A simulation model coupling the behaviour and energetics of a breeding central place forager to assess the impact of environmental changes

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A B S T R A C T

During the breeding season, seabirds are obligate central place foragers, and this may make them vulnerable to impacts of environmental change. An individual based model of a pair of central place foragers and their offspring has been developed for the common guillemot (*Uria aalge*). The behavioural decisions of each adult depend on the state of themselves, their partner and their chick. The behaviour of the adults and the body masses of all three are followed over the chick rearing period. The model was used to investigate how chick fledging mass, proportion of time the chick was left unattended by its parents and change in adult mass are impacted by different foraging ranges, prey abundance and calorific content. Adults in the model typically declined in mass during the chick rearing period, although none died of starvation. Provisioning parents can, to some extent, increase foraging distance from the colony without a reduction in the proportion of chicks reaching a suitable fledging mass or increasing the time they are left unattended. The foraging range at which a decline in fledging success and colony attendance occurs is influenced by changes in either one or both of, prey abundance and prey quality. Patterns produced by the model are consistent with field observations and biological knowledge. As the model outputs can give an indication of the fitness consequences of environmental changes it can be used to address theoretical ecological questions as well as to inform marine spatial management.

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1. Introduction

Seabirds are obligate central place foragers during the breeding season. Adults have to travel regularly between terrestrial breeding colonies and offshore foraging areas in order to feed their offspring. As a result, breeding success may be influenced by the time required to fly to feeding sites and how long adults spend there (Boersma and Rebstock, 2009; Chivers et al., 2012; Uttley et al., 1994), because this affects how frequently the chick is fed. An added constraint on many seabirds is that one parent typically needs to be present at the colony to protect the chick from predation and attacks by conspecifics (Ashbrook et al., 2008). The need to return to a specific location limits the ability of central place foragers to search for more productive foraging areas. Also, any physical disturbance may be encountered repeatedly and so may have a large cumulative influence on a seabird's time and energy budget. This means that environmental changes, such as barriers to movement or a decrease in prey availability, have the potential to negatively impact reproductive success.

Individuals can often buffer against the effects of environmental variation to some extent by adjusting their behaviour budgets. Individuals can spend more time foraging by sacrificing time spent in other activities and therefore, maintain breeding success (Burger and Piatt, 1990; Harding et al., 2007; Piatt et al., 2007; Zador and Piatt, 1999). There is however a limit to this buffering capacity. A reduction in chick provisioning and/or breeding success has been observed in response to a decline in prey abundance or elevated cost of foraging (Chivers et al., 2012; Hamer et al., 1993; Harding et al., 2009; Uttley et al., 1994). In addition, different behaviours have different metabolic costs. Consequently, any change in the behaviour budget of an individual also alters its energy budget. The balance between the energy acquired and energy expended impacts on an individual's body mass, and can therefore influence survival.

Due to the importance of energy reserves to an organism's reproduction and survival (Harding et al., 2011; Keech et al., 2000; Proffitt et al., 2008; Rödel et al., 2004; Wendeln and Becker, 1999), energetic models have frequently been used to study the ecology of seabirds (e.g. Fort et al., 2011, 2009; Grémillet et al., 2003). Seabird energetics have also been considered when trying to predict the

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impact of environmental changes, such as the development of wind farms (Masden et al., 2010) or variations in prey availability (Enstipp et al., 2006). However, these studies did not always take into account the impact of changes to adults' time budgets (Masden et al., 2010) or assumed seabirds were restricted by never being able to leave their chicks unattended (Enstipp et al., 2006). Non-attendance of the chick has now been observed, and can increase fledging success at high-density colonies under severe conditions (Ashbrook et al., 2010). In addition, Enstipp et al. (2006) assumed adults balanced their energy budget, but field observations indicate that body mass of adult seabirds frequently declines during chick rearing (Gaston and Hipfner, 2006b; Harding et al., 2009; Jacobs et al., 2011). These studies provide useful snapshots of how environmental change may impact the energetic and/or time budgets of seabirds, but there has been no attempt to model cumulative impacts on body mass over an extended period or explicitly incorporate the offspring. This makes it difficult to predict the extent that provisioning individuals can buffer against environmental change and therefore whether there will be population level impacts.

The energy budget of a chick both influences, and is influenced by, the behavioural decisions of its parents. Similarly, the behaviour of the two parent birds is affected by each other in order to prevent their offspring being left unattended. These interactions between the different individuals in the seabird family mean that they should be modelled separately (Reuter and Breckling, 1999). Individual-based models provide a framework in which to do this, with autonomously acting individuals whose behaviour adapts to changes in the state of itself and other entities in the model (Martin et al., 2012). Energy budgets are also most suitably considered at the level of the individual (Nisbet et al., 2000) and should be included in individual-based models if variations in food supply affect populations (Sibly et al., 2012).

There are now multiple studies which incorporate energetics into individual-based models in order to make ecological predictions or inform management (e.g. Kaiser et al., 2005; Martin et al., 2012; Reuter and Breckling, 1999; Stillman, 2008; Topping et al., 2010). A series of individual-based models of coastal birds have simulated the foraging behaviour and energetics of individuals, and intraspecific competition (Stillman, 2008; Stillman and Goss-Custard, 2010). These have been applied to predict the impact of environmental change, such as the development of wind farms (Kaiser et al., 2005), on the mortality of wildfowl and waders; although, so far, this has been restricted to overwintering birds. However, to the authors' knowledge, no model has currently been developed which simulates the fine scale behaviour patterns of a breeding central place forager coupled with energetics, nor one that explicitly includes offspring.

The aim of this paper is to present a novel simulation model of a pair of central-place foragers provisioning one offspring. Both the behaviour and energy budget of the adults and the energy budget of their offspring are simulated separately, allowing changes in body mass to be predicted. The model has been developed and parameterised for the common guillemot (*Uria aalge* Pontoppidan, hereafter guillemot). The model was then used to test the ability of adults to provision and attend their offspring over the chick rearing period, as well as maintain themselves, with different foraging ranges, prey abundances and prey qualities.

2. Materials and methods

2.1. Model description

The model was developed in R (R Core Team, 2012) and annotated code is provided in Appendix A. The model is described below using the ODD (Overview, Design concepts, Details) protocol for individual-based models (Grimm et al., 2010, 2006), with additional details in Appendix B, and the values for model constants in Table 1.

2.1.1. Purpose

The purpose of the model is to predict how environmental variables, such as distance to feeding sites, prey abundance and prey quality, influence the behaviour and body mass of the forager and their ability to feed and attend their offspring. The model can therefore be used to compare breeding success or survival between different environmental scenarios.

2.1.2. Entities, state variables and scales

There are three types of guillemots in the model, adult males, adult females and chicks. The individuals are organised into family groups which include one of each of these three types. All the state variables required for the different entities in the model are set out in Table 2. Chicks in the model are defined as being in one of three conditions (C); *good, critical* or *dead*, based on their current and previous body masses.

The model operates on two temporal scales, days (d) and minutes (m). There are 1440 min time steps in each day. The model runs for 21 day time steps, as this is the average fledging age of guillemots. Minutes 1-1200 each day are classified as daylight and all subsequent minutes are defined as night. Some state variables, such as adult behaviour and gut content, change on a minute by minute basis, whereas change in body mass occurs daily.

The model is not spatially explicit, but the location of prey patches relative to the colony is implied by the foraging range.

2.1.3. Process overview and scheduling

The main processes performed by birds in the model are: making behavioural decisions, performing behaviour and mass change (Fig. 1). Both behavioural decision making and the performance of behaviour occur in discrete time steps of a minute, whereas mass change occurs at coarser, daily time steps. The performance of behaviour step covers a variety of processes which always includes updating the behaviour counters (e.g. total time in current day spent at nest ($T_{nest(d)}$), duration of current rest on the surface (D_{surf}), etc.), gut content (G), and calculating the energy expended by the adult during that minute ($E_{(m)}$). Depending on the behavioural state, performing the behaviour can also involve changes to the content of the adult's beak and feeding the chick. Only the adults undergo behavioural decision making and only their behavioural state ($B_{(m)}$) is altered as a result. Similarly, it is only the parent birds which perform behaviours. However the state of the chick, as well as their own, could change during the process. Both the behavioural decision and performing behaviour processes occur every minute through the day time step, including those defined as night. All birds in the model undertake the mass change process which takes place after the last minute of the day (Fig. 1). The only source of mortality in the model is starvation and whether a bird is still alive at the start of the next day time step depends on the output of this mass change process.

One guillemot family is simulated for the whole time series before moving on to the next pair.

2.1.4. Design concepts
2.1.4.1. *Basic principles.* The change in mass of an organism over a time period is related to the balance between the energy assimilated and the energy expended. The energy budgets of foraging animals are determined by the amount of time spent performing different activities and the rates of energy loss or gain experienced while engaged in them. Furthermore, the energy acquired by the offspring of central place foragers also depends on the time budgets of the parents, as this influences how frequently they are fed.