sizes. Thus, in this case, winter habitat loss leading to increasing densities would have a detrimental effect on both survival and reproductive output. In the case of the barnacle geese, however, this is not the case. Habitat loss leading to an increase in the average density above current levels results in lowered survival, as for brent geese, but the reduction in productivity would be comparatively slight. This difference between the species in the response of productivity to overall density arises essentially because there is a limited number of breeding sites available in the barnacle goose model, because we know that the availability of nest sites with suitable foraging areas is a locally limiting resource (Loonen, Tombre & Mehlum 1998). In contrast, the density-dependence of reproductive output in the brent goose model depends solely on the average fat levels at the beginning of the breeding season. This means that, in the barnacle goose model, a section of the population is always likely to have some breeding success, even at high overall density, preventing the same degree of decline in productivity observed in the brent goose model. This marginal effect of increased density on the productivity of barnacle geese underlies the markedly less severe effect of winter habitat loss on the population size.

CONCLUDING COMMENTS

The dark-bellied brent goose and the Svalbard population of the barnacle goose are both the subject of international flyway management plans (Van Nugteren 1997; Black 1998), as recommended under the African Eurasian Migratory Waterbird Agreement (Bonn Convention; Anonymous 1995). These plans recognize the holistic international approach that has to be adopted in order to conserve these populations of long-distance migrants. Models of migratory populations such as those we have developed here that are spatially explicit and that can generate demographic functions in both the breeding and non-breeding seasons from the behaviour of individuals, provide a valuable predictive tool to inform such flyway management plans. This is because the predictive strength of these models is that they are based on fundamental properties of the organisms that should remain the same in the new environmental circumstances, so allowing population functions to be derived reliably for the new conditions (Goss-Custard 1996). This, of course, is the widely recognized advantage of mechanistic models over phenomenological models that use only empirical population functions such as regression equations (Goss-Custard 1996). They allow the possibility of determining how demographic functions in both seasons might change under new circumstances, and crucially how the changes in such functions relative to one another might interact in new circumstances, to determine the response of global populations of migratory animals to either global or even very local habitat changes. We believe these models, and indeed the approach to understanding population dynamics that they represent, will prove to be of considerable value in our attempts as biologists to answer the increasingly urgent and frequent requests to predict the response of migratory populations to environmental change. Conservation biology ultimately integrates evolutionary, behavioural and population ecology. Without such an approach as we have adopted here, our study of population dynamics will remain limited, and policies designed to manage or conserve populations may be seriously flawed.

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Appendix 1. Input parameters in the barnacle goose model

(a) THE MODEL POPULATION

Parameters	Value
Number of age classes	20
Initial proportion juvenile	0.16
Maximum number of family members	7

(b) THE WINTER MODULE. (Sources: R. A. Pettifor & J. M. Rowcliffe, unpublished data)

(i) Patch availability

Parameters	Value
Number of patches	3
Patch areas (ha)	
Merse Head	591
Caerlaverock	847
Rockcliffe	516
Day length (hours : minutes, summer/winter solstice)	17 : 22 / 7 : 11

(ii) Food resources

Parameters	Value
Initial biomass range (g dry wt m ⁻²)	12
Productivity (p , dry g m ⁻²) in relation to temperature (C , °C), defined by threshold temperature (C_{thr}), threshold biomass (B_{thr})	$B_{thr} = 12$ $C_{thr} = 1$ $b = 0.002$
and a slope constant (b): $p = \begin{cases} 0 & \text{if } C \leq C_{thr} \\ b(C_{thr} - C)(B_{thr} - B) & \text{if } C > C_{thr} \end{cases}$	
Temperature (°C, maximum on 21 July/minimum on 22 January)	15.3/2.2

(iii) Foraging rates

Parameters	Values
Area covered by a flock (a) in relation to flock size (N) and minutes elapsed (m), defined by constants b and c : $a = N(c+bm)$	$b = 0.165$ $c = 4.1$
Intake rate while feeding (I , g dry wt min ⁻¹) in relation to plant biomass available (B), defined by constants I_{\max} (asymptotic maximum rate) and r : $I = I_{\max}(1 - r^B)$	$I_{\max} = 0.385$ $r = 0.78$
Proportion of time spent feeding (f) in relation to flock size (s), defined by minimum time (f_{\min} , at $s = 0$) and maximum time (f_{\max} , at $s = s_{\text{thr}}$ (threshold flock size)):	$f_{\max} = 0.88$
$f = \begin{cases} f_{\max} & \text{if } s \geq s_{\text{thr}} \\ f_{\min} + s \frac{f_{\max} - f_{\min}}{s_{\text{thr}}} & \text{if } s < s_{\text{thr}} \end{cases}$	$f_{\min} = 0.57$ $s_{\text{thr}} = 280$
Individual performance skew in flocks (k), where prior grazing time experienced in flocks (m) is related to flock size (N) and local dominance (d , most dominant = 0, least dominant = 1) by: $m = kdN$	0.054
Maximum intake rate (g dry wt day ⁻¹)	390
Perceptual limit	1%

(c) THE SPRING MODULE

(Sources: Prop & Black 1998; Prop *et al.* 1998; J. Prop, unpublished data)

(i) Patch availability

Parameters	Value				
Habitat and patch types and coverage (ha)	Managed islands	<i>Festuca</i> 83	Hay 124	Herb 82	<i>Phleum</i> 0
	Unmanaged islands	211	0	352	0
	Agricultural islands	0	0	0	99
	Agricultural mainland	0	0	0	150
	Patch area in traditional habitats (m ⁻²)	12			

(ii) Food resources

Parameters	Value			
Mean shoot density (shoots m ⁻²)	<i>Festuca</i> 9801	Hay 6084	Herb 2025	<i>Phleum</i> 9801
Mean initial shoot length \pm SD (mm)	33 \pm 11			
Energy density (kJ g ⁻¹ dry wt)	7.11			
Growth rate (mm day ⁻¹)	1.25			

(iii) Foraging rates

Parameters	Value				
Intake rate (I , dry g min ⁻¹) in relation to shoot height (H), defined by maximum hourly intake determined by gut capacity (I_{\max}), proportion of time spent feeding (p), a habitat-specific intercept (c_H), and a slope constant (b):	$I = \begin{cases} \frac{I_{\max}}{60} & \text{if } 60 * I \geq I_{\max} \\ p(c_H + bH) & \text{if } 60 * I < I_{\max} \end{cases}$	<i>Festuca</i> 0.1	Hay 0.137	Herb 0.005	<i>Phleum</i> 0.137
	c_H $b = 0.004$ (all habitats) $I_{\max} = 19.23$ (all habitats) $P = 0.75$ (all habitats)				
Day length (hours)	19				
Threshold age for changing traditional site (birds older than this cannot change, whatever their experience)	2				
Threshold energy reserves (kJ) at departure for changing traditional site	4000				

Appendix 1. (cont'd)

(d) THE BREEDING SEASON

(Sources: Prop, van Eerden & Drent 1984; Prestrud, Black & Owen 1989; Prop & de Vries 1993)

Parameters	Value				
Maximum number of nest sites	2400				
Fat increment (F) is related to population size (N) and available area (A), determined by maximum and minimum values (F_{\max} , F_{\min}), a density-dependence slope parameter (δ) and a mid-point parameter (m) by:					
$F = F_{\min} + \frac{F_{\max} - F_{\min}}{1 + \left(\frac{N}{mA}\right)^{\delta}}$		F_{\max}	F_{\min}	δ	m
	Non-breeders	3.5	1	1	2000
	Pre-breeders	2.5	-0.3	1	2000
	Brood-rearing	1.5	0	1	2000

(e) ENERGETICS

(Sources: Drent, Ebbinge & Weijand 1980; Bromley & Jarvis 1993; J. Prop and J. M. Black, unpublished data)

Parameters	Value
Fat per abdominal profile unit (g)	100
Energy density of fat (kJ g^{-1})	25.5
Efficiency of fat storage/use	0.7/0.77
Basal metabolic rate (BMR, kJ h^{-1} , where average expenditure is $2 \times \text{BMR}$)	50

(f) MOVEMENTS BETWEEN SITES

(Sources: Butler & Woakes 1998)

Parameters	Value
Migration dates (days from Jan 1, Scotland – Helgeland – Svalbard – Scotland)	122/133/268
Distances (km, Scotland – Helgeland – Svalbard – Scotland)	1540/1350/2880
Migration speed (km h^{-1})	90
Energy requirements (kJ hour^{-1})	126

Appendix 2. Input parameters in the brent goose model

(a) THE MODEL POPULATION

Parameter and source (where published)	Value
Starting population	1000 individuals
Number of age classes	3: Juveniles(0), Yearlings (1), Adults, i.e. 3+ years (2)
Number of sexes	2: Male (0), Female (1)
Initial proportion of birds in each age/sex class	Juvenile males, 0.15; Juvenile females, 0.15 Yearling males, 0.00; Yearling females, 0.00 Adult males, 0.35; Adult females, 0.35
Maximum number of family members (Ogilvie 1978)	8
Range of dominance scores among unpaired individuals in each age class	Yearling females, 0–0.083; Yearling males, 0.083–0.166 Adult females, 0.166–0.250; Adult males, 0.250–0.333
Increment to dominance score of adult males for each additional family member.	0.083
Distribution of between individual variation in proportion of each minute spent ingesting food (present study)	Mean 0.00 Standard deviation 0.03

(b) THE MODEL WORLD

(i) Number, location and size of sites and patches

Parameter and source (where published)	Value
Number of wintering sites (Ebbinge & St Joseph 1992)	10
Distance between neighbouring wintering sites (Ebbinge & St Joseph 1992)	170 km
Number of patch types	2 (intertidal and terrestrial)
Number of patches per site	2: 1 intertidal and 1 terrestrial
Patch areas (estimated based on Exe estuary data and extrapolation to total population size, and then rescaled to match the size of initial model population)	Early spring-staging site: 340 000 m ² All other sites: 34 000 m ²

(ii) Food resources

Parameter and source (where published)	Value
Starting biomass densities on 15 September	
Intertidal	233 g dry mass m ⁻²
Terrestrial	81 g dry mass m ⁻²
Maximum and minimum biomass dependent (proportionate) productivity per day, and date on which maximum attained [Intertidal values derived from data in Percival, Sutherland & Evans (1996). Terrestrial values derived from Sutherland & Allport (1994)]	
Intertidal	Maximum 1-0155 Minimum 0-9855
Terrestrial	Maximum on 1 June Maximum 0-9992 Minimum 0-9992
Coefficients for constant and temperature-dependent productivity per day on grassland patches (Sutherland & Allport 1994)	
	Constant rate of productivity 0-038 g dry mass m ⁻² day ⁻¹ Temperature dependent productivity 0-029 g dry mass m ⁻² day ⁻¹ °C ⁻¹
Maximum and minimum mean daily temperature and day on which maximum is attained	
	Maximum 15.3 °C Minimum 5.3 °C Maximum attained on 1 July
Maximum and minimum digestibility and date on which maximum attained (Charman 1979; Drent, Ebbinge & Weijand 1980; Ebbinge, Canters & Drent 1975)	
Intertidal	Maximum 0-67 Minimum 0-44
Terrestrial	Maximum on 1 June Maximum 0-34 Minimum 0-34
Maximum and minimum energy density of food material (Ebbinge, Canters & Drent 1975; Wyer & Waters 1975; Charman 1979; Black <i>et al.</i> 1992)	
Intertidal	Maximum 20 kJ g ⁻¹ Minimum 10 kJ g ⁻¹
Terrestrial	Maximum on 1 June Maximum 18 kJ g ⁻¹ Minimum 18 kJ g ⁻¹

(c) FORAGING WITHIN SITES

Parameter and source (where published)	Value
Duration of spring–neap tidal cycle	14 days
Duration of longest and shortest days (sunrise–sunset at 52°N)	16.55 h on 21 June, 7.92 h on 21 December
Length of time patches available in daylight on a full neap tide and full spring tide on longest and shortest day	21 June
Neap tide	Intertidal 10.93 h; Terrestrial 16.55 h
Spring tide	Intertidal 5.53 h Terrestrial 16.55 h 21 December
Neap tide	Intertidal 2.79 h; Terrestrial 7.92 h
Spring tide	Intertidal 5.53 h; Terrestrial 7.92 h 21 June
Length of time patches available in darkness on a full neap tide and full spring tide on longest and shortest day	
Neap tide	Intertidal 1.26 h; Terrestrial 0 h
Spring tide	Intertidal 5.07 h; Terrestrial 0 h 21 December
Neap tide	Intertidal 9.38 h; Terrestrial 0 h
Spring tide	Intertidal 5.07 h; Terrestrial 0 h
'Bite' size (mg dry mass per unit of ingestion)	Intertidal: mg dry mass per second head down = $0 + 10.28 \times (1 - \exp(-1 \times 0.1050 \times$ biomass density)) Terrestrial: mg dry mass per peck = $0 + 4.75 \times (1 - \exp(-1 \times 0.1050 \times$ biomass density))
Ingestion rate (units of ingestion per unit time ingesting)	Intertidal: seconds head down per minute head down = 60 Terrestrial: pecks per minute pecking = $179.56 - (42.45 + 6.42 \times \text{sex}) \times$ $(1 - \exp(-1 \times 0.065 \times (\text{biomass density} - 75)))$
Proportion of each minute spent ingesting food	Intertidal: minutes head down per minute active = $0 + (1.0336 - 0.1872 \times \text{age} + 0.0537 \times$ $\text{sex} - 0.0782 \times \text{family size} + 0.1004 \times \text{dominance}) \times$ $(1 - \exp(-1 \times 0.0184 \times \text{biomass density})) \times$ $(1 - \exp(-1 \times 0.2867 \times \text{flock size}))$ Terrestrial: minutes pecking per minutes active = $0.482 + (0.413 - 0.0533 \times \text{age} - 0.0661 \times$ $\text{family size}) \times (1 - \exp(-1 \times 0.071 \times (\text{day} - 57)))$
Perception limit (Goss-Custard <i>et al.</i> 1995b)	3%

(d) ENERGETICS

Parameter and source (where published)	Value
Mass used to calculate lower critical temperature from equation 5.12 of Kendeigh, Dol'nik & Gavrilov (1977)	1350 g
Energy reserve storage and mobilization efficiency (Kersten & Piersma 1987)	Storage 0.884 Mobilization 1.000
Energy density of reserves (Lindstrom & Piersma 1993)	28.0 kJ g ⁻¹
Maximum percentage increase in body mass per day (Ebbinge & Spaans 1995)	0.8%
Overwinter target masses (adult figures from Ebbinge & Spaans 1995; assume yearlings = adults and juveniles = 100 g less than adults)	
Females	Juveniles 1175 g Yearlings 1275 g Adults 1275 g
Males	Juveniles 1325 g Yearlings 1425 g Adults 1425 g
Starvation masses (Ebbinge & Spaans 1995 Adult female starvation mass = 1025 g. Assume Adult male starvation mass = 1.04 × 1025 g on basis of ratio of adult male to adult female wing length. Assume starvation masses of yearlings equal those of adults whereas those of juveniles are 85% of adult values)	
Females	Juveniles 871 g Yearlings 1025 g Adults 1025 g
Juveniles	Males 906 g Yearlings 1066 g Adults 1066 g

(e) MOVEMENTS BETWEEN SITES

Parameter and source (where published)	Value
Initial masses on 15 September	
Females	Juveniles 1336 g Yearlings 1600 g Adults 1600 g
Males	Juveniles 1396 g Yearlings 1671 g Adults 1671 g
Proportion of body mass as reserves at which facultative winter movements triggered (Hulscher 1989, 1990)	0.08
Wingspan (Ebbinge & Spaans 1995)	1.204 m
Ratio of mechanical work done to fuel energy consumed (conversion efficiency) (Pennycuik 1989)	0.23
Induced power factor (Pennycuik 1989)	1.2
Circulation/respiration factor (Pennycuik 1989)	1.1
Profile power ratio (Pennycuik 1989)	1.2
Air density (Pennycuik 1989)	1.00 kg m ⁻³

(f) THE BREEDING SEASON

Parameter and source (where published)	Value
Productivity in successful years (equation based on data in Ebbinge & Spaans 1995) % juveniles = -223 + 0.169 × mean female body mass (g)	$r^2 = 79.7\%$ $P < 0.01$ d.f. = 6.
Proportion dying per age/sex class during non-wintering period (Ebbinge 1992b)	0.1447