S19-5   Annual routine models and the evolution of migration

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Abstract   Annual routine models are state-dependent dynamic models which enable the computation of optimal behavioral schedules in seasonal environments. We provide an outline of the computational scheme, and illustrate the method with results on the optimal timing of breeding and migration in the annual cycle. The results demonstrate that the dynamics of a state variable denoted as condition, which is compromised by demanding activities such as breeding and migration and recovers slowly, can explain the observation that autumn migration is more spread out in time than spring migration. Annual routine models promise to be a useful method for analyzing how physiological processes shape life-histories and are in turn shaped by ecological and behavioral demands.

Key words   Annual routines, Dynamic models, State dependence, Avian migration

1   Introduction

Evolution is in its essence a historical process, but optimality models are usually ahistorical. They can play, nevertheless, an important role in the study of evolution, especially the study of *adaptive* evolution. Given a particular background defined by constraints of all sorts, including phylogenetic constraints, it is possible by optimization methods to identify potential selective regimes that have shaped and currently maintain the trait or traits under consideration. It is also possible to make predictions about the outcome of manipulations — if they are possible — and to identify the possible causes of supposedly adaptive intra- and inter-specific variation.

A widespread criticism of optimality models is that such approaches are usually only concerned with one behavioral trait and not with the interactions among several traits. This is sometimes justified. The advent of dynamic state-variable models has, however, weakened that objection significantly (Mangel and Clark, 1988; Houston and McNamara, 1999; Clark and Mangel, 2000). Only limited by computing power and, far more seriously, by our ability to interpret results, this technique allows us to examine any number of traits, their interactions and trade-offs. The method starts from the insight that decisions should be state-dependent. As decisions are affected by state and decisions change state, optimal strategies will often turn out to be time-dependent. The effects of actions are evaluated in the future; thus it is natural to start computations in the future and to calculate backwards (for technical details, see Houston and McNamara, 1999; Clark and Mangel, 2000).

Weber et al. (1998), Farmer and Wiens (1998, 1999) and Clark and Butler (1999) used this method to study migration strategies. The method, however, presupposes that the reproductive value — the universal currency in dynamic models and evolution — of all possible states is known at some time point in the future. Dynamic models are therefore an excellent technique for modeling behavior over well-defined time intervals in the life-history of an organism, such as overwintering of birds. But this technique can be taken further to address entire life-histories. There are, however, some problems that need to be addressed.

Attempts to model the optimal scheduling of state-dependent behaviors in seasonal environments pose special problems. For example, some periods of the annual cycle may offer good conditions for several, sometimes mutually exclusive activities: which activity should be performed? When should a second brood be attempted or preparations for migration be started? Should molt occur before or after autumn migration? The chosen schedule of actions may also have long-term effects: reproductive effort in one season may determine the condition at which a bird enters the winter, and the bird's condition at the end of winter will affect its ability to breed in the following spring and the quality of its offspring. The consequence of these complications is that there is no obvious point in the annual cycle where a backward calculation should start — the linkages between the seasons, mediated by the state-variables, can be quite complex. Houston and McNamara (1999) present a model that overcomes these problems and allows the calculation of fully consistent optimal annual routines.

2   The model

The basic outline of this model was developed by Welham et al. (1998) and the results reported here are based on a more recent version of it. General technical details of the computational procedure can be found in Houston and McNamara (1999). The environment consists of two locations: a "northern" location with a seasonally chang-

ing food supply and a "tropical" location with a stable supply (Fig. 1). Decisions are calculated on a weekly basis. Birds are characterized by five state variables: reserves, condition, foraging experience, brood age and location. The experience variable describes the foraging proficiency of individuals. It is low after birth and increases slowly with time. This variable is introduced so that juveniles do not start reproducing immediately after independence. Sources of mortality are predation, starvation and disease. Predation and metabolism are mass-dependent, starvation occurs if reserves drop to zero, and the probability of dying from a disease increases with decreasing condition. At each point in time, birds have to decide which activity to perform: to forage, to start breeding, to continue breeding if they have a brood or to abandon, or to start migration. For each activity, a foraging intensity must be chosen as well. Condition is compromised by high foraging intensity.

The computations maximize the number of descendants left far into the future. Calculations start by "breaking" the annual cycle at some convenient point — in the current in midwinter at week 51 — and by defining a terminal reward function at this point in time. As in standard dynamic programming, backward iterations are used to calculate reproductive value and the best action and foraging intensity for each combination of state and time. Reproductive values one year back are obtained and these serve as the starting point for a new round of iterations. This procedure is repeated until convergence occurs, that is until the reproductive values do not change any longer if iterations are repeated. The results are independent of the terminal reward chosen at the beginning of the computations.

3 Results

We illustrate the possibilities offered by annual routine models with two examples based on the above model and a version including molt instead of migration.

Fig. 2 shows the timing of migration and breeding in the annual cycle. There is one breeding attempt, peaking at around week 20, i.e. before the peak in food supply. The
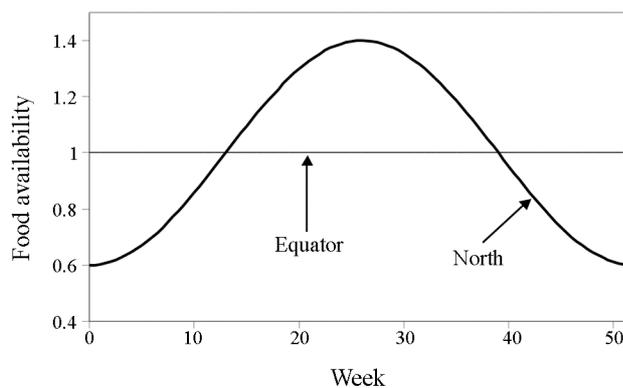
peak in food supply coincides with the raising of the brood. The output reproduces the well-known observation that autumn migration is far more spread out in time than spring migration. With the help of the model we can try to formulate causal hypotheses for why this is the case. Spring migration is concentrated because there are penalties for arriving too early and too late. Individuals that arrive too early encounter a poor food supply, have to work hard to build up reserves, and thus are unable to increase their condition sufficiently fast to breed at all, or to produce offspring that are born early enough to gain their own condition before migration. Late arriving birds are penalized for two reasons: they may arrive too late for successful breeding, or if they are successful, they and their offspring may be low in condition such that their future expectations are bleak.

If the effects of body mass and the condition variables on mortality risk are removed from the model, both autumn migration and spring migration are very concentrated in time. Furthermore, the mean departure time in autumn is delayed by one week: the increased spread and mean of departure times in autumn thus depend on the effects of state. Why migrate early in autumn if condition matters? Early departing birds have high reserves and are in good condition. They arrive early on the wintering ground with decreased condition and have plenty of time to recover before spring migration and breeding. By leaving early they also avoid the need to build up energy reserves for migration at a time when food availability in the breeding area is decreasing. Why migrate late in autumn? Some birds are in such a bad condition after breeding that they need time to recover before they can depart. Without the condition variable there is neither the need to migrate early nor late. With the help of the model we can formulate a causal hypothesis: the slow dynamics of the state variable condition is responsible for the observed departure schedules in spring and autumn.

The following example demonstrates how annual routine models can deal with other questions. One important step is the redescription of the condition variable. Fig. 3 shows the scheduling of molt for a non-migratory species
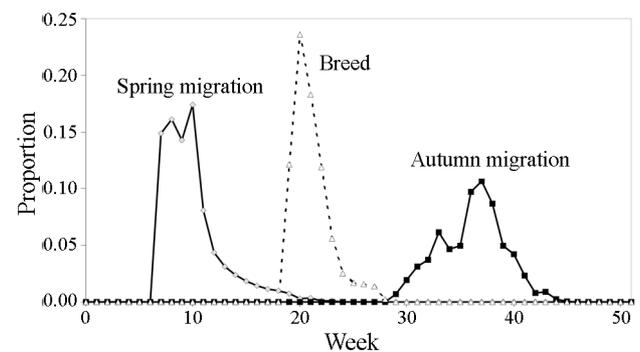

Fig. 1 Food availability as a function of time of year for the two locations in the model
Mean food availability in both environments is 2.

Fig. 2 Proportion of animals migrating and breeding throughout the annual cycle
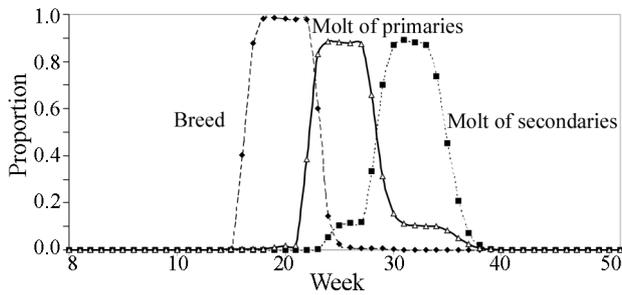
Fig. 3   The optimal scheduling of molt of primaries and secondaries in a resident species
The figure shows the proportion of animals engaged in each activity.

living in the temperate zone. In this model, the above condition variable is replaced by two variables describing the quality of primaries and secondaries respectively. Birds may molt both feather tracts simultaneously or with a variable degree of overlap. Molt can also overlap with breeding. During molt, flight performance is compromised and thus foraging is more costly in terms of predation and metabolic expenditure. The decrease in feather quality depends on foraging intensity. The graph shows that after breeding birds first replace the primaries, which have a substantial effect on flight importance, and then the secondaries.

4   Discussion

What can migration research expect from optimality models now and in the future? Modelers are used to experience two kinds of extreme attitudes towards their efforts: either hope that all problems will at last be solved, or complete disdain. These are two endpoints in a continuum, even though not that rare. Models, however, are just one item in the toolbox of evolutionary biology — and hardly any complex problem can be solved satisfactorily with just one tool.

Annual routine models offer opportunities and, of course, have limitations. The above model can be extended to investigate more locations and problems, such as stop-over choices, choice of wintering latitude and migration routes. Annual routine models seem to offer an especially promising avenue for the linkage of behavioral and physiological processes, and thus may provide insights into the physiological foundations of life-history evolution. A slowly changing state-variable defined as "condition" is responsible for many of the often subtle but complex patterns that arise. This state-variable is responsible for the links between seasons. But what exactly is meant by "condition"? The physiological processes envisaged will depend on the problem studied. In the above model, condition could potentially be identified with immunocompetence (Apanius, 1998).

It still has to be worked out in reasonable detail how immunocompetence enables and constrains life-cycle stages — breeding, migration, molt — and how these events affect immunocompetence. When studying the scheduling of molt

in the annual cycle of migrants and non-migrants, one appropriate condition variable should be feather quality. How do migration and breeding affect feather quality and flight performance? We still do not know the answers to most of such questions about condition variables. They will, however, hopefully spark new research programs, making it possible to ask not only how physiology constrains evolutionary responses but also how physiological processes are shaped by ecological and behavioral demands. Long-distance migration is one of the most demanding of activities, and should offer considerable scope for studying the link between physiological and behavioral adaptations, both experimentally and theoretically.

Annual routine models as they are today have limitations. For example, they do no deal with fluctuating environments. In such environments, all individual without exception are affected by the fluctuations (Lewontin and Cohen, 1969) and the usual fitness measures do not apply. Such models are especially pertinent for annual or short-lived organisms. It remains to be seen how relevant they are for long-lived organisms. More seriously, current annual routine models do not consider frequency-dependence, which most likely is pervasive in nature. This is not an impossible hurdle, but a logical extension to be considered in the future. The models are already complex in their simplest form. An understanding of the current models is needed first before contemplating the addition of further complications.

References

Apanius V, 1998. Stress and immune defence. Adv. Stud. Behav. 27: 133–153.
Clark CW, Mangel M, 2000. Dynamic State Variable Models in Ecology. Methods and Applications. Oxford: Oxford University Press.
Farmer AH, Wiens JA, 1998. Optimal migration schedules depend on the landscape and the physical environment: a dynamic modelling view. J. Avian Biol. 29: 405–415.
Farmer AH, Wiens JA, 1999. Models and reality: Time-energy trade-offs in pectoral sandpiper (*Calidris melanotos*) migration. Ecology 80: 2 566–2 580.
Houston AI, McNamara JM, 1999. Models of Adaptive Behaviour. An Approach Based on State. Cambridge: Cambridge University Press.
Lewontin RC, Cohen D, 1969. On population growth in a randomly varying environment. Proc. Natl. Acad. Sci. USA 62: 1 056–1 060.
Mangel M, Clark CW, 1988. Dynamic Modeling in Behavioral Ecology. Princeton: Princeton University Press.
McNamara JM, Welham RK, Houston AI, 1998. The timing of migration within the context of an annual routine. J. Avian Biol. 29: 416–423.
Weber TP, Ens BJ, Houston AI, 1998. Optimal avian migration: a dynamic model of fuel stores and site use. Evol. Ecol. 12: 377–401.