Optimization of reproductive effort and foraging time in mammals: the influence of resource level and predation risk

LAURI OKSANEN[1] and PER LUNDBERG[2]

[1] *Department of Ecological Botany, University of Umeå, S-901 87 Umeå, Sweden*
[2] *Department of Animal Ecology, Swedish University of Agricultural Sciences, S-901 83 Umeå, Sweden*

Summary

The trade-off between fitness benefits from foraging and associated costs in terms of predation risk is analysed by a simple model which takes into account the differential predation risk for reproducing and non-reproducing individuals. The currency that animals are assumed to maximize is their expected absolute fitness (probability of survival plus half of the expected litter size) after a potential reproductive period. Depending on resource levels and predation risk, this maximization can be achieved by (1) opting for individual survival and behaving as a strict time minimizer, (2) by reproducing at the maximal rate and behaving as a strict energy maximizer or (3) by submaximal reproductive effort and a behaviour intermediate between time minimization and energy maximization. Small changes in the availability of food or cover or in the density of predators can shift the optimum from one strategy to another. The shift is particularly abrupt, if predation pressure increases and the availability of resources remains high. This could explain the spatial and temporal variation in the reproductive effort and body weight observed in boreal small mammals with sustained, multiannual population fluctuations.

Keywords: food, foraging time, lemming, mammal, microtine rodent, optimization, predation, seasonality, risk, reproduction, vole

Introduction

Birds and mammals living at middle and high latitudes tend to have a clear dichotomy between reproductive and non-reproductive seasons. Normally, reproduction takes place only in summer, when resources are plentiful and physical conditions are favourable. There are, however, some notable exceptions. Winter reproduction is common in arctic and alpine lemmings (*Lemmus* spp., *Dicrostonyx* spp.) and root voles (*Microtus oeconomus*) (Tast and Kaikusalo, 1976; Kaikusalo and Tast, 1984; Tast, 1984) and sometimes suffices to generate spectacular numerical increases and reproduction normally only ceases for short periods in the spring and the fall (Fuller *et al.*, 1977; Batzli *et al.*, 1980; Černjavskij and Tkačev, 1982; Oksanen and Oksanen, 1992; Framstad *et al.*, 1993). Boreal small mammals with sustained, periodic density fluctuations (Hansson and Henttonen, 1985; Oksanen, 1990; Hanski *et al.*, 1993) behave still more enigmatically. Body weights are high and winter reproduction is common during population rises (Krebs and Myers, 1974; Tast and Kaikusalo, 1976; Hansson, 1984a; Mihok, 1984; Tast, 1984; Taitt and Krebs, 1985), whereas population declines are characterized by low body weights and compressed breeding season (Hansson, 1984b, 1987, 1988, 1989).

Krebs and Myers (1974) connected this syndrome to genetic changes in microtine populations, whereas North European ecologists have normally regarded it as a consequence of variation in the availability of adequate food due to fluctuations in the production of high-quality plant organs

(Tast and Kalela, 1971), immediate (Hansson, 1987) and time-delayed (Hansson, 1988, 1989) impacts of forage depletion (starving mothers giving rise to small young with low reproductive potential) or induced plant defences (Seldal *et al.*, 1994).

The nutritional status of an organism also depends on its foraging effort, which is sensitive to predation risk and other costs of foraging (Abrams, 1982, 1984, 1991; Sih, 1982, 1984; Lucas, 1983; Lima, 1985; Lima *et al.*, 1985; Mangel and Clark, 1986; Brown, 1988, 1992; Abrahams and Dill, 1989; Magnhagen, 1990; Brown *et al.*, 1992), although detailed theoretical and empirical studies on wintering birds indicate that animals should normally compensate for food stress by accepting a higher predation risk rather than vice versa (McNamara and Houston, 1986, 1987, 1992; Ekman, 1987). However, these studies do not address the broader question of under what conditions should the animals reproduce and when should they 'winter' (i.e. refrain from reproduction and maximize chances for individual survival), which is the scope of our analysis.

The essence of our approach is captured by the Russian proverb 'you cannot be a little bit of pregnant'. A female must either start reproducing and take the risks imposed by the accompanying physiological and behavioural changes (Cushing, 1985) or she must accept that the best imaginable outcome of her feeding effort is individual survival. This trade-off can be analysed in a simple and tractable way by assuming that all animals are equally good carriers of their genes. Then, we can operationally define the fitness of a female as her genetic representation in the population after one potential reproductive period (the time needed from conception to weaning). The impact of age-specific changes in reproductive potential and residual reproductive value will be discussed in the subsequent section of the paper.

The model

Let T_{max} be the maximum foraging time during a potential reproductive period, allowed by environmental and physiological constraints and let T be the time actually spent foraging. When foraging, non-reproducing females are assumed to face a predation risk μ_n, while the corresponding risk for reproducing females is μ_r. Since reproducing females are more vulnerable than non-reproducing ones (see above), we assume that $\mu_n < \mu_r$. For small mammals hiding in burrows, it is reasonable to assume that the predation risk for resting females is small and varies little between reproductive and non-reproductive females. (Predators have difficulty in locating and entering the burrows, but if they do, the chances of escape for the prey are small.) We thus assume that the risk of being captured while resting is ϵ for both reproductive and non-reproductive females. Consequently, the likelihood of a non-reproducing female escaping predation during a potential reproductive period ($E_n(T)$) is obtained from

$$E_n(T) = e^{-\mu_n T} e^{-\epsilon(T_{max} - T)} = e^{-T(\mu_n - \epsilon) - \epsilon T_{max}} \tag{1}$$

The corresponding risk for reproducing females is obtained from

$$E_r(T) = e^{-\mu_r T} e^{-\epsilon(T_{max} - T)} = e^{-T(\mu_r - \epsilon) - \epsilon T_{max}} \tag{2}$$

In the context of animals with relatively safe resting places, it is practical to work on the additional risk of predation due to foraging. We thus let $\mu_n - \epsilon$ be equal to β_n, $\mu_r - \epsilon$ be equal to β_r and $e^{-\epsilon T_{max}}$ be equal to m. Equations 1 and 2 can now be simplified to

$$E_n(T) = m e^{-\beta_n T} \tag{3}$$

and

$$E_r(T) = m e^{-\beta_r T} \tag{4}$$

where m is the per time unit probability of escaping predation while resting, β_r is the additional predation risk while foraging for reproductive females and β_n is the corresponding additional risk for non-reproducing ones. We assume that β_r and β_n are directly proportional to predator density and decreasing functions of the availability of cover. The parameter m depends on predator density as well and on the safety of resting places. $E(T)$ takes the value 1 when predators are absent and asymptotically approaches zero with increasing predator density and time spent foraging.

Next, we define $G(T)$ as the likelihood of survival plus the expected fitness increment due to reproduction of a female using T time units for foraging, provided that she manages to escape predators. The best outcome that a non-reproducing female can expect is individual survival. Thus, for non-reproducing females, $G_n(T)$ asymptotically approaches 1 when T increases (McNamara and Houston, 1987). Logically, there must be some minimum amount of food that a non-reproductive female must obtain in order to have any chances of survival. A simple function fulfilling the above criteria is represented by

$$G_n(T) = 1 - (1 + \eta_n)\, e^{-\theta T} \qquad (5)$$

where the parameter η_n reflects the energy needs of non-reproducing females and θ is the net rate at which they convert foraging time into resources for maintenance.

A reproducing female finds herself in a basically similar situation. She has to obtain a minimum amount of food in order to stand a chance of survival. Moreover, her potential to convert additional food to fitness is bounded by her physiological capacity to produce offspring. Thus, the maximum value for $G_r(T)$ for a reproducing female is $1 + 0.5r$, where r is the female's reproductive capacity. (Multiplication by 0.5 accounts for the cost of meiosis.) We denote this maximum value as y. A further constraint for the $G_r(T)$ function is that the amount of food required for individual survival is independent of reproductive capacity. A function with these properties is represented by

$$G_r(T) = y(1 - (1 + \eta_r)e^{-\rho T} \qquad (6)$$

where η_r reflects the energy needs of reproducing females and ρ represents the rate at which the fitness approaches its maximum value with increasing foraging time.

The physiological and behavioural changes accompanying reproduction are likely to be detrimental to the ability of the female to survive at low resource levels and to accumulate resources for individual survival. It is thus reasonable to assume that $\eta_n < \eta_r$ and $\theta > \rho$. If the adverse effects of attempted reproduction on survival are small, function $G_n(T)$ can be approximated by truncating function $G_r(T)$ (i.e. by assuming that $G_n(T) = Gr(T)$, if $G_r(T) < 1$ and $G_n(T) = 1$, if $G_r(T) > 1$). For the sake of clarity, we will use this approximation in our figures.

McNamara and Houston (1987) computed the total risk of mortality for a non-reproducing animal by adding the risks of predation and starvation. As they noted themselves, this approach is always at least slightly flawed, because a given animal can only die once. We have thus chosen the multiplicative approach, advocated in model IV of Brown (1992), where the expected absolute fitness $(W(T))$ is the product of the chances of escaping predation $(E(T))$ and the expected fitness of the female, provided that she escapes predation $(G(T))$. This product increases as long as $G'(T)/G(T) > -E'(T)/E(T)$. The local optima for foraging time must thus fulfil

$$G'(T)/G(T) = -E'(T)/E(T) \qquad (7)$$

Equation 7 can be contrasted with the result of McNamara and Houston (1987) that the

optimum is found by setting $G'(T) = -E'(T)$. (Only the derivatives count in their model.) The division of derivatives by function values has little impact on the optimal foraging time for wintering animals with high survival rates, because then $G_n(T) \approx E_n(T) \approx 1$. However, the impact can be more substantial, if chances of survival are low or if the females are reproducing.

After differentiating Equations 3 and 4, we immediately see that Equation 7 can be rewritten:

$$-E'(T)/E(T) = \beta \tag{8}$$

which means that, at optimum, the ratio $G'(T)/G(T)$ has to be equal to the additional risk of predation. By substituting this into Equation 5, we obtain the optimum foraging time for non-reproducing females (T^*_n) as

$$T^*_n = \left(\frac{1}{\theta}\right) \log \left(\frac{(\theta + \beta_n)\,(1 + \eta_n)}{\beta_n}\right) \tag{9}$$

The corresponding substitution into Equation 6 yields

$$T^*_r = \left(\frac{1}{\rho}\right) \log \left(\frac{(\rho + \beta_r)\,(1 + \eta_r)}{\beta_r}\right) \tag{10}$$

In both cases, the optimum foraging time has a strong, negative relation to the parameters θ (in Equation 8) and ρ (in Equation 9), which determine how quickly the reward of foraging approaches its maximum value (1 in Equation 8, y in Equation 9). Recall that $\theta \gg \rho$, because it is much easier to satisfy individual energy needs than to get enough food for reproduction at maximum rate. Thus, T^*_n lies much closer to the origin than T^*_r. The distance between the two optima along the T axis has interesting consequences for the relation between the global optimum and parameter values. These consequences can be illustrated by studying the limiting case, where the two local optima are equally high, i.e. the female will have the same expected fitness regardless of whether she chooses to reproduce or not (Fig. 1). If she decides to reproduce, she will spend more time foraging and have a lower probability of survival from predation. On balance, she also has prospects of a substantial fitness reward from producing offspring. If, instead, the female chooses not to reproduce and applies a foraging strategy optimal for this choice, she will forage so much that she is at low risk of starving to death. A foraging strategy giving a zero risk of starvation would be suboptimal, as a small reduction of foraging time would then provide a cost-free way to reduce predation risk. Accumulation of body reserves would be even more suboptimal, unless such reserves are needed as safeguards against environmental stochasticity (see Ekman, 1987).

Now imagine that the local optimum for a reproducing female is slightly higher than the local optimum for a non-reproducing one. In such a situation, a minute decrease in food availability (determining the parameters θ, ρ and η in the $G(T)$ functions) would make it advantageous to refrain from reproduction. A slight reduction in cover or increase in density or activity of predators (determining the parameter β in the $E(T)$ functions) would have the same effect. The model thus predicts that a tiny change in any environmental factor related to food availability or predation risk may result in rapid and profound changes in the reproductive and physiological status of individuals.

The interaction between changing resource availability and predation risk can be studied by means of numerical simulations. Results of such simulations are presented in Fig. 2. Figure 2(a) illustrates a situation with a low resource density and low predation risk. A female facing this situation has to work long days just obtaining enough food for individual survival. Provided that she can obtain some energy surplus with an all-out foraging effort, the model predicts that she should nevertheless reproduce, albeit at a relatively low rate. Her optimal foraging strategy
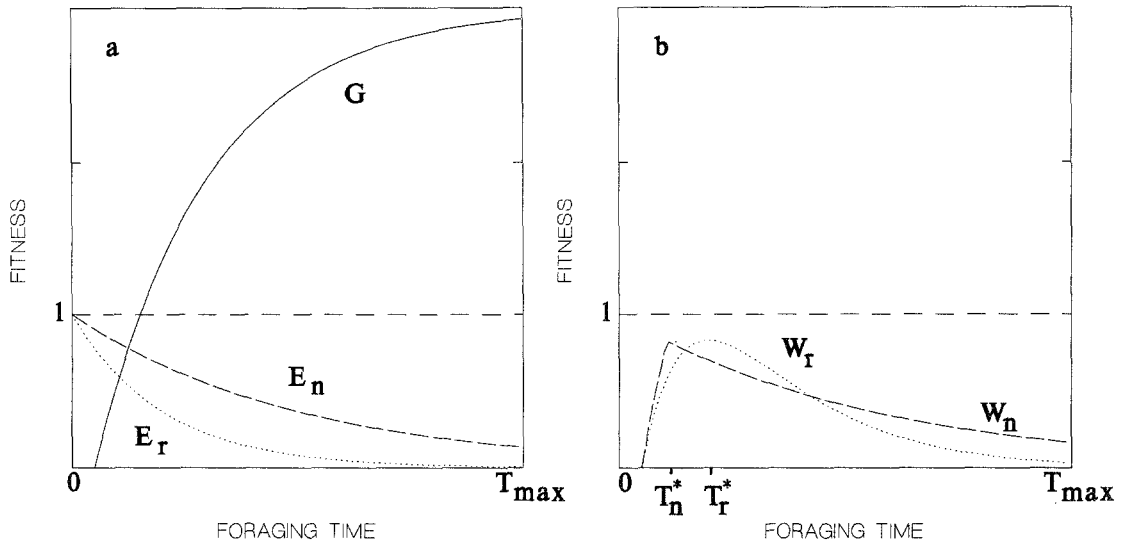
Figure 1. The relation between expected absolute fitness and time spent foraging. (a) Fitness is the product of two components: the contribution of food (energy), G and the probability of escaping predation, E. E_n represents the survival function for non-reproducing females and E_r represent the survival function for reproductive ones. For technical reasons, we have only depicted the G function for reproductive females (G_r); the G function for non-reproductive females (G_n) can be approximated by combining the G function and the line $G = 1$. (b) The resulting fitness functions for reproducing, W_r and non-reproducing, W_n. The situation given in (a) results in W_r and W_n functions with equal maximum height (i.e. equal fitness) but the peak of the W_r function lies further to the right. The optimal foraging times for reproductive and non-reproductive females are denoted as $T_r{}^*$ and $T_n{}^*$, respectively.

would be strict energy maximization. Figure 2(b) represents a situation, where the resource availability is as low as in Fig. 2(a) but the predation risk is high. Now an optimally behaving female should refrain from reproduction and behave as a strict time minimizer. In Fig. 2(c), a high resource availability is combined with a low risk of predation. Under such circumstances, the optimum strategy of a female is to reproduce at a rate which is somewhat below her maximum capacity. Her optimal foraging strategy should be intermediate between energy maximization and time minimization, due to diminishing returns of higher foraging effort. Figure 2(d) represents a situation where food availability is as good as in Fig. 2(c) but the predation risk is high. In this situation, an optimally behaving female should refrain from reproduction and act as a strict time minimizer.

In order to visualize changes between the different situations illustrated in Fig. 2, it is useful to recollect that in Equation 10, the risk parameter lies in the term $\log\left((\rho + \beta_r)/\beta_r\right)$. If ρ is relatively small (i.e. food availability is low), the term within the logarithm is close to 1, i.e. it lies in the range where logarithmic functions are quite sensitive to changes in the value of the argument. The impact of decreasing resource availability on optimal foraging time and reproductive strategy is thus predicted to be gradual. Females react first by reducing their foraging effort and by cutting down on litter size. The shift from reproduction to wintering is only the final step in this gradual adjustment. Conversely, when ρ is large (i.e. food is freely available), the term within the logarithm will lie outside this 'window of sensitivity' and changes in predation risk have little
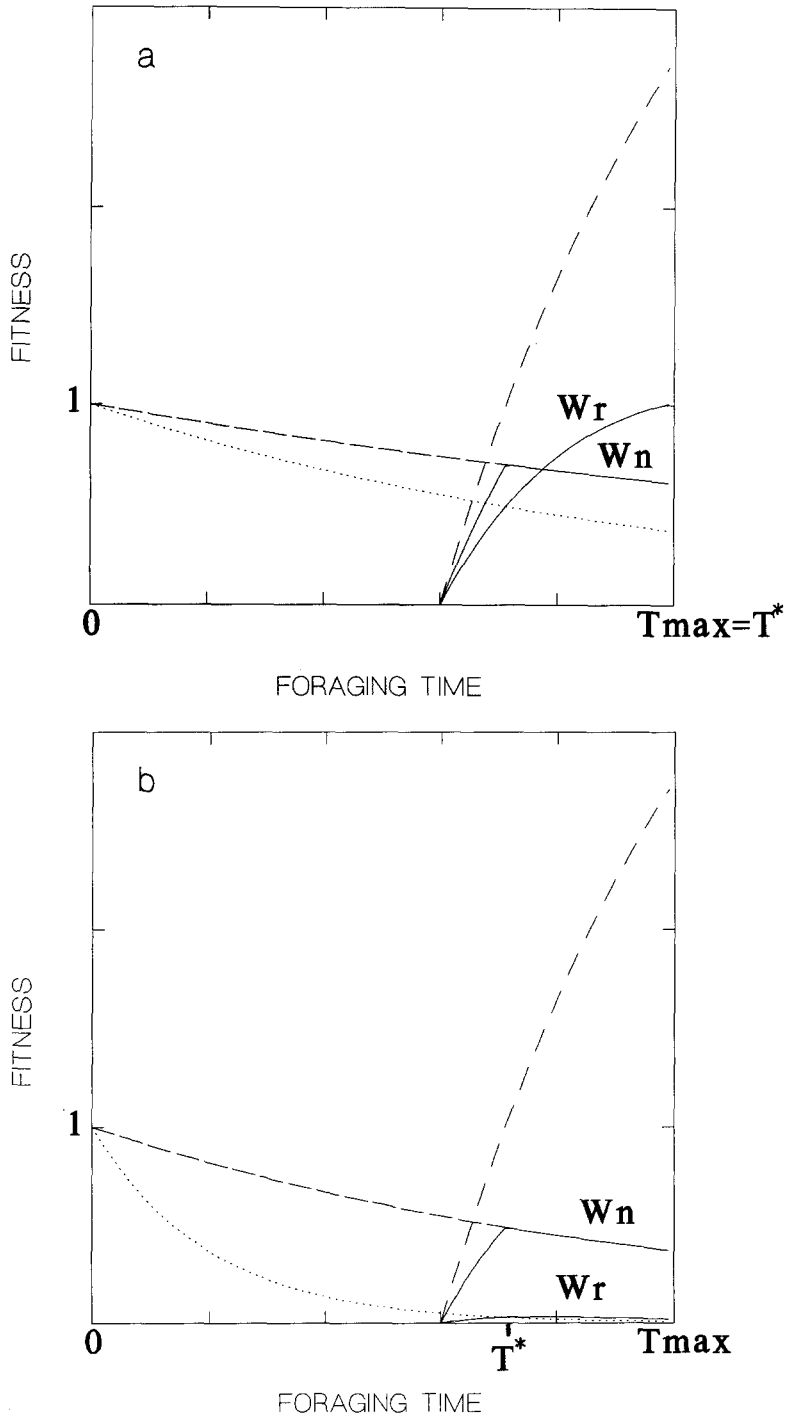
Figure. 2. Four different combinations of resource density and predation risk with the optimal time spent foraging (T^*) indicated on the x-axis. (a) Low resource density and low predation risk, resulting in reproduction being superior to non-reproduction and $T^* = T_{max}$ (energy maximization). (b) Low resource density and high predation risk, favouring wintering (non-reproduction) and strict time minimization.

FITNESS

d

1

Wn

Wr

0   T*   Tmax

FORAGING TIME

FITNESS

c

Wr

1

Wn

0   T*   Tmax
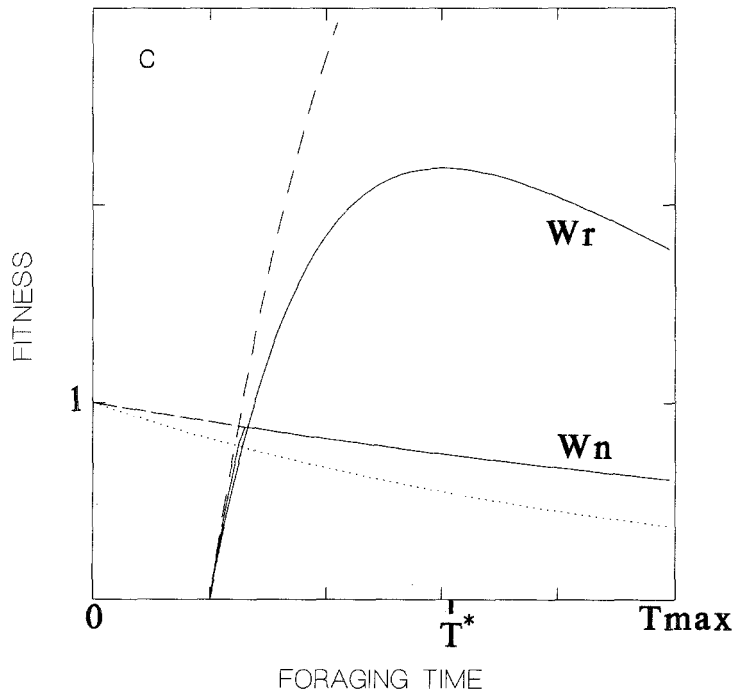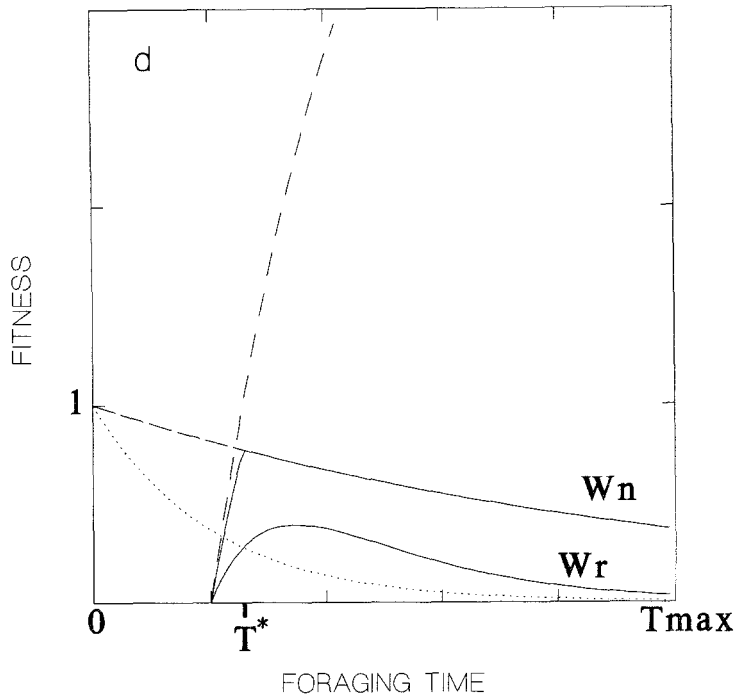
FORAGING TIME

(c) High resource density and low predation risk, favouring reproduction and a foraging strategy intermediate between energy maximization and time minimization. (d) High resource density and high predation risk favouring wintering and strict time minimization.

impact on the optimal foraging time of reproducing females. The response to intensifying predation in a habitat with plentiful food should be much more sudden and dramatic – from nearly maximal reproduction to strict time minimization. Environmental predictability should make the change even more dramatic by eliminating the need for fat reserves and by allowing a relatively risk-free tightrope walk on the brink of starvation. Thus, a sudden and dramatic deterioration in the condition of females should be observed, if food is plentiful and freely accessible and if the individual energy needs are predictable.

Relaxing assumptions

The above analysis is based on the assumption of the equal value of all animals as carriers of their genes. The results are thus sensitive to age-specific differences in the ratio of the current reproductive potential to the residual reproductive value. Young animals with a low reproductive potential but a relatively high residual reproductive value should be more aware of their individual survival than predicted by our model, whereas old animals with a high reproductive potential as compared to their residual reproductive value should be motivated to prioritize reproduction (Stenseth and Framstad, 1980). Consequently, the first readily observable consequence of decreasing food availability or intensifying predation should be that recently weaned juveniles cease to mature. Conversely, old animals with near-zero residual reproductive value should keep on reproducing, no matter how unfavourable the environment has become, as proposed by Stenseth and Framstad (1980).

Another critical assumption looms in the parameter β, which represents the additional predation risk due to foraging, i.e. the difference between the risk faced by foraging animals and resting ones. As pointed out by J. Brown (personal communication) the additional risk is influenced by the safety of the resting places. If their safety is low, e.g. due to a high abundance of snakes adapted to hunt in burrows, reproduction might be superior to wintering even under a relatively high predation risk.

Discussion

In temperate areas Fig 2(c) can be interpreted as summer, with plentiful food and cover, whereas winter conditions should lie somewhere between Fig 2(a) and 2(d) (lower resource availability and higher predation risk than in summer, due to poor cover and arrival of wintering raptors from higher latitudes, see Erlinge *et al.*, 1983; Erlinge 1987). This is reflected in the prevalence of summer reproduction and strongly seasonal numerical dynamics in temperate and south boreal microtines (Zablockaja, 1957; Koškina and Korotkov, 1975; Ivanter, 1981; Erlinge *et al.*, 1983; Hansson, 1984b, 1987; Hansson and Henttonen, 1985; Taitt and Krebs, 1985). Winter reproduction is normally connected to superabundance of food, due to masking of the key food plants (Secher Jensen, 1982). Changes in food availability and predation risk work in the same direction, yielding a rather trivial pattern of reproduction and wintering.

At higher latitudes and altitudes, winter is typically the season with the best cover and lowest predator numbers, whereas food availability in relation to energy needs varies from moderate to low, depending on the density of accessible forage and snow quality (best in shrubby boreal and subarctic – alpine habitats with fairly continuous subnival cavities and benign subnival temperatures, see Dahl, 1957; Eurola, 1974; Kaikusalo and Tast, 1984; worst in typical arctic tundra, characterized by tightly packed snow and frigid subnival temperatures, see Dingman *et al.*, 1980). The production of small winter litters (Kaikusalo and Tast, 1984) can be thus interpreted as

corresponding to Fig 2(a). The environment is harsh, but not harsh enough to prevent reproduction altogether and predation pressure is low. Lemmings choose to reproduce (see Fuller *et al.*, 1977; Batzli *et al.*, 1980; Černjavskij and Tkačev, 1982; Framstad *et al.*, 1993), because they have something to win and nothing to lose.

North European vole populations are characterized by fairly regular, multiannual fluctuations, which differ from the erratic boom–crash pattern of arctic–alpine lemmings and are normally referred to as cyclic, due to their fairly regular period and amplitude (Laine and Henttonen, 1983; Hansson and Henttonen, 1985; Hansson, 1987; Henttonen *et al.*, 1987; Hörnfeldt *et al.*, 1989; Oksanen, 1990; Hanski *et al.*, 1991; Oksanen and Oksanen, 1992; Hörnfeldt, 1994), although in strictly mathematical terms, these fluctuations appear to be chaotic rather than cyclic (Turchin and Taylor, 1992; Hanski *et al.*, 1993). The decline phase is characterized by the high numbers and activity of small mustelids (Fitzgerald, 1977; Viitala, 1977; Hansson, 1984c, 1987; Henttonen, 1985; Järvinen, 1985; Korpimäki *et al.*, 1991; Oksanen *et al.*, 1992) and the pattern of repeated density fluctuations has been interpreted as a predator–prey limit cycle (Oksanen, 1990; Hanski *et al.*, 1991). A standard counterargument, most recently stated by Seldal *et al.* (1994), is that the predation hypothesis fails to account for the high body weights and frequent occurrence of winter breeding during population rises (Tast and Kaikusalo, 1976; Hansson, 1984a; Mihok, 1984; Taitt and Krebs, 1985) and for the low body mass, delayed sexual maturation and compressed breeding season during declines (Krebs and Myers, 1974; Hansson, 1984b, 1987, 1988, 1989). Our model demonstrates that adaptive responses to intensifying predation provide a potential explanation for this syndrome.

Adaptive responses to predation are not only a theoretical possibility. According to the experimental data of Ylönen, and his co-workers (Ylönen, 1989; Ronkainen and Ylönen, 1994; Ylönen and Ronkainen, 1994; Ylönen *et al.*, 1994) individual voles stop reproducing, when exposed to the presence of a caged weasel. (Corresponding experiments have also been performed with other organisms; see Abrahams and Dill, 1989.) In the experiments of Heikkilä *et al.* (1993), the perceived predation risk delayed the rate of maturation of juvenile voles, especially in the case of bank voles (*Clethrionomys glareolus*) and red voles (*Clethrionomys rutilus*) taken from cyclic populations. Moreover, changes in reproductive effort in field populations appear to be better explained by the changing predation risk than by direct or time-delayed impacts of density (Norrdahl, 1993; Korpimäki *et al.*, 1994).

Adaptive changes in foraging time and reproductive effort may have counter-intuitive impacts on numerical predator–prey dynamics. It is conceivable that voles born in a peak population could saturate their predators and reduce predation pressure by quick maturation and copious reproduction. However, every optimally behaving female decides her reproductive effort on the basis of her own fitness prospects. If the current situation favours wintering, juveniles will remain immature and also adults may cease to reproduce. Consequently, adaptive changes in foraging and reproduction are likely to reduce vole peaks and contribute to the initiation of cyclic declines. Relaxation of predation pressure during rock-bottom phases of small mammal cycles should, in turn, favour quick maturation and high reproductive output. The behavioural changes due to reduced predation risk should immediately increase the encounter rates between predators and prey and thus boost the prospects of the few surviving predators. The predicted overall impact of adaptive responses of prey is thus to reduce the amplitude of the cycle. Adaptive changes in predator behaviour work in the same direction (Abrams, 1982; Oksanen *et al.*, 1985; Jedrzejewska and Jedrzejewski, 1989; Oksanen, 1990; Fryxell and Lundberg, 1994). The idea of predator–prey cycles as a path to extinction (Gilpin, 1975) thus appears to be an unnecessarily pessimistic consequence of models based on stereotypic behaviour of predators and their prey.

Acknowledgements

References

Abrahams, M.V. and Dill, L.M. (1989) A determination of the energetic equivalence of the risk of predation. *Ecology* **70**, 999–1007.

Abrams, P.A. (1982) Functional responses of optimal foragers. *Am. Nat.* **120**, 382–90.

Abrams, P.A. (1984) Foraging time optimization and interactions in food webs. *Am. Nat.* **124**, 80–96.

Abrams, P.A. (1991) Life history and the relationship between food availability and foraging effort. *Ecology* **72**, 1242–52.

Batzli, G.O., White, R.G., MacLean, S.F., Pitelka, F.A. and Collier, B.D. (1980) The herbivore based trophic system. In *An Arctic ecosystem: the coastal tundra at Barrow, Alaska.* J. Brown, P.C. Miller, L.L. Tieszen and F.L. Bunnell, eds), pp. 335–410. Dowden, Hutchison & Ross, Stroudsburg, PA.

Brown, J.S. (1988) Patch use as an indicator of habitat preference, predation risk, and competition. *Behav. Ecol. Sociobiol.* **22**, 37–47.

Brown, J.S. (1992) Patch use under predation risk: I. Models and predictions. *Ann. Zool. Fenn.* **29**, 301–9.

Brown, J.S., Morgan, R.A. and Dow, B.D. (1992) Patch use under predation risk: II. A test with fox squirrels, *Sciurus niger. Ann. Zool. Fenn.* **29**, 311–18.

Černjavskij, F.B. and Tkačev, A.V. (1982) *Populjacionnye cikly lemmingov varktike ekologičeskie i endokrinnye aspekti.* Nauka, Moscow.

Cushing, B.S. (1985) Estrous mice and vulnerability to predation by weasels. *Ecology* **66**, 1976–8.

Dahl, E. (1957) Rondane. Mountain vegetation in South Norway and its relation to the environment. *Vidensk. Akad. Skr. I, Mat.-Naturv. Kl.* **1956**(3), 1–374.

Dingman, S.L., Barry, R.G., Weller, G., Benson, C., LeDrew, E.F. and Goodwin, C.W. (1980) Climate, snow cover, microclimate and hydrology. In *An Arctic ecosystem: the coastal tundra at Barrow, Alaska* (J.J. Brown, P.C. Miller, L.L. Tieszen and F.L. Bunnell, eds), pp. 30–65. Dowden, Hutchison & Ross, Stroudsburg, PA.

Ekman, J. (1987) Exposure and time use in willow tit flocks; the cost of subordination. *Anim. Behav.* **35**, 445–52.

Erlinge, S. (1987) Predation and non-cyclicity in a microtine population in southern Sweden. *Oikos* **50**, 347–52.

Erlinge, S., Göransson, G., Hansson, L., Högstedt, G., Liberg, O., Nilsson, I.N., Nilsson, T., von Schantz, T. and Sylvén, M. (1983) Predation as a regulating factor of small mammal populations in southern Sweden. *Oikos* **40**, 36–52.

Fitzgerald, B.M. (1977) Weasel predation on a cyclic population of the montane vole (*Microtus montanus*) in California. *J. Anim. Ecol.* **46**, 367–97.

Framstad, E., Stenseth, N.C. and Östbye, E. (1993) Time series analysis of population fluctuation of *Lemmus lemmus* In *The biology of lemmings* (N.C. Stenseth and R.A. Ims, eds), pp. 97–115. Linnean Society of London, London.

Fretwell, S.D. (1977) The regulation of plant communities by food chains exploiting them. *Perspect. Biol. Med.* **20**, 169–85.

Fryxell, J.M. and Lundberg, P. (1994) Diet choice and predator–prey dynamics. *Evol. Ecol.* **8**, 407–21.

Fuller, W.A. Martell, A.M., Smith R.F.C. and Speller, S.W. (1977) Biology and secondary production of *Dicrostonyx groenlandicus* on Truelove Lowland. In *Truelove Lowland, Devon Island, Canada: a high Arctic ecosystem* (L.C. Bliss, ed.), pp. 437–59. University of Alberta Press, Edmonton.

Gilpin, M.E. (1975) *Group Selection in Predator–Prey Communities.* Princeton University Press, Princeton, NJ.

Hanski, I., Hansson L. and Henttonen, H. (1991) Specialist predators, generalist predators, and the microtine rodent cycle. *J. Anim. Ecol.* **60**, 353–67.

Hanski, I., Turchin, P., Korpimäki, E. and Henttonen, H. (1993) Population oscillations of boreal rodents: regulation by mustelid predators leads to chaos. *Nature* **364**, 232–5.

Hansson, L. (1984a) Winter reproduction of small mammals in relation to food conditions and population dynamics. *Publ. Carnegie Museum Nat. History (Pittsburg)* **10**, 225–34.

Hansson, L. (1984b) Composition of cyclic and non-cyclic vole populations: on the causes of variation in individual quality among *Clethrionomys glareolus* in Sweden. *Oecologia (Berlin)* **63**, 199–206.

Hansson, L. (1984c) Predation as the factor causing extended low densities in microtine cycles. *Oikos* **43**, 255–6.

Hansson, L. (1987) An interpretation of rodent dynamics as due to trophic interactions. *Oikos* **50**, 31–42.

Hansson, L. (1988) Parent–offspring correlations for growth and reproduction in the vole *Clethrionomys glareolus* in relation to the Chitty hypothesis. *Z. Säugetierkunde* **53**, 7–10.

Hansson, L. (1989) Tracking of delay effects in microtine reproduction. *Acta Theriol.* **34**, 125–32.

Hansson, L. and Henttonen, H. (1985) Gradients in density variation of small rodents: the importance of latitude and snow cover. *Oecologia (Berlin)* **67**, 349–402.

Heikkilä, J., Kaarsalo, K., Mustonen, O. and Pekkarinen, P. (1993) Influence of predation risk on early development and maturation in three species of *Clethrionomys* voles. *Ann. Zool. Fenn.* **30**, 153–61.

Henttonen, H. (1985) Predation as a factor causing extended low densities in microtine dynamics: further evidence from shrew dynamics. *Oikos* **45**, 156–7.

Henttonen, H., Oksanen, T., Jortikka, A. and Haukisalmi, V. (1987) How much do weasels shape the microtine cycle at Pallasjärvi, Finnish Lapland? *Oikos* **50**, 353–65.

Hörnfeldt, B. (1994) Delayed density dependence as a determinant of vole cycles. *Ecology* **75**, 791–806.

Hörnfeldt, B., Carlsson, B.-G., Löfgren, O. and Eklund, U. (1989) Effects of cyclic food supply on breeding performance in Tengalm's owl, *Aegolius funereus*. *Can. J. Zool.* **68**, 522–30.

Ivanter, E.V. (1981) Dinamika čislennosti. In *Evropejskaja ryžaja polevka* (N.V. Basenina, ed.), pp. 245–67. Nauka, Moscow.

Järvinen, A. (1985) Predation causing extended low densities in microtine cycles: implications from predation on hole-nesting birds. *Oikos* **45**, 157–8.

Jedrzejewska, B. and Jedrzejewski, W. (1989) Seasonal surplus killing as hunting strategy of the weasel, *Mustela nivalis*, in Poland. *Acta Theriol.* **34**, 347–59.

Kaikusalo, A. and Tast, J. (1984) Winter breeding of microtine rodents at Kilpisjärvi, Finnish Lapland. In *Winter ecology of small mammals* (J.F. Merrit, ed.), pp. 243–52. Carnegie Museum of Natural History, Special Publication 10, Pittsburg, PA.

Korpimäki, E., Norrdahl, K. and Rinta-Jaskari, T. (1991) Responses of stoats and least weasels to fluctuating food abundances: is the low phase of the cycle due to mustelid predation. *Oecologia (Berlin)* **88**, 552–61.

Korpimäki, E., Norrdahl, K. and Valkama, J. (1994) Reproductive investment under fluctuating predation risk: microtine rodents and small mustelids. *Evol. Ecol.* **8**, 357–68.

Koškina, T. and Korotkov, J.S. (1975) Regulative adaptation in populations of the red backed vole (*Clethrionomys rutilus*) under optimal conditions of its range. *Mouse News* **1977** (3), 2–29. (English translation by W.A. Fuller. Original publication: *Fauna i ekologija gryzunov* **12**, 6–61).

Krebs, C.J. and Myers, J.H. (1974) Population cycles in small mammals. *Adv. Ecol. Res.* **8**, 267–399.

Laine, K. and Henttonen, H. (1983) The role of plant production in microtine cycles in northern Fennoscandia. *Oikos* **40**, 407–18.

Lima, S.L. (1985) Maximizing feeding efficiency and minimizing time exposed to predators: a trade-off in the black-capped chickadee. *Oecologia* **66**, 60–7.

Lima, S.L., Valone, T.J. and Caraco, T. (1985) Foraging-efficiency–predation-risk trade-off in the grey squirrel. *Anim. Behav.* **33**, 155–65.

Lucas, J.R. (1983) The role of foraging time constraints and variable prey encounter in optimal diet choice. *Am. Nat.* **122**, 191–209.

McNamara, J.M. and Houston, A.I. (1986) The common currency for behavioral decisions. *Am. Nat.* **127**, 358–78.

McNamara, J.M. and Houston, A.I. (1987) Starvation and predation as factors limiting population size. *Ecology* **68**, 1515–19.

McNamara, J.M. and Houston, A.I. (1992) Risk-sensitive foraging: a review of the theory. *Bull. Math. Biol.* **54**, 355–78.

Magnhagen, C. (1990) Predation risk as a cost of reproduction. *Trends Ecol. Evol.* **6**, 183–6.

Mangel, M. and Clark, C.W. (1986) Towards a unified foraging theory. *Ecology* **67**, 1127–38.

Mihok, S. (1984) Life history profiles of boreal meadow voles (*Microtus pennsylvanicus*). In *Winter ecology of small mammals* (J.F. Merrit, ed.), pp. 91–102. Carnegie Museum of Natural History, Special Publication 10, Pittsburg, PA.

Norrdahl, K. (1993) Regulation of cyclic small mammal populations by avian and mammalian predators. PhD thesis, University of Helsinki.

Oksanen, L. (1990) Exploitation ecosystems in seasonal environments. *Oikos* **57**, 14–24.

Oksanen, L. and Oksanen, T. (1992) Long-term population dynamics of microtine rodents in the Fennoscandian tundra: the vole cycle and the lemming chaos. *Ecography* **15**, 226–36.

Oksanen, T., Oksanen, L. and Fretwell, S.D. (1985) Surplus killing in the hunting strategy of small predators. *Am. Nat.* **126**, 328–46.

Oksanen, T., Oksanen, L. and Norberg, M. (1992) Habitat use of small mustelids in the North Fennoscandian tundra: a test of the hypothesis of patchy exploitation ecosystems. *Ecography* **15**, 237–44.

Ronkainen, H. and Ylönen, H. (1994) Behaviour of cyclic bank voles under risk of mustelid predation: do females avoid copulation. *Oecologia*, **97**, 377–81.

Secher Jensen, T. (1982) Seed production and outbreaks of non-cyclic rodent populations in deciduous forests. *Oecologia (Berlin)* **54**, 184–92.

Seldal, T., Andersen, K.-J. and Högstedt, G. (1994) Grazing-induced proteinase inhibitors: a possible cause for lemming population cycles. *Oikos* **70**, 3–11.

Sih, A. (1982) Foraging strategies and the avoidance of predation by an aquatic insect, *Notonecta hoffmanni*. *Ecology* **63**, 786–96.

Sih, A. (1984) Optimal behavior and density-dependent predation. *Am. Nat.* **123**, 314–26.

Stenseth, N.C. and Framstad, E. (1980) Reproductive effort and optimal reproductive rates in small rodents. *Oikos* **34**, 25–34.

Taitt, M.J. and Krebs, C.J. (1985) Population dynamics and cycles. In *Biology of New World Microtus* (R. Tamarin, ed.), pp. 576–60. American Society of Mammal, Special Publication 8.

Tast, J. (1984) Winter success of root voles, *Microtus oeconomus*, in relation to population density and food conditions at Kilpisjärvi, Finnish Lapland. In *Winter ecology of small mammals* (J.F. Merrit, ed.), pp. 59–66. Carnegie Musuem of Natural History, Special Publication 10, Pittsburg, PA.

Tast, J. and Kaikusalo, A. (1976) Winter breeding of the root vole, *Microtus oeconomus*, in 1972/73 at Kilpisjärvi, Finnish Lapland. *Ann. Zool. Fenn.* **13**, 174–8.

Tast, J. and Kalela, O. (1971) Comparisons between rodent cycles and plant production in Finnish Lapland. *Ann. Acad. Sci. Fenn., A IV Biol.* **186**, 1–14.

Turchin, P. and Taylor, A.D. (1992) Complex dynamics in ecological time series. *Ecology* **73**, 289–305.

Ylönen, H. (1989) Weasels, *Mustela nivalis*, suppress reproduction in cyclic bank voles, *Clethrionomys glareolus*. *Oikos* **55**, 138–40.

Ylönen, H. and Ronkainen, H. (1994). Breeding suppression in the bank vole as antipredatory adaptation in a predictable environment. *Evol. Ecol.* **8**, 1–9.

Ylönen, H., Koskela, E., and Mappes, T. (1994) Small mustelids and breeding suppression of cyclic microtines: adaptation or general sensitivity. *Ann. Zool. Fenn.*, in press.

Zablockaja, L.V. (1957) Materiali po ekologii osnovnyh vidov myševidnyh gryzunov Prioksko-Terrasnogo Zapovednika i smežnyh lesov. *Trudy Priosksko-Terrasnogo gosudarstvennogo darstvennogo Zapovednika* **1957**(1), 190–241.