

The origin and adaptive advantages of delayed implantation in *Mustela erminea*

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One of the recurrent fascinations of ecological discussion at present is why apparently similar and sympatric animals can have different reproductive strategies. *Mustela erminea* and *M. nivalis* are a particularly puzzling pair, recently discussed by King (in press) and Sandell (1983). These two papers have much in common, but on first reading they appear to be advocating opposing hypotheses.

In fact, the difference is mainly one of approach. The problem of delayed implantation has two aspects, origin and maintenance. Discussion of the two must be clearly distinguished, otherwise confusion results. Tuomi and Haukioja (1979) identify various kinds of models of life-history theory, including *tactic models*, explaining the present adaptive variations and maintenance of life history traits, and *historical models*, explaining the past establishment of life history traits. Sandell is mainly concerned with a tactic model, King with a historical one.

The basic question asked in both papers is the same: why does *M. erminea* have delayed implantation, while *M. nivalis* does not? This is really two questions:

(a) what is the adaptive value of delayed implantation to *erminea*? and (b) if it is valuable, why does not *nivalis* have it too?

The trouble with all explanations of adaptive value is that they tend to sound like Just-so stories, and many are just as unconvincing, for two reasons. The first is the difficulty of distinguishing a *function*, produced by design, from an *effect* that follows secondarily or by chance. The second is it is seldom possible to avoid the trap of confusing sequence with consequence. In contemporary experimental biology, the second problem is dealt with by ensuring adequate replicates and controls, but in phylogeny, controlled observations are impossible. We cannot say what adaptations a species might have evolved if it had not evolved the ones it did. Delayed implantation may well have many advantages to *erminea*, but it is obligate; therefore we cannot ascribe the biological success of the species to that character, since for all we know, it could have been as successful without it.

Before we can use the term "adaptation" we have to show that the attribute in question has been produced by design, that is, by natural selection between alternate alleles in Mendelian populations (Williams 1966). From observing populations of contemporary mustelids, we cannot say how delayed implantation first arose, because we do not know enough about the conditions in which natural selection was operating on the ancestral populations. But no character so intimately concerned with reproductive success could be maintained in a population for long if it were detrimental. So, looking at the contemporary mustelids, it is valid to ask whether delayed implantation has been *maintained* by design. There is every sign that it has.

The mechanism requires complex hormonal control, which in *erminea* is extremely precise and consistent, with practically no variation between individuals or years. Virtually all females of all ages display it every year, in all temperate habitats; apparently there is never any profit in deviation. It is easy to suggest lists of advantages that this arrangement may have for individual *erminea*, as both King (1981 and in press) and Sandell (1983) have done; but we cannot tell if these advantages are the purpose or the effects of delayed implantation, and they are relevant only to the first part of the question (why *erminea* has delay) – and even then, only by circular reasoning, as Sandell honestly admits. The second question (why *nivalis* does not have it too) remains, and it brings up the problem of origin. Here Sandell stops, because "the breeding strategies of these species are determined not by phylogenetic constraints, but by the selection pressures that act on the animals in their present ecological situations". Of course: but how did the present situations arise?

The rather late appearance of the modern *erminea* and *nivalis* in the Pliocene (Kurtén 1968), was, I suggest, a response by existing mustelid types to the opportunity presented by the radiation of the voles and lemmings (King in press). Increasing specialisation on unreliable small rodent prey in a cooling climate required a shift to a more opportunistic life-history strategy – e.g. by developing earlier maturity and/or

more litters per female per year. The existing mustelids could have included marten-like animals, which already had delayed implantation, and polecat-like animals, which had not, and possibly also intermediate form(s), known (Anderson 1970), or unknown. (Of course, these "ancestors" are not visualised as being much like the existing martens and polecats, any more than ancestral hominids need have looked like existing great apes.) In addition, there is one more important character to be considered, the extremely early puberty of juvenile female *erminea*, which I think is as important as delayed implantation to the reproductive strategy of the species (King 1981 and in press). Whereas delayed implantation is a common character among mustelids (particularly in the older genera), and it is reasonable to suggest that *erminea* descended from an ancestor that already had it, such extreme precocity is rare, and may well be an invention special to *erminea* (and *frenata*); any explanation of the reproductive strategy of *erminea* must account for it just as convincingly as for delayed implantation.

In theory, the modern *erminea* and *nivalis* could have descended to us in one of four ways.

1) *Both are derived from a common ancestor without delayed implantation, but erminea acquired it.* This hypothesis demands that *erminea* acquire two new characters – and with the additional condition that delayed implantation had to be added *before* juvenile precocity. It would not give a juvenile female *erminea* much of an advantage in reproductive competition to conceive young that would be born before she is strong and experienced enough to provide for them; and the addition of delayed implantation by itself would impose such a disadvantage to a small rodent predator that it is hard to see how it could have been selected in favour of the alternative of direct implantation. So, on ecological grounds, this first possibility seems the least likely. Moreover, the statement of Flint (1981), that the development of embryonic diapause is a "relatively small step in evolutionary development", seems too naive in view of the ecological consequences, and the complexity of the control mechanisms involved, at least in mustelids (Mead 1981).

2) *Both are derived from a common ancestor with delayed implantation, but nivalis lost it.* This suggestion is more reasonable, at least on *erminea*'s side. In a population of females where the mean age at death is 2.5 yr and delayed implantation obligatory, a single heritable change in strategy allowing a female to mate as a nestling, instead of at one year old, would double her lifetime fecundity compared with any other female, and, provided survival and other life-history characters were not too much altered thereby, this would certainly be a strong selective advantage in the demographic environment of that animal. Note that we do not have to believe that this is the purpose of the change, only that it is the effect. Females inheriting the combination of infant precocity and delayed implantation, linked to-

gether as a stable set of genes, would have higher individual life-time breeding success, plus other advantages as side-effects, e.g. certain fertilisation before dispersal. The same set of genes would greatly increase the number of mates available to successful males; hence, if all other things are equal, the set would spread. But on the other side, this alternative postulates that *nivalis* abandoned the delayed implantation of its ancestors. This would certainly be as effective a way of increasing lifetime fecundity as the other, except that it raises the question, if *nivalis* could take this line, why not *erminea* too? What would prevent the individual female *erminea* from "cheating", abandoning delayed implantation and producing a second litter in rodent-peak years?

3) *Both are derived from a common ancestor in which delay was facultative and variable* (as, for example, in modern *Mustela vison* and *Mephitis mephitis*; Mead 1981), but since then, each has lost the ability to take up the other option. This hypothesis implies some kind of reproductive isolation, as in, for example, the separate geographic distributions of the eastern and western forms of the spotted skunk (Mead 1968): otherwise, it meets the same problems, of how different reproductive strategies can develop in sympatric animals of common ancestry, as were outlined in (1) and (2) above.

4) *Each is descended from different ancestors, one with delayed implantation and one without it.* The third and fourth alternatives do not require answers to the question of how *erminea* acquired delayed implantation, or to the question of why only *nivalis* abandoned it. They need only to postulate *erminea* acquiring juvenile precocity, which is probably the easiest to explain both in ecological terms (the original advantage of increasing lifetime fecundity) and in physiological control (e.g. by juvenile females developing a means of perceiving and responding to maternal oestrogen in the milk when the lactating female comes into post-partum oestrus). They are the basis of my historical model, which proposes that delayed implantation is an ancestral character, whose original value we cannot know, but which has been retained in modern *erminea* because of the beneficial effects of it in combination with juvenile precocity. Like many previous authors, I have been unable to suggest a positive, unarguable function for delayed implantation without circular argument, but this model does not require one – nor is it necessary to make the impossible distinction between function and effect. The mere persistence of the character in *erminea* provides grounds for assuming its effects are, on balance, beneficial. Whether it most benefits the females or (perhaps more likely) the dominant males, is another question.

There are two main objections to this model. First, recent chromosomal and cranial studies (quoted by Sandell) concluded that *nivalis* and *erminea* are closely related, hence arguing against alternative (4). But neither study included martens, nor considered all possible characters, especially the morphology of the baculum. The baculum of *erminea* is much more like

that of *Martes*, and that of *nivalis* is more like *Putorius*, than either is to each other. Unfortunately, it is well known that different methods of deducing phylogenetic relationships can give different answers. A new and comprehensive study is required, free of the prior assumption of a close relationship between *nivalis* and *erminea*.

The second point concerns one of my suggested advantages of delayed implantation for female *erminea*, that of certain fertilisation before dispersal. Sandell points out that Swedish studies (Erlinge 1977) show that it is the male, not the female, which is the dispersing sex. I agree (King and McMillan 1982), although that does not prove that females never disperse; and it may be worth pointing out that, in small predators relying on food supplies that may be unevenly distributed and temporarily variable, dispersal is not the only way by which a female might find herself alone in spring. Females are more efficient at hunting in rodent burrows, and surviving on short rations, when prey is scarce (Moors 1980) (and they are also generally less often caught in traps), so are more likely than males to survive a local population decline. Nevertheless, the combination of delayed implantation and sexual bimaturism could still be retained even if it were of little or only incidental advantage to the individual female, because it also confers the strong advantage to the dominant male (including eventually some of her sons) of providing an instant and submissive harem in every breeding den he can get into. Perhaps the males seen carrying food to dens were actually either appeasing the temporarily dominant adult female, in order to gain entry, or investing in their future mates.

Sandell's tactic model is based on the present reproductive strategies of *nivalis* and *erminea*, and in this it is perfectly valid; but it does not distinguish function from effect, and it hinges on a supposed difference in selection pressures acting on the two species (favouring early breeding in *erminea*, versus high r_{max} in *nivalis*). This difference seems disproportionately small and variable, compared with the size and constancy of the difference in breeding biology it tries to explain.

The early breeding argument is best applied to herbivores and hibernators, where the young are able to grow only during summer, and must reach a critical minimum size to survive the winter. Sandell adapts it for *erminea* by assuming it would be advantageous to the adults to avoid mating during winter, a time of severe energetic stress for northern weasels generally. In fact both species are quite well adapted to life under the insulating snow blanket, and when prey are abundant, *nivalis* can breed there (Fitzgerald 1981). If *nivalis*, why not *erminea*? In *Mustela* spp. the most favorable seasons for growth and development of young are probably determined more by density of prey than by temperature, even in the Arctic. When prey are abundant, hunting

trips can be brief, and adults and young can spend most of their time in thickly insulated nests. It seems simpler to assume that the earlier breeding of *erminea* compared with *nivalis*, pointed out by Sandell, is an effect, not a function, of delayed implantation.

Concerning *nivalis*, Sandell suggests that the strongest selection pressure should be for a high potential rate of increase. I strongly agree (although not for the reason suggested by Heidt); but this argument applies to *erminea* too. The interesting point is that the two species have evolved almost opposite tactics (King 1981), and strategies (King, in press) in response. Delayed implantation itself is only a part of these differences. The historical model presented above aims to provoke discussion of their wider evolutionary implications and ecological consequences.

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