BREEDING SUPPRESSION AND PREDATOR–PREY DYNAMICS

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Abstract. In a biotic environment, current reproduction will affect future population sizes, but these future changes may also affect the optimality of current reproductive decisions. We investigate the dynamics of predator–prey cycles if both predators and prey respond to each other's (and their own) population density by adjusting their breeding effort. We find that adaptive breeding strategies of predators can produce equally profound changes to the dynamics as those produced by analogous strategies of their prey. Contrary to earlier, more limited models, we find that breeding suppression can be either destabilizing (i.e., generating cycles or chaotic behavior) or stabilizing, in cases where predators, prey, or both can adopt adjustable strategies. The direction of change depends on the shape of the density dependence in the growth rates, as well as how it is affected by the breeding decisions. We discuss these findings in light of the Fennoscandian vole cycle, where antipredatory behavior of voles has been evoked to explain some properties of the cycle, and where many predators show pronounced variability in their breeding effort according to the phase of the cycle.

Key words: antipredatory behavior; behavioral mechanism; breeding suppression; cyclicity; density dependence; predation; predator–prey dynamics; population dynamics; survival; vole.

INTRODUCTION

Much of life history theory concerns the optimal timing of reproductive effort (Roff 1992). Specifically, in a variable environment (either predictable or unpredictable), individuals are expected to take advantage of favorable conditions and vary their reproductive output accordingly (e.g., Kisdi et al. 1998). If the important aspects of the environment are biotic, this gives rise to an interesting interaction between current reproductive decisions and the future environment. Current reproduction obviously affects future population sizes, but the future population size will partly determine the reproductive rate that is optimal at present, as it forms the future environment that the offspring will face (Hirschfield and Tinkle 1975, Mangel et al. 1994). In such cases, an evolutionarily stable strategy of behavior (i.e., a reaction norm of reproduction) will also determine the population-level dynamical properties that will emerge from the life history strategies of individuals.

Recently, much interest has focused around the question of optimal breeding adjustment in predator–prey cycles. This question forms a two- or multi-species example of the above two-way interaction. It has been suggested that antipredatory behavior can give rise to

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predator–prey cycles (Abrams and Matsuda 1997*a, b*), that breeding suppression is an adaptive mechanism of prey individuals to avoid predation (Magnhagen 1991), and, specifically, that this phenomenon could explain at least some properties of the Fennoscandian vole cycles (Ylönen 1994). According to this hypothesis, enhanced survival brings about a selective advantage for females that raise smaller broods or delay breeding until more favorable conditions exist (Ylönen 1994, Koskela and Ylönen 1995). This would enhance the crash in prey population density, thus encouraging the persistence of cycles. However, although observational and experimental evidence exists that supports the notion of suppressed breeding as an antipredatory behavior of voles (Heikkilä et al. 1993, Korpimäki et al. 1994, Ylönen and Ronkainen 1994, Koskela and Ylönen 1995, Norrdahl and Korpimäki 1995, Mappes and Ylönen 1997), it is currently disputed whether this effect is real and whether it occurs in nature at all (Lambin et al. 1995, Wolff and Davis-Born 1997, Klemola et al. 1998, Mappes et al. 1998, Prévot-Julliard et al. 1999). Likewise, theoretical models addressing the possibility of the evolution of breeding suppression have given mixed results (Kokko and Ranta 1996, Kaitala et al. 1997). It has also been suggested that breeding suppression would not maintain cycles, but instead stabilize the dynamics (Gyllenberg et al. 1996, Ruxton and Lima 1997).

On the other hand, the evidence that predators react

TABLE 1. List of predator species with documented reductions in brood or clutch sizes, or that refrain from breeding altogether, in years with low prey density.

Species	Common name	Literature citations
Aegolius funereus	Tengmalm's Owl	Korpimäki (1987, 1989)
Strix uralensis	Ural Owl	Pietiäinen (1988), Pietiäinen and Kolunen (1993)
Strix aluco	Tawny Owl	Southern (1970)
Bubo virginianus	Great Horned Owl	Houston and Francis (1995)
Nyctea scandiaca	Snowy Owl	Portenko (1972)
Buteo lagopus	Rough-legged Buzzard	Hagen (1969)
Circus cyaneus	Northern Harrier	Simmons et al. (1986)
Accipiter gentilis	Goshawk	Sulkava (1964)
Falco tinnunculus	Eurasian Kestral	Korpimäki and Wiehn (1998)
Alopex lagopus	Arctic fox	Angerbjörn et al. (1995), Kaikusalo and Angerbjörn (1995), Tannerfeldt and Angerbjörn, (1998)

to low densities of their prey is overwhelming. Reduced brood or clutch sizes, or refraining from breeding altogether in years with low prey density, have been observed in several predator species (Table 1). In view of the considerable effort expended in search of the (possibly subtle) effects of predation risk on prey reproduction, it is surprising that both verbal and mathematical models of predator–prey cycles have so far neglected the effects of predators adjusting their breeding output (e.g., Korpimäki and Krebs 1996). Furthermore, intraspecific interactions should not be neglected: vole population size itself has an adverse effect on vole reproduction and may delay maturation of young voles (Kalela 1957, Rodd and Boonstra 1984, Nakata 1989, Pusenius and Viitala 1993, Ostfeld and Canham 1995, Saitoh et al. 1997). Together with the possibility of similar responses in the predator species, such factors should be taken into account when striving towards better understanding of cyclicity.

THE DYNAMIC CONSEQUENCES OF BREEDING SUPPRESSION

We illustrate the requirements for breeding adjustment to generate cycles through the relationship between breeding adjustment and density dependence. Density dependence is the critical determinant of the emerging dynamics. As a general rule of thumb, a steep reduction in population growth with increasing density implies unstable dynamics. As a simple illustrative example, consider a hypothetical one-species model where reproductive success decreases with density (Fig. 1). The type of dynamics in Fig. 1A marked with a solid line (alternative 1) is stable, since the slope of population growth rate at the equilibrium is shallow, whereas it is unstable in Fig. 1B due to the steep slope of population growth rate at equilibrium. Now, if it were optimal for individuals in the populations shown in Fig. 1A and Fig. 1B to suppress breeding at high densities (perhaps because survival prospects of juveniles would be very low in a competitive environment), this would affect the shape of the population growth curve. Density dependence would also be affected, since reproduction decreases or ceases at high

density. The new curve might take several alternative shapes depending on the exact breeding strategies of individuals and on the relationship between survival, density, and breeding effort (alternatives 2 and 3 in Fig. 1A, B). It is important to realize that behavioral reductions in reproduction at high density produce density dependence in population growth rates, as do direct factors, such as lowered survival.

When the population-wide effects of breeding suppression, i.e., a reduction in the growth rate at unfavorable conditions, are added to this simple model of population growth, it turns out that qualitative changes in the dynamics are possible in either direction: originally stable dynamics may remain stable or become destabilized (Fig. 1A), and originally unstable dynamics may stay unstable or become stable (Fig. 1B). Without knowledge of the density-dependent growth rates of both the "original" and the suppression-affected population, there is no a priori way to tell the direction in which suppression will affect the dynamics.

Both the breeding suppression strategies and the stability conditions become still more complicated in two-species systems such as predator–prey interactions. If breeding suppression occurs at unfavorable conditions, this means high predator density for the prey, but low prey density for the predator. In addition, high density of conspecifics might imply lower survival in either species (although a dilution effect of predation risk might have an opposite effect in the prey, i.e., increasing per capita survival of prey with increasing prey density).

All of these effects can be combined into a phase plane that describes the regions of increase and decrease in the prey and predator populations (Fig. 2). The null isoclines give the threshold of zero growth for each of the two species, and their intersection specifies the equilibrium point. The four slopes (i.e., rate of change in the growth rate of the prey or predator for a unit increase in the prey or predator population, measured at the equilibrium) of the surfaces that describe population growth (and pass from positive to negative values at the null isocline) determine local stability at this equilibrium (May 1973). Cyclicity in
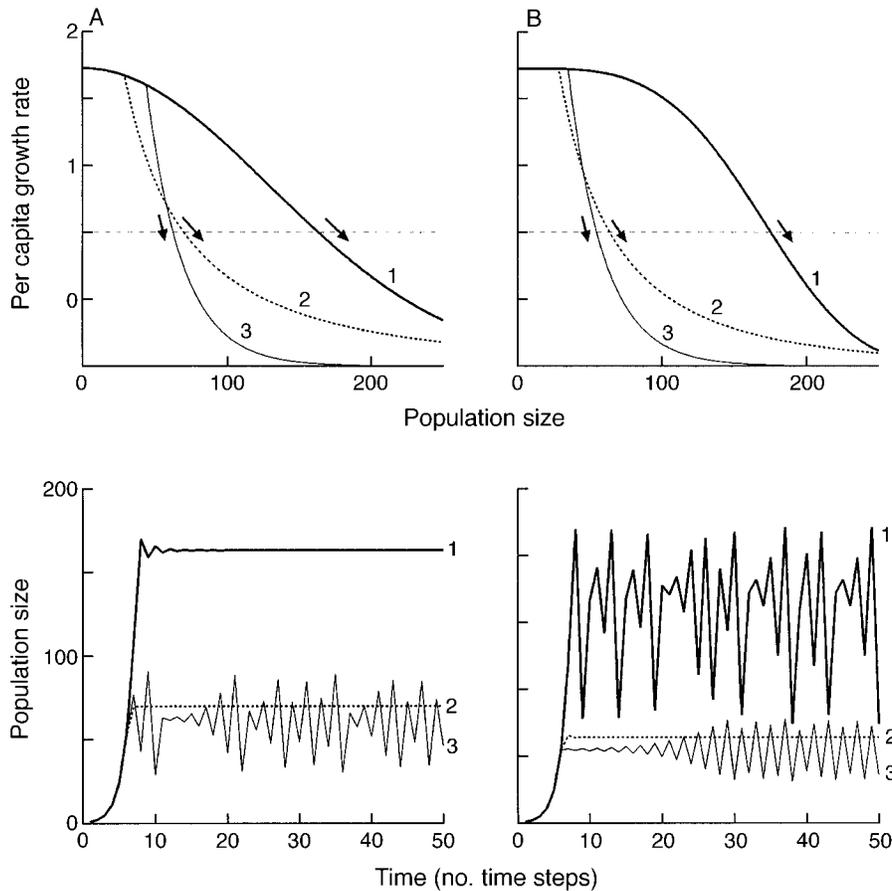
FIG. 1. Breeding suppression in a single-species model, where the original dynamics were (A) stable, or (B) unstable. The upper panels show three different density-dependent per capita growth rates: in example 1, it was assumed that reproduction was maximal regardless of population density, but that growth rates decreased with density because of lower survival; in examples 2 and 3, it was assumed that breeding effort decreased after a threshold density, such that growth rates dropped more rapidly with population size than in example 1. The lower panels give the corresponding dynamics. Population equilibrium size was smaller with than without breeding suppression, whereas the slope of density dependence at equilibrium, marked with arrows, was either steeper or shallower in the suppressed alternatives, compared to the original density dependence. Hence, the new dynamics may be either stable or unstable, regardless of whether the original dynamics was stable or unstable.

population dynamics requires that the equilibrium point of the predator–prey system is locally unstable (or, as a limit case, neutrally stable).

Assuming that breeding suppression corresponds to reduced growth rates in a part of the phase plane, the area of negative growth will either increase or remain the same in Fig. 2, if either species suppresses breeding. This means a shift downwards or to the left in the prey null isocline (if the prey suppresses), or a shift downwards or to the right in the predator isocline (if the predator suppresses). These shifts imply that the equilibrium population sizes will shift as well. However, as in the example of Fig. 1, the movement of the equilibrium does not yet tell how the slopes at equilibrium will change. Depending on whether they become steeper or shallower, we may observe opposite changes in the dynamics.

It is easy to find examples where breeding output is reduced and stability conditions (May 1973) are either met or not met at the new equilibrium point. As a particularly tractable two-species example, we assume an equal mortality rate for mature prey of any age, such that cycles will not be generated by a senescence-related mechanism (Boonstra 1994). This rate may, however, differ from the rate for immature prey. We will use X and Y to represent the prey and predator populations, respectively. The juvenile (immature) parameters are denoted by lowercase lettering throughout (subscripts x and y). We assume that juveniles enter the adult population after one generation, so that the adult population size can be used as a basis for density dependence. Denoting the survival probability from one breeding opportunity to the next by S_X and s_x for mature and immature prey, respectively, and the brood size by
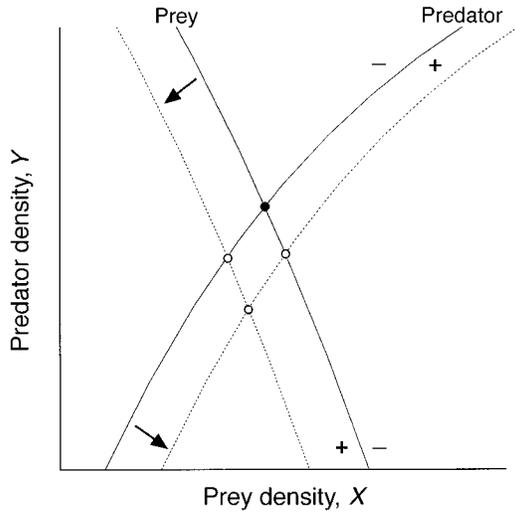
FIG. 2. A schematic presentation of the effect of breeding suppression to population equilibrium densities. Solid lines give the null isoclines for both predator and prey, with positive growth below the corresponding line; the solid circle marks the equilibrium. If parent and offspring survival in breeding individuals are not so small that subsequent population size is increased by choosing not to breed, breeding suppression will increase the area of negative growth. This means shifting the prey isocline downward and/or to the left (as a response to high predator and/or high prey density), and shifting the predator isocline to the right and/or downward (as a response to low prey density and/or high predator density). Examples for new isoclines are presented as dotted lines, and open circles mark the possible new equilibria. The result is a decline in predator density in all cases. However, the effect on prey equilibrium density is negative if prey suppress breeding, but positive if predators suppress.

m_X, we find that the prey dynamics obeys the following equation:

$$X(t + 1) = X(t)[S_X(X(t), Y(t), m_X(t))$$
$$+ m_X(t)s_x(X(t), Y(t), m_X(t))]. \quad (1a)$$

Similarly, for the predator,

$$Y(t + 1) = Y(t)[S_Y(X(t), Y(t), m_Y(t))$$
$$+ m_Y s_y(X(t), Y(t), m_Y(t))]. \quad (1b)$$

Our model is an extension of that of Kokko and Ranta (1996). We incorporate the possibility of varying the brood size as an alternative to a complete suppression of breeding, which was the only possible form of breeding suppression in Kokko and Ranta (1996). Optimal brood sizes m_X and m_Y will follow from the dependency of S and s on X, Y, and m. In diploid, sexually reproducing species with overlapping generations, optimally behaving individuals at time t will maximize the sum of reproductive values of themselves and their offspring at time $t + 1$, weighted by the coefficient of relatedness r_i and the probability of survival $s_i(t)$ from time step t to step $t + 1$ (Kokko and Ranta 1996). We

assume that individuals born at time t mature by time $t + 1$, which is the next opportunity for the parent to breed. The reproductive values $v_i(t + 1)$ thus refer to mature individuals, which are all identical by assumption. The values to be maximized are thus the following for the prey and predator, respectfully:

$$V_X = S_X(X, Y, m_X) + \frac{1}{2}m_X s_x(X, Y, m_X) \quad (2a)$$

$$V_Y = S_Y(X, Y, m_Y) + \frac{1}{2}m_Y s_y(X, Y, m_Y). \quad (2b)$$

In order to derive optimal breeding decisions, we have to assume a form for the functions S_X and s_x. Both are likely to be decreasing functions of m_X: the survival of the parent decreases with parental effort, and the survival of each offspring decreases with the number of siblings. In our examples we assume the following model of survivability for mature and immature prey, and mature and immature predators, respectively:

$$S_X(X, Y, m_X) = S_X(X, Y, 0)\exp(-\alpha_X m_X) \quad (3a)$$

$$s_x(X, Y, m_X) = s_x(X, Y, 0)\exp(-\alpha_X m_X) \quad (3b)$$

$$S_Y(X, Y, m_Y) = S_Y(X, Y, 0)\exp(-\alpha_Y m_Y) \quad (3c)$$

$$s_y(X, Y, m_Y) = s_y(X, Y, 0)\exp(-\alpha_Y m_Y) \quad (3d)$$

(i.e., that brood size affects parents and offspring by the same factor). Substituting Eq. 3a, b into Eq. 2a and differentiating gives

$$\frac{\partial V_X}{\partial m_X} = \exp(-\alpha_X m_X)$$

$$\times \{-\alpha_X S_X(X, Y, 0)$$

$$+ 0.5[s_x(X, Y, 0) - \alpha_X m_X s_x(X, Y, 0)]\}. \quad (4)$$

Solving for $\partial V_X/\partial m_X = 0$ then gives the optimal prey brood size m_X^*:

$$m_X^*(X, Y) = \frac{1}{\alpha_X} - 2\frac{S_X(X, Y, 0)}{s_x(X, Y, 0)}. \quad (5a)$$

A similar derivation for the predator gives

$$m_Y^*(X, Y) = \frac{1}{\alpha_Y} - 2\frac{S_Y(X, Y, 0)}{s_y(X, Y, 0)}. \quad (5b)$$

These results imply that optimal brood sizes will decrease if changes in X or Y cause the ratio of adult to juvenile survival, S_X/s_x (for the prey) or S_Y/s_y (for the predator), to increase. In other words, if deteriorating conditions induce a larger proportional reduction in juvenile than adult survival, it becomes optimal for the parents to respond by reproductive suppression. This conclusion can be shown to apply whenever the effects of brood size and population density act multiplicatively, as in Eq. 3 (G. D. Ruxton and H. Kokko, *unpublished manuscript*); however, other forms of den-

sity and brood size dependence may lead to different forms of the optima m_X^* and m_Y^*.

To explore the effects of brood size adjustment on dynamics, we present numerical examples that use the following form:

$$S_X(X, Y, m_X) = S_{X0}\exp(-\beta_{XX}X)\exp(-\beta_{YX}Y)\exp(-\alpha_X m_X)$$

$$s_x(X, Y, m_X) = s_{x0}\exp(-\beta_{Xx}X)\exp(-\beta_{Yx}Y)\exp(-\alpha_x m_X)$$

$$S_Y(X, Y, m_Y) = S_{Y0}(1 - \exp(-\beta_{XY}X))\exp(-\beta_{YY}Y)$$
$$\times \exp(-\alpha_Y m_Y)$$

$$s_y(X, Y, m_Y) = S_{X0}[1 - \exp(-\beta_{Xy}X)]\exp(-\beta_{Yy}Y)$$
$$\times \exp(-\alpha_y m_Y). \qquad (6)$$

The functions are chosen such that an individual's survival approaches its maximum value S_{i0} in the most advantageous environment (low prey and predator density and a small brood size for the prey; and high prey but low predator density and a small brood size for the predator).

The simulations are calculated by the following algorithm. For each time step t, we know the population sizes $X(t)$ and $Y(t)$, starting initially at low values. Hence, Eq. 6 gives survival values S_X, s_x, S_Y, and s_y for any choice of m_X and m_Y, if $\alpha_X = \alpha_x$ and $\alpha_Y = \alpha_y$. Eq. 5a, b is then used to determine the optimal m_X^* and m_Y^* values (zero is used if the optimum falls into a negative region); otherwise, m_X^* and m_Y^* can be determined numerically. The next population size will now follow from Eq. 1a, b, where m_X and m_Y are set to the optimum values m_X^* and m_Y^*, and survival values are those that follow from X, Y, and the chosen brood sizes. Each of the $X(t)$ prey adults thus produce m_X offspring, of which the fraction s_x survives to become adults of the next time step; additionally, a fraction S_X of the adults themselves survive to remain as living adults in the next time step. The predator population is updated likewise. To simulate nonbrood size adjusting dynamics for comparison, we assume that populations use a single brood size equal to the optimum at favorable conditions.

Even with this quite restricted subset of all possible forms of $S(X, Y, m)$ functions, we find that brood size adjustment can have either stabilizing or destabilizing effects, and the roles of predators and prey can be co-incident or opposing in this respect. Three examples of the resulting dynamics are shown in Fig. 3 (Table 2, examples 1–3). Further examples can be generated to produce, for example, chaotic oscillations via breeding suppression, or, equally well, a stabilization of chaotic dynamics. The results confirm that a variety of stable and locally unstable dynamics can be generated by optimal breeding decisions of predator and prey, as suspected by the general analysis of reshaping the density dependence of population growth. Of particular interest is that brood size adjustment by the predator

alone can give rise to cyclic dynamics (Fig. 4). This confirms that not only the possible antipredatory response of the prey, but also the predator response to altered food levels should be taken into account in behavior-based models of predator–prey cycles. Again, the effect of such predator responses on dynamics is dependent on the shape of density dependence, and stabilization is also possible.

DISCUSSION

An increasing number of studies focus on the interrelationship of individual behavior and population dynamics (see Sutherland [1996] for a recent review). A good example is the antipredatory behavior of prey such as voles, forming a possible behavior-based explanation for persistent cycles in predator–prey interactions. Views on the consequences of antipredatory behavior on population dynamics have undergone rapid changes in recent years. Breeding suppression was first presented as an adaptive mechanism in individuals to avoid predation (Ylönen 1994), but the possible generation of cycles by this mechanism was refuted by models that suggested that the effect is likely to be a stabilization of the dynamics (Gyllenberg et al. 1996, Ruxton and Lima 1997). Here, we present a general model that addresses not only the possibility of breeding suppression in the prey, but in the predator as well.

Our results are surprising. A general analysis of the effect of reduced growth rates in unfavorable conditions suggest that breeding suppression in either predators or their prey may profoundly change the dynamical properties of the two-species system. The effect can be either stabilizing or destabilizing. There seems to be no simple general rule to the effects of optimal breeding strategies on the dynamics, except that suppression will move the equilibrium towards smaller density of the suppressing species. Even this assumption may be violated if survival prospects are so low, both for breeding individuals and their offspring, that breeding suppression actually prevents or lessens a population decrease. In any case, it is not the movement of the equilibrium densities itself, but the slopes of density-dependent growth rate at the new equilibrium that determine the new stability properties of the system. These slopes encompass all the processes responsible for determining the growth rate in any given circumstance; here, breeding strategies and behavioral processes such as territoriality are likely to be as important as predation and starvation.

Our results conflict with earlier models that suggest stabilization as the only possible outcome of breeding suppression (Gyllenberg et al. 1996, Ruxton and Lima 1997). This emphasizes the importance of considering density-dependent responses of different shapes. In addition, the model of Gyllenberg et al. (1996) assumes discrete, nonoverlapping generations. In such a model, sexuality, and the resulting difference in relatedness to offspring and the individual itself, are ignored; the most
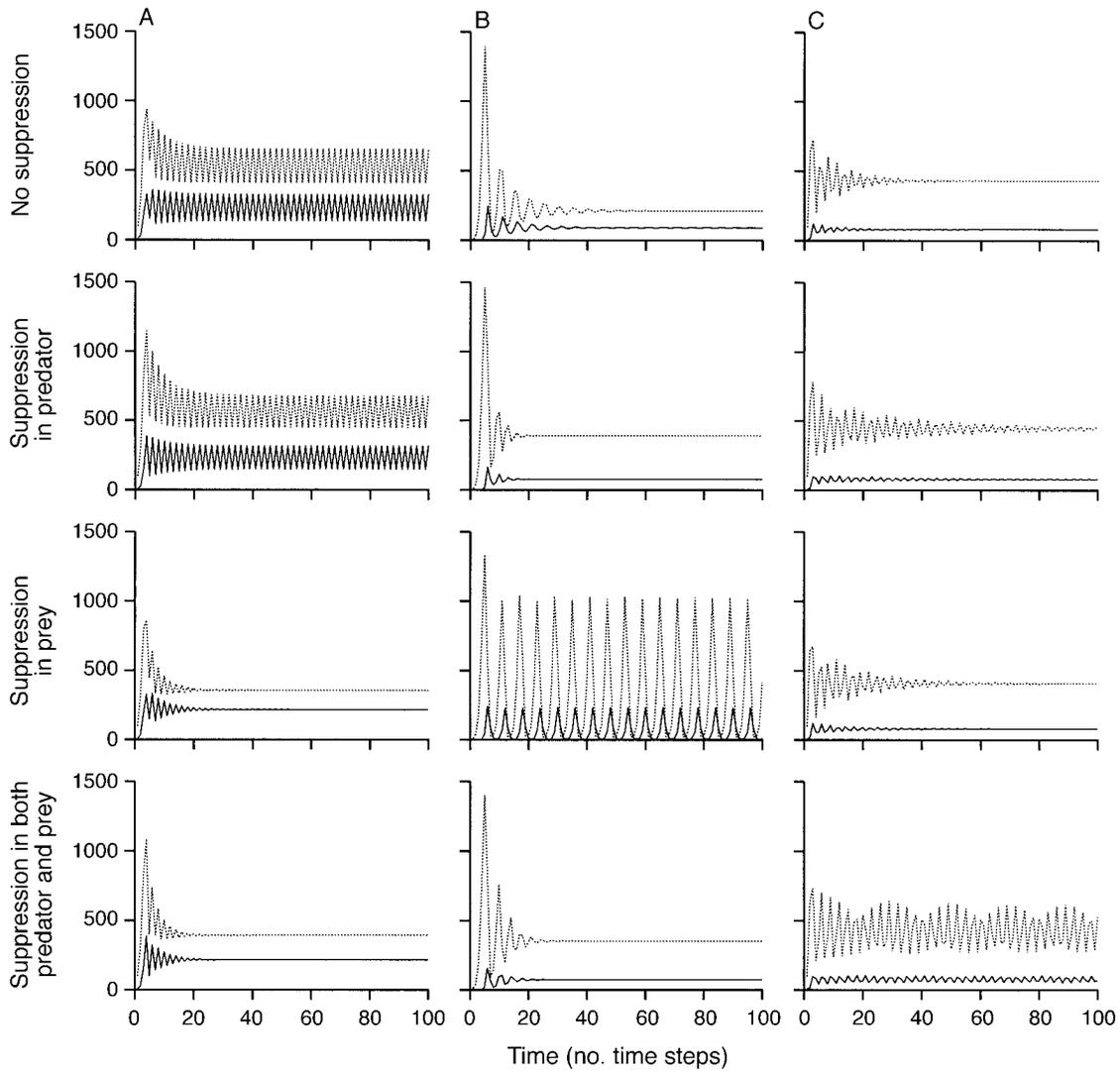
FIG. 3. Examples 1–3 (see Table 2 for parameters) of the dynamics of the optimal suppression model with equal $\alpha_X = \alpha_x$. Solid lines depict predator density; dotted lines, prey density. Upper panels give dynamics with optimal fixed brood size in a favorable environment, where $m_X^* = 1/\alpha_X - 2S_{X0}/s_{x0}$. These can be compared with the dynamics of optimal suppression allowed in predator only, in prey only, or in both predator and prey. Optimal brood sizes at each density are derived from Eqs. 5a, b. (A) Example 1: breeding suppression in the prey has a stabilizing effect, damping a two-year cycle, in this case. (B) Example 2: breeding suppression in the prey generates cycles from originally stable dynamics, but breeding suppression by predators as well as prey maintains stability. (C) Example 3: suppression in both the predator and its prey maintains quasiperiodic dynamics, whereas dynamics are stable when one or both populations do not adjust brood sizes.

successful strategy will simply maximize the production of surviving offspring. Allowing parents to survive as well, as in our present model, will produce a larger variety of breeding strategies. We also predict suppression being optimal perhaps more often than previously supposed (Kokko and Ranta 1996), if reductions in brood or clutch sizes are considered in addition to completely abandoning breeding.

We also note that the dynamical effects of breeding suppression do not depend on whether suppression is considered an adaptive ''choice,'' or if it is interpreted as a ''forced'' reduction in the brood size, if the female

is in physiologically poor condition. Both alternatives describe changes in the optimal brood size, among feasible ones. The interpretation of a ''forced'' reduction applies to cases where survival of both parent and offspring would be zero if the female attempted breeding despite her poor condition, hence restricting the set of feasible alternatives.

Changes in the relative performances of immature and mature individuals with changes in population density form the essential evolutionary basis of suppression, although a complete analysis of this problem is not easy when more general forms of the interaction

TABLE 2. Values of parameters appearing in Eq. 6 used to build the examples in Figs. 3 and 4.

Parameter	Example 1	Example 2	Example 3	Example 4
Prey				
S_{X0}	0.1	0.1	0.1	0.75
s_{x0}	0.1	0.1	0.1	0.4
α_X	0.03	0.02	0.01	0.05
α_x	0.03	0.02	0.01	0.15
β_{XX}	0.0001	0.0003	0.001	0.001
β_{Xx}	0.0001	0.0012	0.003	0.002
β_{YX}	0.001	0.003	0.0025	0.001
β_{Yx}	0.005	0.015	0.0125	0.005
Predator				
S_{Y0}	0.9	0.9	0.9	0.95
s_{y0}	0.7	0.7	0.7	0.95
α_Y	0.05	0.05	0.05	0.2
α_y	0.05	0.05	0.05	0.1
β_{XY}	0.01	0.0045	0.05	0.01
β_{Xy}	0.003	0.0045	0.002	0.002
β_{YY}	0.01	0.0015	0.025	0.0005
β_{Yy}	0.01	0.0018	0.025	0.0005

between reproductive costs and density dependence are considered (G. D. Ruxton and H. Kokko, *unpublished manuscript*). Some evidence exists in favor of a larger proportional reduction in juvenile, as compared to adult, survival in deteriorating conditions. It is commonly found that young inexperienced predators are more likely to starve as food becomes scarce (e.g., Packer et al. 1988, Newton et al. 1997). As an example, in a recent study that quantified survival of Great Horned Owl *Bubo virginianus,* the survival of young floaters was indistinguishable from that of adult territory owners in peak years of the snowshoe hare (*Lepus americanus*) cycle, whereas the reduction in survival in a low-hare year was 13.2% in territory owners, but 60% in floaters (Rohner 1996). In prey species, evidence for differences in predation risk among social classes exists, at least for the field vole *Microtus agrestis* (Mappes et al. 1993), where males and subordinates were taken disproportionately often by the Pygmy Owl *Glaucidium passerinum.* Also, young snowshoe hares suffer more from predation by Great Horned Owls than adults (Rohner and Krebs 1996).

On the other hand, the original form of the breeding suppression hypothesis assumes that breeding individuals, especially lactating females, are at higher risk if predators are abundant (Ylönen 1994). In light of the current model, an increased risk of death of offspring must be considered together with the direct risk that the female faces. These two risks may also be correlated, since the death of a lactating female brings about the death of her offspring, as well. In any case, we suggest considering the role of brood size adjustments in predators in more detail, as they are likely to be as important in shaping the properties of the cycle, as are the possible decisions of their prey. The lack of studies on litter size variation in mustelid predators is an ob-
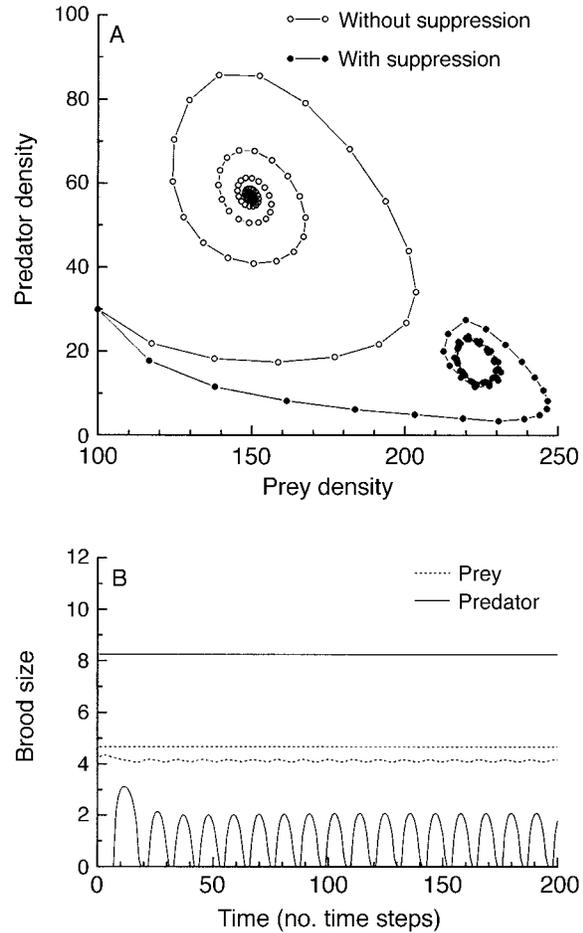
FIG. 4. Example 4 (see Table 2 for parameters), showing predator-induced oscillations. (A) Without suppression, the populations converge to a stable equilibrium (–○–○–). Allowing predators to adjust breeding effort leads to sustained cycles around an equilibrium point (–●–●–), where prey density is higher and predator density lower than at the original equilibrium. (B) Optimal brood size in predators when adjustment is allowed for (solid line with humps) varies according to the cycle phase and often equals zero. In the hypothetical case where individuals were not allowed to adjust breeding effort according to population density, the optimal brood size of predators would be much higher (solid straight line). Breeding adjustment in the prey is slight in this example and contributes little to the dynamics. If suppression occurs in prey only, the dynamics are indistinguishable from the nonadjustment dynamics (–○–○–).

vious gap in empirical knowledge, since their role is central in the Fennoscandian vole cycles (Hanski et al. 1993, Norrdahl 1995).

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