

The life-history strategies of *Mustela nivalis* and *M. erminea*

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Mustela nivalis and *M. erminea* are small, boreal carnivores living mainly on voles and lemmings. The population fluctuations of these prey create alternately good and bad conditions for mating and reproduction of the two small mustelids. The difference in means by which each has adapted to this variable environment is associated with the presence of prolonged delayed implantation in one and not the other.

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1. Introduction

Mustela nivalis and *M. erminea* are two apparently closely-related small mustelids of similar appearance and habits. Both are very widespread in the cool temperate and boreal zones north of about 40°N. Both are highly specialised for hunting small rodents in their burrows and under snow, and over the northern part of their ranges there is often little alternative food available for most of the year (Nasimovich 1949).

The niche of the specialist predator of small rodents is precarious. The population fluctuations of voles and lemmings create alternate feasts and famines over a three or four year cycle, during which the chances of a female *nivalis* or *erminea* producing surviving young range from very high to practically nil. The population densities of small mustelids fluctuate over the same period, during which the chances of a male *nivalis* or *erminea* establishing priority of access to a high number of females range from good to bad. The common problem for all short-lived predators living in such a variable environment is to minimise their chances of leaving no young. *M. nivalis* and *erminea* have each evolved entirely different strategies in response to that problem. (I define a strategy as a long-term characteristic of a species, alterable only in evolutionary time; a tactic as a short-term response of individuals alterable in ecological time).

2.1. Female strategies

The female *nivalis* matures at about three months, and, when food is abundant, spring-born young females may produce young in the summer of their own birth, and adults a second litter. Litters average 5-6, and the

mean life expectancy from independence is < 1 year, though some individuals may live 3-4 years (King 1980). The combination of early maturity and capacity for extra summer litters allows female *nivalis* to respond very quickly when rodents become abundant; but in poor years, spring-born young females delay their first breeding attempt until next spring, and in very bad springs, many adults produce no young at all (Tapper 1979). The probability of a given female meeting a disastrous season is significant, since the 3-4 year rodent cycle is about the same length as her maximum lifespan. Local extinctions and recolonisations by dispersal are therefore frequent.

The female *erminea* becomes sexually mature whilst still a nestling (5-8 weeks old) and almost all young females are fertilised by an adult male before leaving the family group (King & Moody 1982). Physical maturity is reached at about 6 months, unaffected by the negligible maintenance cost of the blastocysts in delay. The ovulation rate is high (average 8-10 ova per female, up to 19) with a remarkably constant mean in a wide range of temperate environments. The number of young produced depends on the supplies of food, especially of small rodents, from the time of implantation to weaning. In poor conditions large numbers of potential young die before or soon after birth (King 1981). No second litter is possible, because delayed implantation is obligate. In a peak season an adult female *erminea* realising her entire available fecundity can produce as many young in one litter as an adult *nivalis* can produce in two, but the total productivity for the season of a female *erminea* is much lower (King & Moors 1979). This disadvantage may be offset to some extent by a longer maximum lifespan, possibly 5-6 years (King, unpubl.). Hence, female *erminea* losing all their young in seasons of scarcity have some chance of surviving to the next good

season, though the proportion that do so is unknown, probably small.

2.2. Male strategies

Males of both species are polygynous or promiscuous, and take no direct part in the rearing of the young. The variance in reproductive success among males is determined by the number of females each mates. There is therefore likely to be intense competition (direct or indirect) between males for access to, or selection by, the most females. This is most pronounced among *erminea*, where the precocity of the juvenile females results in a great excess and clumping of fertile females in the breeding population. *Erminea* are an outstanding exception to the general rule that extreme polygyny is rare among the smaller carnivores (Clutton-Brock & Harvey 1978). However, in poor years the density of breeding females may be lower, reducing the males' opportunities to obtain several mates, or even one.

3. Delayed implantation

Individuals of both species adjust their reproductive effort to the population fluctuations of their prey, but by different tactics (defined and summarised in King 1981). The difference is due to delayed implantation in one and not the other. Its origin, in only one of two similar, sympatric species, is puzzling. The problem is not only physiological, but also ecological: delay prevents *erminea* reproducing as fast as its competitor, *nivalis*. It is difficult to understand how a mutation for delay in age at first littering could establish in relatively short-lived predators requiring rapid productivity in peak years, when fecundity does not increase with age (King & Moody 1982). Wright's (1963) temporary family-bond explanation is invalid if a male *erminea* can gain more breeding success from promiscuity than from investment in young that are not guaranteed to be his own.

I suggest that the key to the life-history strategy of *erminea* is the combination of delayed implantation and juvenile precocity. This combination confers the advantage, to the females, of certain fertilisation before dispersal, and to the males, of huge possible breeding success. The combination could have arisen if *erminea* evolved from an ancestral mustelid stock that already had delayed implantation. The first *erminea* appeared in the late Pliocene (Kurtén 1968), at the time of rapidly cooling climate, and explosive evolution of voles, and the first appearance of the tundra and the early lemmings (Kowalski 1980). They had the opportunity to occupy a new niche by becoming small enough to hunt voles and lemmings in their own runways — incidentally also becoming pre-adapted for undersnow hunting in the following glacial periods.

Because the niche of a specialist predator of small rodents is one of fluctuating risks and rewards, natural selection favoured a shortened generation time, and greater insurance against periodic reproductive failure, in the early *erminea*. These requirements could be met simply by adding juvenile precocity to the pre-

existing delayed implantation. The reproductive advantages of this innovation, to both sexes, would ensure its spread through the population. Synchronising oestrus in adult and juvenile females requires a post-partum oestrus, and the delay in implantation, so far from being a handicap, might have had to be extended to meet this condition.

There are at least two possible explanations for the lack of delayed implantation in *nivalis*. One is that the two species are not as closely related as they look: in details of the cranium, baculum, and reproduction, *erminea* has closer affinities to the martens, and *nivalis* to the polecats, than either has to each other (Pohl 1910). Possibly *erminea* and *nivalis* are independently-evolved vole-specialists descended from different ancestral stocks, one with delayed implantation and one without it. There are palaeontological arguments against this idea: The form and number of the teeth of even the earliest *Mustela* are different from those of *Martes*. An alternative explanation is that both are descended from stock which had delayed implantation, but *nivalis* eliminated it in the process of reducing its body size and generation time to match those of its prey. There are ecological arguments against this idea: It does not explain why *erminea* has not done the same.

The alternatives can be tested by various modern genetic and biochemical techniques. The results would be interesting either way. If the two species are from different stocks, they are a remarkable example of convergence; if from the same stock, they pose a problem for the theory of reproductive strategies.

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