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# STARVATION AND PREDATION AS FACTORS LIMITING POPULATION SIZE<sup>1</sup>

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**Abstract.** We consider a simple model in which an animal can control both its probability of starvation and its probability of predation. Probability of starvation is decreased by increasing the mean amount of food obtained in the day, but this increases the probability of predation. The optimal mean gain minimizes the total mortality. It is shown that as the amount of food that is required per day increases, the probability of starvation does not necessarily increase, and may actually decrease. This result arises because as the food requirement increases, the animal increases its predation risk in order to avoid starvation.

The results suggest that it is inappropriate to argue that food alone or predation alone limits the size of a population when there is a strong interaction between them. Furthermore, the number of animals that die from starvation may not provide a reliable indication of the importance of food.

*Key words:* mortality; predation; starvation; trade-off.

## INTRODUCTION

A long-standing problem in ecology is that of determining the factors that limit the growth of a population (e.g., Andrewartha and Birch 1954, Lack 1954, 1966, MacArthur 1964, Connell 1975, Weins 1977, Newton 1980, Schoener 1982). Two obvious limiting factors are food shortages and predation. There is growing evidence that animals can control, either behaviorally or ecologically, both the quality of the food supply and their risk of predation, and that there is a trade-off between these factors. In particular, animals can increase the mean rate at which they gain food at the cost of an increase in predation risk. An animal can make this trade-off behaviorally by varying the rate at which it scans the environment for predators, or ecologically by choice of its foraging habitat (e.g., Sih 1980, Werner et al. 1983, Werner and Gilliam 1984, Mangel and Clarke 1986). Work in this area is reviewed by Milinski (1986), Dill (*in press*), and Sih (*in press*).

In this paper, we present a simple model in which an animal can decrease its probability of starvation by increasing its probability of being killed by a predator. The animal can control the mean rate at which it gains food. We determine the percentage of animals that die as a result of starvation and the percentage of animals that die as a result of predation under various environmental conditions. We look at the effect of a decrease in temperature, a decrease in food availability, and an increase in the variability of the food supply.

All these changes increase the total mortality, but decreasing either temperature or food availability does not necessarily increase the probability of starvation. Under some circumstances, the probability of starvation may actually decrease. We conclude that changes in the level of starvation across environmental conditions can not be used to make deductions about whether food availability is limiting a population. More important, it may not be meaningful to say that either predation or starvation limits a population. Because of the potential interaction, both factors must be considered simultaneously.

## RESULTS

We assume that an animal can choose its mean energy gain  $\mu$  over the day. This mean determines both the probability  $S(\mu)$  that the animal dies of starvation and the probability  $P(\mu)$  that the animal is taken by a predator. Typically,  $S(\mu)$  will be a decreasing function of  $\mu$  and  $P(\mu)$  will be an increasing function of  $\mu$ . We consider an animal that is not reproducing, and assume that the optimal behavior is the one that minimizes total mortality  $M(\mu)$  where

$$M(\mu) = S(\mu) + P(\mu). \quad (1)$$

This optimality criterion may not be valid for all animals, but is likely to be appropriate in many cases (see McNamara and Houston 1982). The optimal value  $\mu^*$  of  $\mu$  satisfies

$$-S'(\mu^*) = P'(\mu^*). \quad (2)$$

It is clear from Eq. 2 that there is no a priori reason for the levels of starvation and predation to be equal;

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it is the slopes of  $S(\mu)$  and  $P(\mu)$  that should be equal and opposite.

We now illustrate the optimal balance of starvation and predation within the framework of a simple model of starvation. If the animal gets less than a critical amount of energy  $G$  during the day, then it starves during the night. There is no starvation during the day. The amount of energy obtained during the day has a normal distribution with mean  $\mu$  and standard deviation  $\sigma$ .

In this model, the probability of starvation in the absence of any predation is

$$S_0(\mu) = 1 - \Phi(z), \quad (3)$$

where  $\Phi$  is the standard normal distribution function and

$$z = (\mu - G)/\sigma. \quad (4)$$

To obtain  $S(\mu)$ , we must correct  $S_0(\mu)$  to account for any animals that die of predation before they get a chance to starve. Assuming that given the choice of  $\mu$ , starvation and predation are independent, the probability of death by predation for an animal that would otherwise have starved is  $S_0(\mu) \times P(\mu)$ . Thus

$$S(\mu) = S_0(\mu)[1 - P(\mu)]. \quad (5)$$

For all the cases that we consider, the correction term  $S_0(\mu) \times P(\mu)$  is very small, and our results would not be changed if the correction term were omitted.

We present all our results in terms of  $10^4$  times the actual probability of death during a day. This measure of mortality is approximately equal to the percentage of animals that die during 100 d, and will be referred to as the percentage mortality.

Fig. 1 shows total percentage mortality, together with the percentage mortalities that result from starvation and predation, when  $P(\mu) = 10^{-4}\mu$ . It can be seen that starvation decreases rapidly with  $\mu$ , while predation increases slowly. As a consequence, the optimal value of  $\mu$  occurs when starvation is extremely low. At  $\mu^*$ , the percentage mortality from starvation is 0.23, whereas the percentage mortality from predation is 14.07.

We now explore the variation in  $S(\mu^*)$  and  $P(\mu^*)$  as the environment becomes harsher. We consider three cases of  $P(\mu)$ . In case I,  $P(\mu) = 10^{-4}\mu$ , so  $P'(\mu)$  is constant. In case II,  $P(\mu) = 10^{-5}\mu^2$ , so  $P'(\mu)$  is an increasing function of  $\mu$ . In case III,  $P(\mu) = 10^{-3.5}\mu^{0.5}$ , so  $P'(\mu)$  is a decreasing function of  $\mu$ . All three cases have the same level of predation when  $\mu = 10$ . These specific predation probabilities give percentage mortalities between 10 and 30 under an optimal policy, but as we show below, the general features of our analysis do not depend on the absolute values of  $P(\mu)$  but on the sign of its second derivative.

The first deterioration in the environment that we consider is a decrease in temperature. This has the effect of increasing the daily energy gain  $G$  that is re-

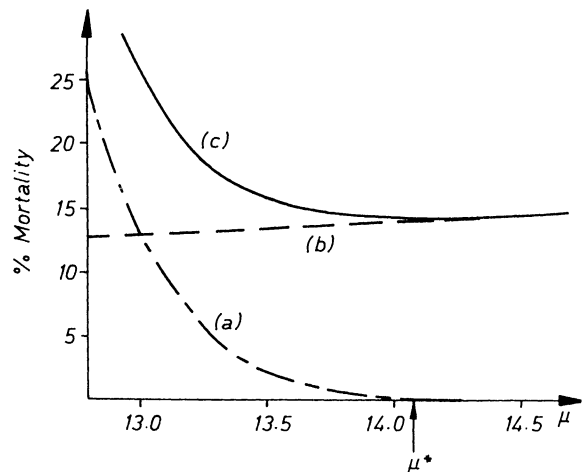


FIG. 1. The change in percentage mortality ( $10^4$  times the daily probability of death) as the mean gain  $\mu$  increases. Curve (a) shows  $10^4 \times S(\mu)$ , (b) shows  $10^4 \times P(\mu)$ , and (c) shows  $10^4 \times M(\mu) \equiv 10^4 \times [S(\mu) + P(\mu)]$ . Total mortality is minimized at  $\mu = \mu^*$ . Daily energy requirement  $G = 10$ ; SD of energy gain  $\sigma = 1$ .

quired for survival. We look at the effect of an increase in  $G$  while keeping the variability  $\sigma$  constant. Table 1 gives examples of the effect of  $G$  for the three cases of  $P(\mu)$ . In all three cases predation increases as  $G$  increases since increasing  $G$  increases  $\mu^*$ . However, starvation does not necessarily increase with increasing  $G$ . To understand this effect we consider the cases I, II, and III separately.

In case I, starvation is constant as  $G$  increases. This result can be understood as follows. Since  $P(\mu)$  is small, Eq. 5 shows that  $S(\mu) \approx S_0(\mu)$ . Thus by Eqs. 3 and 4

$$-S'(\mu) \approx \frac{f(z)}{\sigma}, \quad (6)$$

where  $f(z)$  is the normal density function. Since  $z = (\mu - G)/\sigma$ , the graph of  $-S'(\mu)$  is a bell-shaped curve centered on  $\mu = G$ . Fig. 2 illustrates this curve for the two values  $G_1$  and  $G_2$  of  $G$ . The curve for  $G = G_2$  is identical in shape to that of  $G = G_1$ , but shifted to the right by an amount  $G_2 - G_1$ . In case I,  $P(\mu)$  is a linear function of  $\mu$  so that  $P'(\mu)$  is a constant. This constant function is also illustrated in Fig. 2. By Eq. 2 the optimal value  $\mu^*$  of  $\mu$  satisfies  $-S'(\mu^*) = P'(\mu^*)$ . Thus we can find  $\mu^*$  graphically by finding the point of intersection of the curves  $-S'(\mu)$  and  $P'(\mu)$ . Fig. 2 illustrates the values  $\mu^*_1$  and  $\mu^*_2$  of  $\mu^*$  corresponding to the values  $G_1$  and  $G_2$  of  $G$ , respectively. It can be seen that  $\mu^*_2 - \mu^*_1 = G_2 - G_1$ . Let  $z^* = (\mu^* - G)/\sigma$ . Then, since  $\sigma$  is held constant,  $z^*_1 = z^*_2$  where  $z^*_1$  and  $z^*_2$  are the values of  $z^*$  corresponding to the values  $G_1$  and  $G_2$  of  $G$ , respectively. Since  $S_0(\mu^*)$  is a function of  $z^*$  alone it can be concluded that increasing  $G$  from  $G_1$  to  $G_2$  does not change  $S_0(\mu^*)$ . It follows that the starvation probability  $S(\mu^*)$  also remains approximately constant as  $G$  is increased.

TABLE 1. The effect of the amount of energy  $G$  that is required per day on the value  $\mu^*$  of daily energy gain  $\mu$  that minimizes total mortality  $S(\mu) + P(\mu)$ , together with the resulting percentage starvation  $10^4 \times S(\mu^*)$  and percentage predation  $10^4 \times P(\mu^*)$ .  $\sigma$  (standard deviation of daily energy gain) = 1.

	Daily energy requirement $G$						
	4	6	8	10	12	14	16
Case I							
$\mu^*$	8.07	10.07	12.07	14.07	16.07	18.07	20.07
$10^4 \times S(\mu^*)$	0.23	0.23	0.23	0.23	0.23	0.23	0.23
$10^4 \times P(\mu^*)$	8.07	10.07	12.07	14.07	16.07	18.07	20.07
Case II							
$\mu^*$	7.96	9.90	11.85	13.81	15.78	17.75	19.72
$10^4 \times S(\mu^*)$	0.38	0.48	0.58	0.69	0.79	0.90	1.00
$10^4 \times P(\mu^*)$	6.33	9.80	14.05	19.08	24.90	31.50	38.88
Case III							
$\mu^*$	8.22	10.24	12.26	14.28	16.30	18.31	20.32
$10^4 \times S(\mu^*)$	0.13	0.11	0.10	0.10	0.09	0.09	0.08
$10^4 \times P(\mu^*)$	9.06	10.12	11.07	11.95	12.76	13.53	14.26

In case II, starvation increases as  $G$  increases. Fig. 2 can again be used to analyze this effect. It can be seen from the figure that increasing  $G$  from  $G_1$  to  $G_2$  increases  $\mu^*$  but that  $\mu^*_2 - \mu^*_1 < G_2 - G_1$ . Consequently  $z^*_2 < z^*_1$ . Thus starvation is higher when  $G = G_2$  than when  $G = G_1$ . In case III  $P'(\mu)$  is a decreasing function of  $\mu$ . Fig. 2 shows that this implies that  $\mu^*_2 - \mu^*_1 > G_2 - G_1$  so that  $z^*_2 > z^*_1$  and starvation is lower when  $G = G_2$  than when  $G = G_1$ . Table 1 illustrates the changes in starvation with increasing  $G$  for three specific cases, but the graphical argument based on Fig. 2 shows that the qualitative results obtained are quite general. If  $P(\mu)$  increases linearly with  $\mu$ , so that  $P'(\mu)$  is constant, starvation remains constant as  $G$  increases. If  $P(\mu)$  is an accelerating function of  $\mu$ , so that  $P'(\mu)$  is increasing, starvation increases with increasing  $G$ . Finally, if  $P(\mu)$  is an increasing but decelerating function of  $\mu$ , so that  $P'(\mu)$  is decreasing, starvation decreases with increasing  $G$ .

A slight modification of this analysis allows us to look at the effect of a decrease in food availability while keeping temperature and variability in the food supply constant. In this context,  $\mu$  is not the mean gain but is rather the mean rate at which the animal is working to obtain food. The predation rate remains as  $P(\mu)$ , but the mean gain is now  $\mu - \beta$ , where  $\beta$  is a measure of the availability of food;  $\beta$  increases as food becomes more scarce. The  $z$  value, which was  $(\mu - G)/\sigma$ , is now modified to  $[\mu - (\beta + G)]/\sigma$ . It follows that an increase in  $\beta$  for fixed  $G$  is equivalent to an increase in  $G$  for  $\beta = 0$ . We conclude that the analysis of a decrease in temperature also applied to a decrease in food availability.

Table 2 gives some examples of the effect of increasing the variability in the amount of food gained while keeping  $G$  constant. Both starvation and predation increase in all cases. Starvation increases most rapidly in case II and least rapidly in case III.

The different effects of  $G$  and  $\sigma$  on starvation prob-

ability in case I can be understood from Eq. 6. Since  $P'(\mu^*)$  is constant, so is  $-S'(\mu^*)$  and so Eq. 6 shows that  $f(z^*)$  is proportional to  $\sigma$ . Thus, increasing  $G$  has no effect on  $z^*$  but increasing  $\sigma$  increases  $f(z^*)$  and hence decreases  $z^*$  [ $f(z)$  is decreasing for  $z > 0$ ]. Decreasing  $z^*$  increases starvation probability.

DISCUSSION

Our analysis shows that when an animal can decrease its probability of starvation by increasing its probability of predation, there is no reason to expect the levels of starvation and predation to be equal when behavior is optimal. A low level of starvation does not justify the inference that animals are not in danger of starving; it is possible that in order to avoid starvation the animals are increasing their probability of predation. Gibb (1954) reached a similar conclusion from his study of the behavior of small animals in winter (see also Jansson et al. 1981).

We have also shown that comparing the levels of starvation under various environmental conditions may not provide obvious evidence about the importance of food. When the probability of predation is a decelerating function of mean gain, the probability of starvation can actually decrease as the environment gets worse.

Lima (1986) points out that previous discussion of population control has often been phrased in terms of determining which single factor limits population size. Analysis of winter fattening as a trade-off between starvation and predation (Lima 1986 and J. M. McNamara and A. I. Houston, *personal observations*) shows that the combined effects of weather, food availability, and predation are important in determining optimal levels of fat and hence mortality rates. Our analysis supports Lima's conclusion that one cannot argue that the population is limited by starvation or predation alone. These factors cannot be considered in isolation.

Within our model, decreasing the temperature has

the same effect as decreasing the availability of food while keeping the variance in the food supply constant. The effect can differ from the effect produced by increasing the variability of the food supply. Both effects involve an increase in total mortality, but increasing the variability has a much more pronounced effect on the probability of starvation and consistently increases this probability for the parameter values that we have used.

The results that we have presented in Tables 1 and 2 are based on a particular model of starvation and three forms of the predation function  $P(\mu)$ . Arguments based on Fig. 2 have been used to show that the trends in these tables depend only on the qualitative features of  $P(\mu)$ . The model of starvation is very simple. It ignores both the possibility of starvation during the day and the value of gaining more energy than  $G$  by dusk. It also does not allow the animal to change its policy during the day as a function of the outcomes of its previous foraging behavior. McNamara and Houston (1986) include all three modifications. There, we consider the case when  $P(\mu)$  is an accelerating function. Our results and subsequent work suggest that including the above modifications do not change the qualitative conclusions reached here.

Although we have not included, explicitly, density dependence in our model, an increase in the population size may decrease the availability of food (i.e., increase  $\beta$ ). Our results show that such a decrease in food availability may not produce an increase in the percentage of animals that starve.

It should be emphasized that Eq. 2 is completely general; it will apply to any case of a trade-off between starvation and predation. Two possible examples are:

- 1) An animal feeding its young. The parent can choose

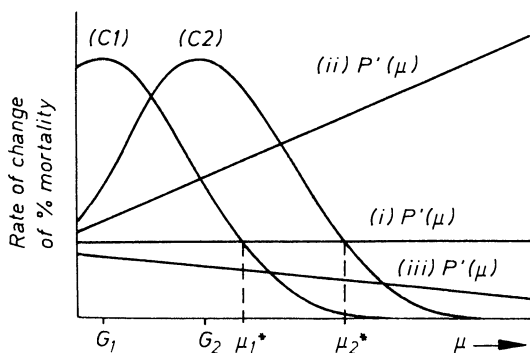


FIG. 2. Dependence of the optimal value of mean energy gain  $\mu$  on daily energy requirement  $G$ , for three different forms of the predation function  $P(\mu)$ . The bell-shaped curve (C1) is that of  $-S'(\mu)$  when  $G = G_1$ . The curve (C2) is that of  $-S'(\mu)$  when  $G = G_2$ . The three lines labelled  $P'(\mu)$  are (i) constant, (ii) increasing with increasing  $\mu$ , and (iii) decreasing with increasing  $\mu$  (cf. cases I, II, and III in Results). The optimal value  $\mu^*$  of  $\mu$  is the value of  $\mu$  at which the curves  $-S'(\mu)$  and  $P'(\mu)$  intersect. When  $P'(\mu)$  is given by curve (i),  $\mu_1^*$  and  $\mu_2^*$  are the values of  $\mu^*$  corresponding to the values  $G_1$  and  $G_2$  of  $G$ .

TABLE 2. The effect of the variability in energy gain on the value  $\mu^*$  of  $\mu$  that minimizes total mortality  $S(\mu) + P(\mu)$ , together with the resulting percentage starvation  $10^4 \times S(\mu^*)$  and percentage predation  $10^4 \times P(\mu^*)$ . Daily energy requirement  $G = 10$ .

	Standard deviation of daily energy gain, $\sigma$				
	0.5	1.0	1.5	2.0	2.5
Case I					
$\mu^*$	12.12	14.07	15.96	17.80	19.60
$10^4 \times S(\mu^*)$	0.11	0.23	0.36	0.48	0.61
$10^4 \times P(\mu^*)$	12.12	14.07	15.96	17.80	19.60
Case II					
$\mu^*$	12.01	13.81	15.52	17.13	18.71
$10^4 \times S(\mu^*)$	0.29	0.69	1.18	1.83	2.48
$10^4 \times P(\mu^*)$	14.43	19.08	24.03	29.33	34.98
Case III					
$\mu^*$	12.21	14.28	16.30	18.29	20.25
$10^4 \times S(\mu^*)$	0.05	0.09	0.13	0.17	0.21
$10^4 \times P(\mu^*)$	11.05	11.95	12.77	13.52	14.23

a feeding strategy that determines its predation probability and the starvation probability of the young. There are now four possible outcomes. The parent may die of predation, in which case the young starve, the young may starve while the parent survives, the young may die of predation, or both the parent and the young may survive. Regardless of the exact details of the situation, there will be a trade-off between the conflicting pressures of predation and starvation.

- 2) An animal can choose the size of group in which it feeds. Group size in turn determines feeding rate (and hence starvation probability) and predation rate.

In both these examples, our results suggest it is difficult to determine the importance of food from an observation of the rates at which animals die from starvation.

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#### LITERATURE CITED

- Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago, Illinois, USA.
- Connell, J. H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. Pages 460–490 in M. L. Cody and J. M. Diamond, editors. Ecology and evolution of communities. Harvard University Press, Cambridge, Massachusetts, USA.
- Dill, L. M. *In press*. Animal decision making and its ecological consequences: the future of aquatic ecology and behaviour. Canadian Journal of Zoology.
- Gibb, J. A. 1954. Feeding ecology of tits, with notes on treecreeper and goldcrest. *Ibis* 96:513–543.
- Jansson, J., J. Ekman, and A. von Brömssen. 1981. Winter mortality and food supply in tits *Parus* spp. *Oikos* 37:313–322.
- Lack, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford, England.
- . 1966. Population studies of birds. Clarendon, Oxford, England.

- Lima, S. L. 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. *Ecology* **67**:377–385.
- MacArthur, R. H. 1964. Environmental factors affecting bird species diversity. *American Naturalist* **98**:387–397.
- Mangel, M., and C. W. Clark. 1986. Towards a unified foraging theory. *Ecology* **67**:1127–1138.
- McNamara, J. M., and A. I. Houston. 1982. Short term behaviour and lifetime fitness. Pages 60–87 in D. J. McFarland, editor. *Functional ontogeny*. Pitman, London, England.
- McNamara, J. M., and A. I. Houston. 1986. The common currency for behavioural decisions. *American Naturalist* **127**:358–378.
- Milinski, M. 1986. Constraints placed by predators on feeding behaviour. Pages 236–252 in T. J. Pitcher, editor. *The behaviour of teleost fishes*. Croom Helm, London, England.
- Newton, I. The role of food in limiting bird numbers. *Ardea* **68**:11–30.
- Schoener, T. W. 1982. The controversy of interspecific competition. *American Scientist* **70**:586–595.
- Sih, A. 1980. Optimal behavior: can foragers balance two conflicting demands? *Science* **210**:1041–1043.
- . *In press*. Predators and prey lifestyles: an evolutionary and ecological overview. In W. C. Kerfoot and A. Sih, editors. *Predation: direct and indirect impacts on aquatic communities*. University Press of New England, Hanover, New Hampshire, USA.
- Weins, J. A. 1977. On competition and variable environments. *American Scientist* **65**:590–597.
- Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* **15**:393–425.
- Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* **64**:1540–1548.