ORIGINAL ARTICLE

Breeding migration and population stability

T. Nakazawa · N. Yamamura

Abstract We have modeled habitat shift for reproduction to examine the relationship between the timing of migration and population stability, by modifying Takimoto's (Am Nat 162:93–109, 2003) consumer–resource model with a consumer's ontogenetic niche shift. We found that equilibrium was always locally unstable if migration occurs at a fixed time or level of energy storage, whereas it could be stable if the timing of migration was adaptively flexible to maximize reproductive output. The general conditions for stability were safer breeding rather than feeding habitat and abundant resources at the feeding habitat. These results imply that both adopting an adaptive plastic strategy in the timing of migration and choosing to migrate from a rich feeding habitat to a safe breeding habitat can contribute to population stability. We also found that reduced reproductive success with delays in migration, and the survival rate after reproduction, had complicated effects on stability, depending on resource availability at the feeding habitat. The equilibrium was more likely to be stable when reproduction success was only slightly (or greatly) reduced or survival rate was high (or low) if the feeding habitat was rich (or poor). These are significant predictions for ecological study of migrating animals.

Keywords Adaptive behavior · Mortality risk · Phenotypic plasticity · Resource availability · Trade-off

T. Nakazawa (✉) · N. Yamamura
Center for Ecological Research, Kyoto University,
2-509-3 Hirano, Otsu 520-2113, Japan
e-mail: nkzw@ecology.kyoto-u.ac.jp

Introduction

Breeding migration is known in a variety of animal taxa, for example crustaceans (Taylor et al. 1985; Moksnes et al. 1997), fish (Leggett 1977; Hendry and Stearns 2004), amphibians (Madison and Shoop 1970; Gittins 1983), reptiles (Luschi et al. 2003), birds (Berthold 2001; Both and Visser 2001), and mammals (Stone et al. 1990; McConnell and Fedak 1996). Migratory birds and sea turtles are well known long-distance migrants, but a smaller scale of migration within a localized area, as in fish that migrate from offshore to the shore within a lake (Hidaka and Takahashi 1987), is also widespread (Vøllestad and L'Abee-Lund 1987; Heggberget et al. 1988; Aoyama et al. 2003). The move to a different habitat for reproduction thus seems to be a common strategy in nature.

One of the greatest concerns for migrants is when to migrate. It is, for example, reported that global warming has advanced the timing of migration of birds that use temperature as a signal for migration (Cotton 2003; Jonzén et al. 2006), indicating that yearly regular migration is advantageous to these birds. In some species, furthermore, the timing of migration varies annually depending on pre-migration conditions, for example resource availability or energy accumulation (Drent et al. 1980; Albon and Langvatn 1992; Prop and Black 1998; Prop et al. 2003); this also suggests more directly the significance of the problem of timing.

Although many researchers have examined the mechanisms triggering migration, its ecological aspects, i.e. how population dynamics are related to characteristics of the migrant and the surrounding environmental conditions, are insufficiently understood

(Farmer and Wiens 1999). This is because of the difficulty of conducting long-term and broad-scale research. Here, we addressed this problem using a consumer–resource model with a consumer ontogenetic niche shift in which two life-history stages result in different growth rates for the consumer. The model considers the relationship between population stability and the timing of the niche shift from one stage to the other. The framework of the model may therefore be useful for analysis of migration for breeding, with the first and second consumer stages corresponding to the pre-migration and post-migration periods, respectively.

There are several theoretical works on ontogenetic niche shifts. For example, De Roos et al. (2002) used the bifurcation diagram of a size-structured model to consider flexible changes in resource use from one type to the other (see also Persson and De Roos 2003). They assumed the niche shift occurred when the instantaneous net gains (the ratio of individual growth over mortality) at the first stage decreased to that of the next stage. This is called the "μ/g rule" (Werner and Gilliam 1984).

More recently, an ontogenetic niche-shift model containing a different rule was proposed by Takimoto (2003). This model showed that niche shifts occurred in such a way to maximize the fitness defined over the entire life-span (but see also Claessen and Dieckmann 2002). Although he considered only semelparous cases, for example ontogenetic resource shift in fishes or metamorphosis in insects, the model has advantages in that it can be used to describe different types of mechanism of niche shift—final, rather than instantaneous, energy gain can be the criterion for niche-shift timing, and more conveniently, the model can be analyzed because of the relative simplicity of its formulation compared with previous models. In this study, therefore, we used the ontogenetic niche-shift model by Takimoto (2003), with some variations.

– First, we assumed a change in the risk of mortality after migration. In the original model (Takimoto 2003) the mortality rate was assumed to be constant throughout the life-span. This may be inappropriate for breeding migration because enemy behavioral patterns, species composition, and physical environments should differ in the feeding and breeding habitats, which are usually separated by a distance (Wilbur 1980; Werner et al. 1983a, b).
– Second, we assumed that reproductive success depends on the timing of migration. In the original model (Takimoto 2003), the timing of ontogenetic niche shift did not directly affect individual fitness. If, however, a fixed period of time is necessary to

prepare for reproduction after migration (e.g. for finding territory, nest making, competing among mating rivals, or mating), reproductive success may decrease as a result of delays in migration (Møller 1994; Kokko 1999; Prop et al. 2003; Smith and Moore 2005; see also Daan et al. 1990; Rowe et al. 1994).
– Third, Takimoto (2003) assumed that all individuals die after reproduction, i.e. they are semelparous. This assumption is valid for salmon or aquatic insects, for which habitat shift occurs only once during the life-span. In general, however, many animals have more than one reproductive opportunity before their death. We therefore included iteroparity in the original model by assuming that reproductive individuals have a specific rate of survival after reproduction.
– Finally, we assumed that accumulation of reproductive energy is achieved at the feeding habitat only and ceases thereafter, under the assumption that most of the time and effort at the breeding habitat is spent on preparation for reproduction. We also assumed natal homing, which means the surviving individuals migrate back to their original place of birth (Meylan et al. 1990; Quinn 1993; Rhodes et al. 1996; Thorrold et. al. 2001), and no cost of migration.

In these ways, we formulated a modified Takimoto's (2003) model appropriate for analysis of breeding migration.

Takimoto (2003) suggested three patterns of niche-shift timing—fixed-age, fixed-size, and adaptive plasticity. In the fixed-age and fixed-size models, niche shifts are assumed to occur at a specific age and body size, respectively. In the adaptive plasticity model, niche-shift timing is assumed to be flexible, to maximize fitness. Takimoto (2003) showed analytically that only the adaptive plasticity model could achieve local stability, because of density-dependent negative feedback. For example, niche shift occurs earlier when resources are scarce in the initial niche, which facilitates recovery of resource abundance. Here, the adaptive plasticity model assumes phenotypic plasticity or flexible behavioral change in the timing of migration, rather than evolutionary response.

Our concern is with breeding migration. If the timing of breeding migration is determined by day length (Gwinner 1986) or temperature (Reading 1998), it would correspond to a fixed-age model. Prop and Black (1998) suggested a mass threshold in avian migration, which would correspond to a fixed-size model. If the timing of migration seems to be adaptively flexible and migration occurs when it becomes no longer profitable to remain at the feeding habitat, this would correspond to an adaptive plasticity model. In the latter

circumstance a stagnant growth rate or deteriorating environmental conditions may trigger migration (Drent et al. 1980; Prop et al. 2003; Olsson et al. 2006).

The purpose of the new model is to examine how population stability is related to life-history or environmental conditions. We also tried to verify whether only the adaptive plasticity model was stable, even when the model assumptions were altered to approximate conditions determining the timing of migration. The model predictions will provide useful insight into the ecological conditions necessary for population stability for species that migrate for reproduction, which is a difficult subject for empirical research. The results may also be used in other circumstances, for example ontogenetic niche shifts or age at maturity, as well as spatial movement to different habitats for reproduction.

Model

First, we briefly explain Takimoto's (2003) ontogenetic niche-shift model. He developed a consumer–resource model including consumer size-dynamics within the consumer's life-span. Population dynamics before and after niche shift are expressed as follows:

$$\frac{dR_n(t)}{dt} = \begin{cases} rR_n(t) - aR_n(t)C_n(t) & (0 < t < T_n) \\ rR_n(t) & (T_n < t < S) \end{cases}, \quad (1a)$$

$$\frac{dW_n(t)}{dt} = \begin{cases} baR_n(t) & (0 < t < T_n) \\ \omega & (T_n < t < S) \end{cases}, \quad (1b)$$

$$\frac{dC_n(t)}{dt} = -xC_n(t) \quad (0 < t < S), \quad (1c)$$

where R_n, C_n, and W_n represent resource density, consumer density, and body mass, respectively, of the individual consumer at time t in the nth year; S is the span of 1 year and $0 < t < S$; niche shift occurs at $t = T_n$; r is the intrinsic growth rate of the resource; a is the efficiency of resource consumption by the consumer; b is the resource conversion rate to body mass by the consumer; ω is constant individual growth rate after niche shift; and x is the mortality rate of the consumer, which is constant during the life-span. Takimoto (2003) did not consider any density-dependent factors for the purposes of elucidating the stabilizing effect of the adaptive timing of migration and facilitating the analysis.

Integrating Eq. 1 for each interval, Takimoto (2003) obtained the following between-generation dynamics (see Takimoto 2003 for the process used):

$$R_{n+1}(0) = R_n(0) \exp\left[rS - \frac{a}{x}C_n(0)\{1 - \exp(-xT_n)\}\right] \quad (2a)$$

$$C_{n+1}(0) = c\{W_n(T_n) + \omega(1 - T_n)\}C_n(0) \exp\{-xS\}, \quad (2b)$$

where

$$W_n(T_n) = \int_0^{T_n} baR_n(0) \exp\left[r\tau - \frac{a}{x}C_n(0)\{1 - \exp(-x\tau)\}\right] d\tau. \quad (2c)$$

and c is a constant for size-dependent reproduction. Here, the initial body mass of the consumer $W_n(0)$ was set to 0 for simplicity. Later we will analyze the local stability of this difference equation after model modification.

In this study, we modify several model assumptions for breeding migration (see Introduction). First, we assume mortality rate changes after migration. Therefore, Eq. 1c for the population dynamics of the consumer is expressed as follows:

$$\frac{dC_n(t)}{dt} = \begin{cases} -xC_n(t) & (0 < t < T_n) \\ -yC_n(t) & (T_n < t < S) \end{cases}. \quad (3)$$

where y is the mortality rate after migration.

Next, we consider $(1 - T_n/S)^z$ as the probability of reproduction when migration occurs at $t = T_n$. This decreasing function of T_n represents reduced reproductive success as a result of delays in migration. The reproductive opportunity is assumed to be completely lost if migration occurs at the end of the year. The functional form is convex toward T_n when $0 < z < 1$, and concave when $z > 1$ (Fig. 1).

We also assume the consumer survives after reproduction at a rate of s, where $s = 0$ for semelparity, and
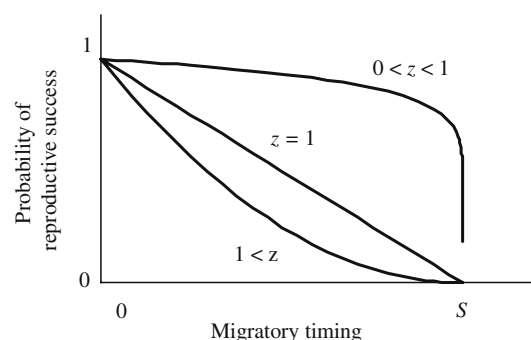

Fig. 1 Probability of reproduction with timing of migration for $z = 0.1$, 1, and 2

$0 < s < 1$ for iteroparity. W_n represents the body size of the consumer in Takimoto's model (2003) that assumes semelparity, but here we set accumulated reproductive energy in this iteroparous model. We assume that storage of reproductive energy W_n is nullified at the start of each year, such that $W_n(0) = 0$, whether or not reproduction is successful. Although this assumption may occasionally be inappropriate, it facilitates analysis of iteroparity and may be a good assumption if preparation for reproduction is energetically costly. For the same reasons we also assume the offspring of the next year are equivalent to the surviving adults in all characteristics.

Finally, substituting $\omega = 0$ for stagnant growth after migration, we obtained the following between-generation dynamics for breeding migration:

$$R_{n+1}(0) = R_n(0) \exp\left[rS - \frac{a}{x}C_n(0)\{1 - \exp(-xT_n)\}\right], \tag{4a}$$

$$C_{n+1}(0) = \{cW_n(T_n)(1 - T_n/S)^z + s\} \\ \times C_n(0) \exp\{-xT_n - y(S - T_n)\}, \tag{4b}$$

where

$$W_n(T_n) = \int_0^{T_n} baR_n(0) \exp\left[r\tau - \frac{a}{x}C_n(0)\{1 - \exp(-x\tau)\}\right]d\tau. \tag{4c}$$

Substituting $R_n(0) = R_n/cbaS$, $C_n(0) = C_n/aS$, $T_n = ST_n$, $W_n(T_n) = W_n/c$, $r = r/S$, $x = x/S$, and $y = y/S$ into Eqs. 4a–4c, we obtain the following normalized model:

$$R_{n+1} = R_n \exp\left[r - \frac{C_n}{x}\{1 - \exp(-xT_n)\}\right], \tag{5a}$$

$$C_{n+1} = \{W_n(1 - T_n)^z + s\}C_n \exp\{-xT_n - y(1 - T_n)\}, \tag{5b}$$

where

$$W_n = \int_0^{T_n} R_n \exp\left[r\tau - \frac{C_n}{x}\{1 - \exp(-x\tau)\}\right]d\tau. \tag{5c}$$

This basic model includes five nondimensional parameters (Table 1): resource growth rate (r), mortality rates at the feeding and breeding habitats (x and y, respectively), the extent of reduction of reproductive success (z), and the survival rate after reproduction (s). We then analyzed the local stability of the fixed-age, fixed-size, and adaptive plasticity models derived from this basic model, adopting the same analytical method of Takimoto (2003).

In the adaptive plasticity model we assumed the timing of migration T_n changed each year in a way which maximized per-individual fecundity ($0 \le T_n \le 1$), obtained from Eq. 5b by dividing by C_n:

$$F(T_n) = \{W_n(1 - T_n)^z + s\} \exp\{-y - (x - y)T_n\}. \tag{6}$$

Eq. 6 does not mean evolutionary fitness defined over the entire life-span, because we consider phenotypic plasticity or flexible behavioral change in the timing of migration. The model therefore assumes the migrants have a reaction norm that maximizes Eq. 6.

Results

It has been demonstrated analytically, by substituting $T_n = T$ or $W_n = W$, respectively (Appendix), that population dynamics are always locally unstable when breeding migration occurs at a specific time (fixed-age model) or level of energy storage (fixed-size model). In contrast, we found that only the adaptive plasticity model was indicative of stability (Appendix).

In the adaptive plasticity model, when the initial resource density is high (or low), it is adaptive to delay (or advance) migration. Thus, the period during which

Table 1 The symbols used in the basic model

|	Symbol	Definition
Populations	R_n	Resource density at time 0 in the nth year
	C_n	Consumer density at time 0 in the nth year
	W_n	Consumer reproductive energy at migration in the nth year
	T_n	Time of migration in the nth year
Parameters	x	Mortality rate at the feeding habitat
	y	Mortality rate at the breeding habitat
	z	Exponent of reproductive probability
	r	Resource growth rate
	s	Survival rate after reproduction

the resource is vulnerable to predation becomes longer (or shorter), which in turn reduces (or increases) its density. Takimoto (2003) called this process density-dependent negative feedback. In the fixed-age model the period during which the resource is vulnerable to predation is always constant, and thus no feedback occurs. In the fixed-size model, when the initial resource density is high (or low), the period during which the consumer remains at the feeding habitat becomes shorter (or longer), and thus the resource increases (or decreases) in the following year. This is positive feedback, which destabilizes population dynamics. These two models are, therefore, always locally unstable. We confirmed that the stabilizing effect found by Takimoto (2003) was also present under the changes in assumptions considered here (different risk of mortality, timing-dependent reproductive success or iteroparity).

We next examined the dependence of local stability in the adaptive plasticity model on the five basic model parameters (Fig. 2). The most notable trend is that the regions of stability are biased toward the lower right portion within each panel, where the breeding habitat

is safer than the feeding habitat (x is high and y is low). The reason is quite simple—if the breeding habitat is extremely dangerous, early migration is absurd. The consumer therefore remains at the feeding habitat until the end of the year, and T_n is close to 1, which corresponds to the fixed-age model, and the system then becomes unstable (Appendix). If, however, the breeding habitat is safer than the feeding habitat, optimum timing of migration is at an intermediate time determined by the trade-off between the gain in reproductive energy and the costs of mortality and the probability of reproduction. Consequently, the population dynamics are more likely to be stable when the breeding habitat is safer than the feeding habitat (Fig. 3a).

We observed an exception, however, for the semelparous condition ($s = 0$), for which the equilibrium is unstable when the breeding habitat is extremely safe (Fig. 2a). Under these conditions T_n first converges to 0, because an extremely short stay at the feeding habitat ensures the subsistence of the consumer during its life-span and maintains the reproductive opportunity. The resource density increases, however, because

Fig. 2 Dependence on model parameters of local stability for $s = 0$ (**a**), 0.2 (**b**), 0.4 (**c**), and 0.6 (**d**). In each *small panel*, the *horizontal* and *vertical* axes represent the mortality rates at the feeding and breeding habitats (x and y), respectively. We arranged these panels along the exponent of the probability of reproduction ($z = 0.1$, 1, and 2) and the resource growth rate ($r = 2$, 4, and 6). The *white* and *black* areas represent regions in which the equilibrium is locally stable or unstable, respectively
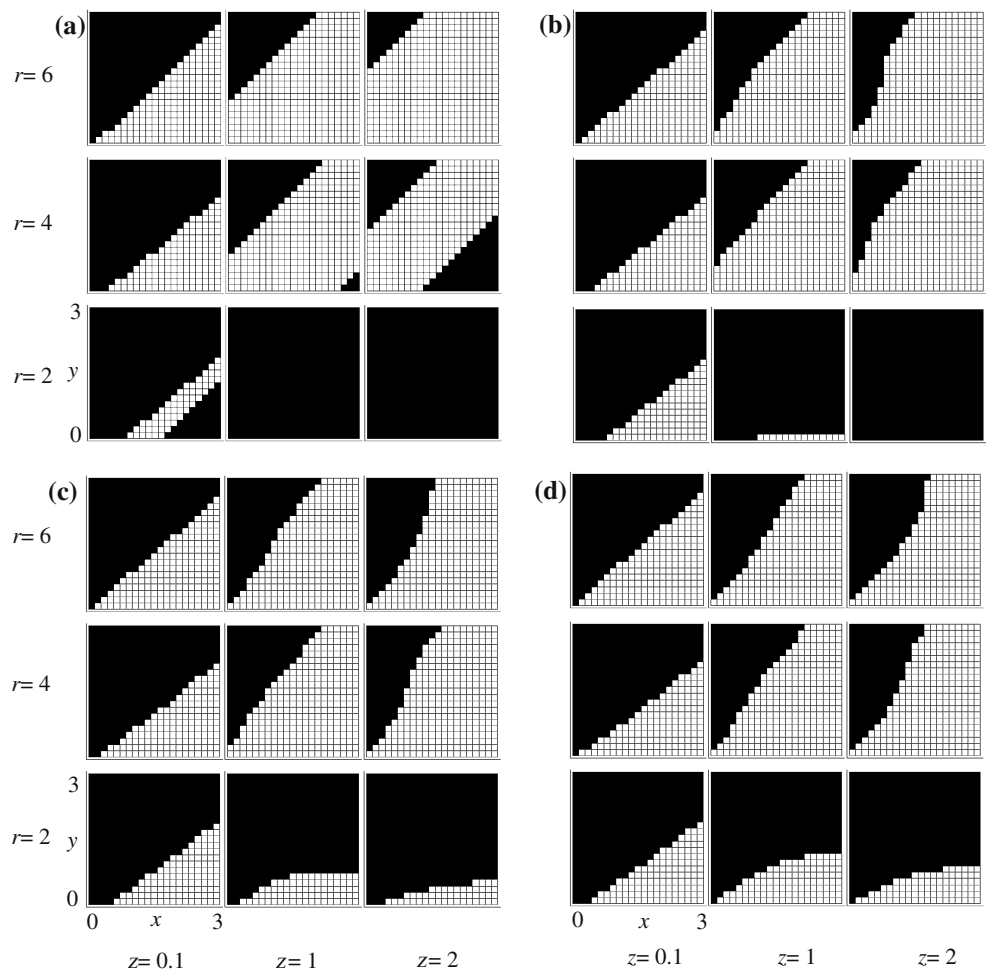
of the release from consumption, and the increased energy gain (W_n) outweighs the costs of mortality and the probability of reproduction, causing T_n to increase. T_n therefore fluctuates between 0 and a specific value (Fig. 3b). The regions of instability are larger for larger values of z, because T_n also becomes more likely to converge to 0 to ensure reproductive opportunity. Enlargement of unstable regions may extinguish stable regions (Fig. 2a, $r = 2$, $z = 1$ and 2). When s is high, this mechanism does not work because the need for earlier migration declines in anticipation of future reproduction.

Another notable result is that the region of stability expands with an increase in resource growth rate (r; Fig. 2). When r is very low, reproductive energy (W_n) is small, and thus T_n approaches 0, because the costs of mortality and the reduced probability of reproduction become relatively large. Thereafter, T_n increases because of the recovery of the resource density, and then fluctuates. The equilibrium is, therefore, likely to be unstable when r is low.

The exponent of the probability of reproduction (z) and the survival rate after reproduction (s) have complicated effects on the stability. First, the region of stability usually shrinks with an increase in z when the resource growth rate (r) is low, whereas it expands when r is high (Fig. 2). T_n should decrease with in-creases in z, because it becomes more difficult to ensure a reproductive opportunity. Thus, T_n is more likely to approach 0 (and then fluctuate) when z is high. This is greater when r is lower, because lower r also facilitates convergence to 0. In contrast, an increase in z prevents T_n from converging to 1, because of the same mechanism. This effect is evident when r is higher, because T_n is more likely to approach to 1 when r is high. Convergence of T_n to extreme values (0 or 1) indicates the population dynamics are unstable (Appendix). Thus, z has a stabilizing effect when r is high. We found that z has opposite effects, depending on r.

The region of stability shrinks with increases in s when r is high, whereas it expands when r is low (compare panels arranged at the same coordinates in Figs. 2a–d). In contrast with z, T_n should decline with a decrease in s because of the lower probability of future reproduction (in the extreme case, semelparous species have only a single reproductive opportunity and should avoid delaying migration, so they do not to lose this opportunity). Thus, if r is low and T_n is likely to ap-proach 0 (and then fluctuate), it is more likely to do so when s is low. If, in contrast, r is high, T_n is more likely to converge to 1 when s is high. s therefore has a sta-bilizing effect when r is low and a destabilizing effect when r is high.

Fig. 3 Dynamics of resource and consumer densities and timing of migration in **a** stable and **b** unstable regions; $r = 4$ (**a**) and 2 (**b**); $x = 3$, $y = 1$, $z = 0.1$, and $s = 0$
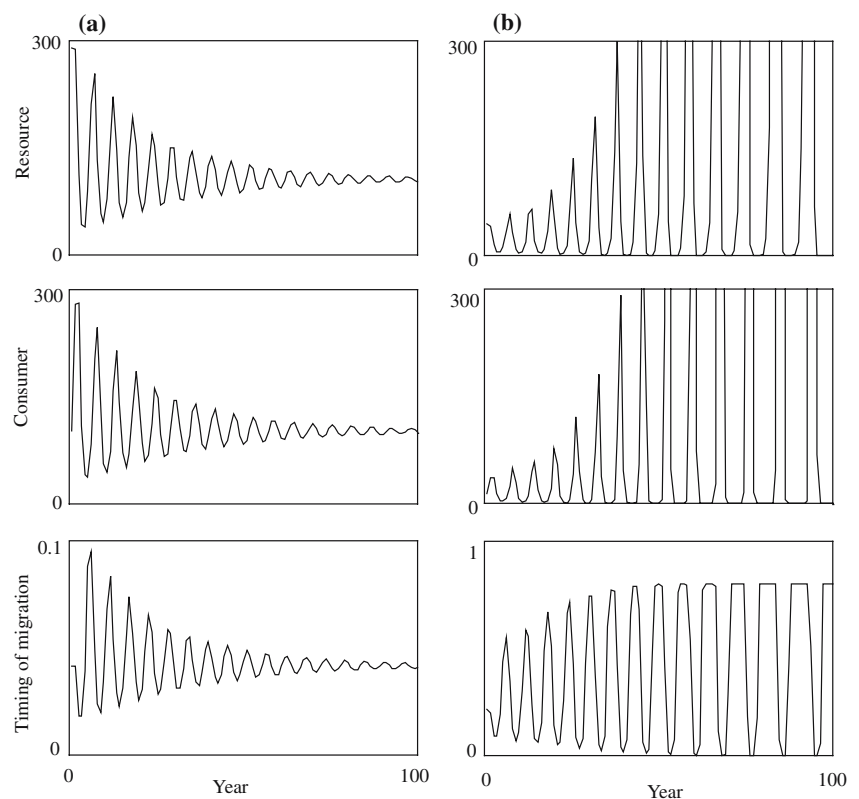
Finally, we summarize the conditions for a stable equilibrium:

– the timing of migration is adaptively plastic;
– the breeding habitat is safer than the feeding habitat;
– the feeding habitat has abundant resources;
– if the feeding habitat is poor, reproductive success is weakly reduced with a delay in migration or the survival rate after reproduction is high; and
– if the feeding habitat is rich, reproductive success is severely reduced or survival is low.

Discussion

Ontogenetic habitat shifts are observed for many animals (Wilbur 1980; Werner and Gilliam 1984) and theoretical works have been performed on the phenomenon. Some models consider population dynamics that include ontogenetic niche shifts (e.g. Hastings 1983, 1984; McCann and Yodzis 1998) whereas others consider adaptive strategies in terms of life-history evolution (e.g. Krivan 1997; Weber et al. 1998; Kokko 1999; van Baalen et al. 2001; Claessen and Dieckmann 2002). Few researchers, however, have considered both processes (cf. De Roos et al. 2002). In this respect, the ontogenetic niche-shift model of Takimoto (2003) is outstanding. His model is, however, too simple for most examples in nature. We therefore modified the assumptions of the original model to consider breeding migration (Introduction).

We confirmed that this model was stable only under conditions of adaptive plasticity, despite many differences in the model assumptions. This result corroborates the idea that, in the context of the model studied here, adaptive plasticity in the timing of niche shift has more effect on population stability than some other model changes, for example risk of mortality or iteroparity.

The adaptive plasticity model was not always stable, however, and some conditions were necessary for stability. The equilibrium is more likely to be stable when the breeding habitat is safer than the feeding habitat (x is high and y is low) and the feeding habitat is rich (r is high; Fig. 2). According to Takimoto (2003), who assumed a constant mortality rate throughout the lifespan, local stability was achieved if the mortality rate was intermediate (see Fig. 2 in Takimoto 2003). Our results, in contrast, imply that not only adaptive plasticity in the timing of migration but also adaptive habitat choice, which means growing in a rich habitat and breeding in a safe habitat, if possible, contributes to population stability. In animals that migrate for

breeding, one of the purposes of the habitat shift is pursuit of the safety area (Northcote 1978). We believe this is a highly suggestive concept, not only ecologically but also evolutionarily.

Takimoto (2003) showed that the equilibrium of the adaptive plasticity model was unstable within a substantial range of values if growth rate after niche shift was very low (Fig. 2 in Takimoto 2003). Our results suggest, however, that if the risk of mortality changes after niche shift, the adaptive plasticity model could be stable, even when the individual growth rate is 0. Our predictions make an important suggestion with regard to the general dynamics of models that include ontogenetic niche shifts. The risk of mortality may change with a shift in resource use even if environmental factors do not change, because different foraging strategies are believed to be necessary for use of different resources (Werner and Gilliam 1984). It is, therefore, also suggested that a reduced risk of mortality in later stages of the life history would also contribute to the population stability of animals for which there is a shift in resource use without a change in habitat. Some animals may stop resource consumption during the breeding season. Our model can be applied to such cases even if breeding migration does not occur. The probability of stable population dynamics should be greater than that predicted by Takimoto's (2003) ontogenetic niche-shift model.

The ontogenetic niche-shift model may be applicable to other problems. There are, for example, many theoretical studies of optimal age at maturity (Abrams and Rowe 1996; Takada and Caswell 1997). Our model formulation could be applied to this problem as a special case of semelparity if resource consumption or individual growth is suppressed after sexual maturity. We think our predictions could be useful because previous studies have been mainly concerned with evolutionary aspects of this problem.

Our study may also be applicable to the adaptive switching theory in consumer–resource systems (Holt 1984; Abrams 1999). In general, optimum switching may promote persistence of nonequilibrium dynamics (Abrams 1999) whereas the habitat switch in the current model contributed to local stability. Takimoto (2003) discussed this point briefly, and stated that the difference between his results and earlier results was because of the combination of differential and difference equations for within-year and between-year dynamics. This means population dynamics are locally stable from the viewpoint of between-year dynamics but unstable from the viewpoint of within-year dynamics, because they oscillate periodically (refer to

Takimoto 2003 for further discussion). It would be intriguing to consider how population stability is affected by a change in the risk of mortality because of sexual maturity or switching.

We found that reproductive success depends on the timing of migration and that survival rate after reproduction had complex effects on population stability. These parameters were not included in the original model (Takimoto 2003). In our model we assumed constant values for them. It is more realistic, however, to assume that these parameters fluctuate depending on a variety of factors (e.g. reproductive effort), because a trade-off should occur among some reproductive traits from the viewpoint of evolutionary ecology (Stearns 1992). For example, the mortality rate of reproducing individuals may increase with increasing reproductive effort (Stearns 1992). Reproductive effort may also depend on environmental factors, for example resource availability or predation risk (Bronson 1989). If both these conditions are satisfied, the following logic may occasionally be valid: when resources are abundant, reproductive effort is high and the survival rate of parents is reduced because of the trade-off, resulting in a negative correlation between survival rate after reproduction and resource availability. According to our results, population dynamics are more likely to be stable when r is low and s is high, or when r is high and s is low (Fig. 2). The negative correlation, if any, may therefore result in a greater probability of stability. For this to occur, reproductive effort (c in Eq. 4b) must be negatively correlated with s, and optimized each year, depending on resource availability or expected reproductive output. Further analysis and empirical research are required to address this with any certainty, however.

Our modified ontogenetic niche-shift model still retains several simplifications, even though we modified Takimoto's (2003) original model. For example, we did not consider density-dependence, stage structure, size structure, spatial structure, environmental fluctuations, nonlinear consumer functional or numerical responses, and individual variation. Most notably, we assumed identical characteristics for surviving parents and newborns. These simplifications enabled us to use an analytical approach. In future work, however, it will be necessary to conduct numerical studies by developing more realistic (but more complicated) models that take these assumptions into account (cf. Claessen and Dieckmann 2002; De Roos et al. 2002). When a carrying capacity of resource dynamics is assumed, for example, we expect a greater probability of stability, because it has the same effect as density-dependent negative feedback.

The stability conditions would also change with nonlinear interaction (refer to Oaten and Murdoch 1975a, b, 1977; Levin 1977 for the analysis of the effects of consumer functional response on population stability for exponential resource growth rates). Levin (1977), for example, showed that stabilizing functional response was not always necessary for population stability if the mortality rate of the consumer was density-dependent.

In addition, we assumed no cost of migration. Migration itself can be costly (Baudinette and Schmidt-Nielsen 1974; Owen and Black 1989; Rankin and Burchsted 1992; Witter and Cuthill 1993; Kinnison et al. 2003), especially long-distance migration. If the cost of migration depends on energy storage or the timing of migration, it should affect the optimum timing of migration. This consideration may produce different results and should be incorporated into future models. If, however, the cost of migration is independent of these factors and similarly imposed on all migrants irrespective of the timing of migration, the cost term is integrated with c in Eq. 4b, which represents reproductive efficiency. Under these conditions we can conclude that stability is independent of the cost of migration.

We modeled breeding migration in the simplest manner by assuming that migrants grow at the feeding habitat and migrate to a different habitat for reproduction. Because of insufficiency of the model assumptions mentioned above, however, the model would fail to predict real population stability. For example, population may occasionally be stable even without adaptive plasticity. There is, in fact, little evidence for population cycle in birds (Kendall et al. 1998), even though migratory timing does not change very much; this may be related to foraging in breeding habitat and interactions with other species. We argue, however, that adaptive plasticity has a potentially stabilizing effect.

Our results, especially the dependence of stability on the values of specific parameters, will depend on details of the model assumptions, for example the functional form of the probability of reproduction or the size-dependence of the cost of migration. Although there have been many empirical studies of breeding migration, few have investigated the actual forms of these factors. Furthermore, little is known about the relative risk of mortality at each stage of life-history during the life-span for many animals for which habitat shift is observed. This study would provide useful predictions of the population stability of migrating animals, which is still unsolved because of the large number of unknowns.

Appendix

Here, we analytically illustrate that both fixed-age and fixed-size models are always unstable and only adaptive plasticity model can be stable, basically following Takimoto (2003).

We define the right hand sides of Eqs. 5a and 5b as F_R and F_C, respectively. The equilibrium (R^* and C^*) is locally stable if the absolute values of both roots of the following equation are <1.

$$x^2 - (a_{11} + a_{22})x + a_{11}a_{22} - a_{12}a_{21} = 0, \qquad (A1a)$$

where

$$\begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} = \begin{pmatrix} \frac{\partial F_R}{\partial R_n}\Big|_{R^*,C^*} & \frac{\partial F_C}{\partial R_n}\Big|_{R^*,C^*} \\ \frac{\partial F_R}{\partial C_n}\Big|_{R^*,C^*} & \frac{\partial F_C}{\partial C_n}\Big|_{R^*,C^*} \end{pmatrix}. \qquad (A1b)$$

This condition is satisfied (Edelstein-Keshet 1988; see also Takimoto 2003) when:

$$2 > 1 + a_{11}a_{22} - a_{12}a_{21} > |a_{11} + a_{22}|. \qquad (A2)$$

In the fixed-age model, the timing of migration is fixed by setting $T_n = T$, and the equilibrium is

$$R^* = \frac{W^*}{\int_0^T \exp\left[r\tau - \frac{C^*}{\mu}\{1 - \exp(-x\tau)\}\right]d\tau}, \qquad (A3a)$$

$$C^* = \frac{rx}{1 - \exp(-xT)}, \qquad (A3b)$$

where

$$W^* = \frac{\exp\{y + (x - y)T\} - s}{(1 - T)^z}. \qquad (A3c)$$

Furthermore:

$$a_{11} = \frac{\partial F_R}{\partial R_n}\Big|_{R^*,C^*} = 1, \qquad (A4a)$$

$$a_{12} = \frac{\partial F_R}{\partial C_n}\Big|_{R^*,C^*} = -\frac{R^*}{x}\{1 - \exp(-xT)\}, \qquad (A4b)$$

$$a_{21} = \frac{\partial F_C}{\partial R_n}\Big|_{R^*,C^*} = C^*(1 - T)^z \exp\{-y - (x - y)T\}$$
$$\times \int_0^T \exp\left[r\tau - \frac{C^*}{x}\{1 - \exp(-x\tau)\}\right]d\tau, \qquad (A4c)$$

$$a_{22} = \frac{\partial F_C}{\partial C_n}\Big|_{R^*,C^*} = 1 - \frac{R^*C^*}{x}(1 - T)^z \exp\{-y - (x - y)T\}$$
$$\times \int_0^T \{1 - \exp(-x\tau)\} \exp\left[r\tau - \frac{C^*}{x}\{1 - \exp(-x\tau)\}\right]d\tau. \qquad (A4d)$$

Therefore,

$$1 + a_{11}a_{22} - a_{12}a_{21}$$
$$= 2 + \frac{R^*C^*}{x}(1 - T)^z \exp\{-y - (x - y)T\}$$
$$\times \int_0^T \{\exp(-x\tau) - \exp(-xT)\}$$
$$\times \exp\left[r\tau - \frac{C^*}{x}\{1 - \exp(-x\tau)\}\right]d\tau. \qquad (A5)$$

Eq. A5 is >2 because the second term in Eq. A5 is not negative for $0 < t < T$ ($0 \le T \le 1$), and thus A2 is not satisfied. Therefore, the equilibrium of the fixed-age model is always locally unstable.

In the fixed-size model, consumer reproductive energy at the time of migration is fixed by setting $W_n = W$, and the equilibrium is

$$R^* = \frac{W}{\int_0^{T^*} \exp\left[r\tau - \frac{C^*}{x}\{1 - \exp(-x\tau)\}\right]d\tau}, \qquad (A6a)$$

$$C^* = \frac{r\mu}{1 - \exp(-xT^*)}, \qquad (A6b)$$

where T^* is obtained by solving the equation:

$$W = \frac{\exp\{y + (x - y)T^*\} - s}{(1 - T^*)^z}. \qquad (A6c)$$

Furthermore,

$$a_{11} = \frac{\partial F_R}{\partial R_n}\Big|_{R^*,C^*} = 1 - R^*C^* \exp(-xT^*)\frac{\partial T_n}{\partial R_n}\Big|_{R^*,C^*}, \qquad (A7a)$$

$$a_{12} = \frac{\partial F_R}{\partial C_n}\Big|_{R^*,C^*} = -R^*\left\{\frac{1 - \exp(-xT^*)}{x} + C^* \exp(-xT^*)\frac{\partial T_n}{\partial C_n}\Big|_{R^*,C^*}\right\}, \qquad (A7b)$$

$$a_{21} = \frac{\partial F_C}{\partial R_n}\bigg|_{R^*,C^*} = \frac{C^*}{R^*}[1 - s(1 - T^*)^z \exp\{-y - (x - y)T^*\}]$$

$$+ C^*\bigg[R^*(1 - T^*)^z \exp\{-r(1 - T^*)\} \exp\{-y - (x - y)T^*\}$$

$$- \left(x - y + \frac{z}{1 - T^*}\right)\bigg]\frac{\partial T_n}{\partial R_n}\bigg|_{R^*,C^*}, \tag{A7c}$$

$$a_{22} = \frac{\partial F_C}{\partial C_n}\bigg|_{R^*,C^*} = 1 - \frac{C^*}{\mu}[1 - s\exp\{-y - (x - y)T^*\}]$$

$$\times \frac{\int_0^{T^*}\{1 - \exp(-x\tau)\}\exp\left[r\tau - \frac{C^*}{x}\{1 - \exp(-x\tau)\}\right]\mathrm{d}\tau}{\int_0^{T^*}\exp\left[r\tau - \frac{C^*}{x}\{1 - \exp(-x\tau)\}\right]\mathrm{d}\tau}$$

$$+ C^*\bigg(\frac{[1 - s\exp\{-y - (x - y)T^*\}]\exp\{-r(1 - T^*)\}}{\int_0^{T^*}\exp\left[r\tau - \frac{C^*}{\mu}\{1 - \exp(-x\tau)\}\right]\mathrm{d}\tau}$$

$$+ \frac{sz\exp\{-y - (x - y)T^*\}}{1 - T^*} - \left(x - y + \frac{z}{1 - T^*}\right)\bigg)\frac{\partial T_n}{\partial C_n}\bigg|_{R^*,C^*}, \tag{A7d}$$

where

$$\frac{\partial T_n}{\partial R_n}\bigg|_{R^*,C^*} = -\frac{\exp\{r(1 - T^*)\}}{R^*}$$

$$\times \int_0^{T^*}\exp\left[r\tau - \frac{C^*}{x}\{1 - \exp(-x\tau)\}\right]\mathrm{d}\tau, \tag{A7e}$$

$$\frac{\partial T_n}{\partial C_n}\bigg|_{R^*,C^*} = \frac{\exp\{r(1 - T^*)\}}{x}\int_0^{T^*}\{1 - \exp(-x\tau)\}$$

$$\times \exp\left[r\tau - \frac{C^*}{x}\{1 - \exp(-x\tau)\}\right]\mathrm{d}\tau. \tag{A7f}$$

The partial derivatives Eqs. A7e and A7f are calculated from Eq. 5c. Then,

$$1 + a_{11}a_{22} - a_{12}a_{21}$$

$$= 2 + C^*\exp(-xT^*)\exp\{r(1 - T^*)\}$$

$$\times \int_0^{T^*}\exp\left[r\tau - \frac{C^*}{x}\{1 - \exp(-x\tau)\}\right] + \frac{C^*}{x}\exp\{r(1 - T^*)\}$$

$$\times \left[x - y + \frac{z}{1 - T^*} - \frac{sz\exp\{-y - (x - y)T^*\}}{1 - T^*}\right]$$

$$\times \int_0^{T^*}\{\exp(-x\tau) - \exp(-xT^*)\}$$

$$\times \exp\left[r\tau - \frac{C^*}{x}\{1 - \exp(-x\tau)\}\right]\mathrm{d}\tau. \tag{A8a}$$

$$a_{11} + a_{22} = 2 + C^*\exp(-xT^*)\exp\{r(1 - T^*)\}$$

$$\times \int_0^{T^*}\exp\left[r\tau - \frac{C^*}{x}\{1 - \exp(-x\tau)\}\right]\mathrm{d}\tau - \frac{C^*}{x}\exp\{r(1 - T^*)\}$$

$$\times \left(x - y + \frac{z}{1 - T^*} - \frac{sz\exp\{-y - (x - y)T^*\}}{1 - T^*}\right)$$

$$\times \int_0^{T^*}\{1 - \exp(-x\tau)\}\exp\left[r\tau - \frac{C^*}{x}\{1 - \exp(-x\tau)\}\right]\mathrm{d}\tau. \tag{A8b}$$

If $x - y + \frac{z}{1-T^*} - \frac{sz\exp\{-y-(x-y)T^*\}}{1-T^*} > 0$, Eq. A8a is >2 and condition A2 is not satisfied. If $x - y + \frac{z}{1-T^*} - \frac{sz\exp\{-y-(x-y)T^*\}}{1-T^*} < 0$, Eq. A8b is >2 and, again, condition A2 is not satisfied. Therefore, the equilibrium of the fixed-size model is always locally unstable.

In the adaptive plasticity model, the per-individual fecundity Eq. 6 is maximized every year, and the equilibrium is:

$$R^* = \frac{W^*}{\int_0^{T^*}\exp\left[r\tau - \frac{C^*}{x}\{1 - \exp(-x\tau)\}\right]\mathrm{d}\tau}, \tag{A9a}$$

$$C^* = \frac{rx}{1 - \exp(-xT^*)}, \tag{A9b}$$

where

$$W^* = \frac{\exp\{y + (x - y)T^*\} - s}{(1 - T^*)^z}. \tag{A9c}$$

Differentiation of Eq. 6 by T_n produces

$$\frac{\mathrm{d}F}{\mathrm{d}T_n} = \exp\{-y - (x - y)T_n\}(1 - T_n)^z$$

$$\times \left\{\frac{\partial W_n}{\partial T_n} - \left(x - y + \frac{z}{1 - T_n}\right)W_n - \frac{s(x - y)}{(1 - T_n)^z}\right\}. \tag{A10}$$

Therefore, we can obtain T^* numerically from the equation:

$$\frac{[1 - s\exp\{-y - (x - y)T^*\}]\exp\{-r(1 - T^*)\}}{\int_0^{T^*}\exp\left[r\left\{\tau - \frac{1 - \exp(-x\tau)}{1 - \exp(-x\overline{T})}\right\}\right]\mathrm{d}\tau}$$

$$- \left[x - y + \frac{z}{1 - T^*} - \frac{sz\exp\{-y - (x - y)T^*\}}{1 - T^*}\right] = 0. \tag{A11}$$

The left side of Eq. A11 is $+\infty$ when $T^* = 0$ and $-\infty$ when $T^* = 1$, and we have confirmed the solution is always between 0 and 1. Then:

$$a_{11} = \left.\frac{\partial F_R}{\partial R_n}\right|_{R^*,C^*} = 1 - R^* C^* \exp(-xT^*)\left.\frac{\partial T_n}{\partial R_n}\right|_{R^*,C^*}, \quad \text{(A12a)}$$

$$a_{12} = \left.\frac{\partial F_R}{\partial C_n}\right|_{R^*,C^*} = -R^*\left\{\frac{1-\exp(-xT^*)}{x}\right. \\ \left. + C^* \exp(-xT^*)\left.\frac{\partial T_n}{\partial C_n}\right|_{R^*,C^*}\right\}, \quad \text{(A12b)}$$

$$a_{21} = \left.\frac{\partial F_C}{\partial R_n}\right|_{R^*,C^*} = \frac{C^*}{R^*}[1 - s\exp\{-y-(x-y)T^*\}], \quad \text{(A12c)}$$

$$a_{22} = \left.\frac{\partial F_C}{\partial C_n}\right|_{R^*,C^*} = 1 - \frac{1}{x}(C^*-r) \\ \times [1 - s\exp\{-y-(x-y)T^*\}] - \frac{1}{x}[1 - \exp\{r(1-T^*)\}] \\ \times \left[x-y+\frac{z}{1-T^*} - \frac{sz\exp\{-y-(x-y)T^*\}}{1-T^*}\right] \quad \text{(A12d)}$$

where

$$\left.\frac{\partial T_n}{\partial R_n}\right|_{R^*,C^*} = \frac{s\exp\{-y-(x-y)T^*\}\left(1-\frac{z}{1-T^*}\exp\{r(1-T^*)\}\int_0^{T^*}\exp\left[r\tau-\frac{C^*}{x}\{1-\exp(-x\tau)\}\right]d\tau\right)}{R^*\left\{C^*\exp(-xT^*)-r+\left(x-y+\frac{z}{1-T^*}\right)\right\}+\frac{z\exp\{r(1-T^*)\}}{(1-T^*)^{z+1}}\left[\frac{\exp\{y+(x-y)T^*\}}{1-T^*}+s\left(x-y-\frac{1}{1-T^*}\right)\right]}, \quad \text{(A12e)}$$

$$\left.\frac{\partial T_n}{\partial C_n}\right|_{R^*,C^*} = \frac{R^*}{xC^*}$$

$$\times \frac{C^*\{\exp(-xT^*)-1\}+\left(x-y+\frac{z}{1-T^*}\right)\left\{1-[1-\exp\{r(1-T^*)\}]\left(1-(C^*-r)\int_0^{T^*}\exp\left[r\tau-\frac{C^*}{x}\{1-\exp(-x\tau)\}\right]d\tau\right)\right\}}{R^*\left\{C^*\exp(-xT^*)-r+\left(x-y+\frac{z}{1-T^*}\right)\right\}+\frac{z\exp\{r(1-T^*)\}}{(1-T^*)^{z+1}}\left[\frac{\exp\{y+(x-y)T^*\}}{1-T^*}+s\left(x-y-\frac{1}{1-T^*}\right)\right]}. \quad \text{(A12f)}$$

Using Eq. A12 we have numerically examined the local stability of the adaptive plasticity model.

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