

CHAPTER 11

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## The Advantages and Disadvantages of Small Size to Weasels, *Mustela* Species

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The weasels (*Mustela* spp.) are a group of small mustelid carnivores that originated in the late Pliocene and are now distributed throughout the Holarctic region. *Mustela erminea*, the stoat or ermine, is circumboreal north of about 40°N. *M. nivalis* is sympatric with *erminea* over most of the same area. It includes two distinct subspecies, the common weasel of western Europe and Britain (*M. n. vulgaris* Erxleben 1777), and the least weasel of northern Scandinavia, USSR, and North America (*M. n. nivalis* Linnaeus 1766), which are different in appearance and range (Stolt 1979) but interbreed in captivity (F. Frank, pers. comm.). A third species, *M. frenata*, the long-tailed weasel, is confined to America, from about 50°N to about 15°S.

All have the characteristic "weasel" look (Figure 11.1): small (all under 600 mm total length) with long, thin bodies, short legs, flattish triangular heads, bright black eyes, and long whiskers. They form a size-graded set of two (rarely three) sympatric carnivores, in which *frenata* (or, in the absence of *frenata*, *erminea*) is always the largest, and *nivalis* is always the smallest; where all three are sympatric, *erminea* is the middle-sized one. All have rather short fur, brown above and white or cream below, turning totally white in winter in the northern races. All are, to different degrees, specialist predators of small mammals, willing to take birds, insects, lizards, or invertebrates if hungry, but preferring to concentrate on whatever varieties of rodents and lagomorphs are provided by the local fauna; and they hunt these prey very effectively, with seemingly boundless energy.

The way of life of the weasels is extremely successful; as a group, they are without doubt the most abundant mammalian carnivores in the world. But their small size and specialized hunting strategies give them high efficiency as predators at the price of substantial inefficiency in physiology and uncertainty in reproductive success. These strategies and their penalties, and the ecological consequences that follow, are the subject of this chapter.

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Figure 11.1.  
A typical weasel,  
*Mustela erminea*.  
(Drawing by  
L. Douglas.)

## The Evolutionary Origin of Small Size in Weasels

The evolutionary history of many groups of mammals shows a tendency toward gradual increase in size, by no means universal but common enough to have been labeled "Cope's Rule" (Stanley 1973; Peters 1983:192). Evolutionary trends toward decreased size are much less common, perhaps because at any one time "all the smaller niches will be occupied, [so] the only way to conquer new worlds is to make larger niches. It is only through . . . some peculiar change of conditions that the smaller niches will be vacated [or created], and there might be a selection pressure for a reversion to smaller size" (Bonner 1965:190). I have suggested that the weasels are an example of this process (King 1983a, 1984a). In the Miocene period, when the subfamily Mustelinae originated, the ancestors of the weasels were forest-dwelling hunters, probably somewhat similar to martens. Several marten-like carnivores are known from the Miocene (see Martin, this volume), and by the early Pliocene there were at least three separate lines of true *Martes* already established, as well as some other forms intermediate between *Martes* and *Mustela* (Anderson 1970:122). Throughout the Pliocene period the northern climate was cooling toward the Pleistocene; the forests were being replaced by grassland; and the evolution of the voles was presenting a new niche for predators small enough to make best use of an abundant but unreliable resource.

Such circumstances would favor a decrease in size and a shift along the  $r$ - $K$  spectrum in the direction of a more  $r$ -selected or opportunistic life-history strategy (King and Moors 1979a). In the late Pliocene the tundra and the earliest lemmings appeared (Kowalski 1980), and also the first of the modern weasels, *M. plioerminia* and *M. pliocaenica* in Eurasia (Kurtén 1968) and *M. rexroadensis* in North America (Kurtén and Anderson 1980). The small size of these predators was, I suggest, originally an adaptation for hunting voles on Pliocene grasslands; but as climatic cooling continued and conditions became more and more severe, small size also became a useful preadaptation for hunting lemmings under snow. The timing of these events implies that the characteristic that later became one of the most critical advantages of small size to the northern weasels, the ability to use the nests of rodents and the insulating snow blanket to escape the infinite heat sink of the clear night sky (Pruitt 1978), started as a side benefit of the more obvious advantage of the ability to pursue voles through their runways in matted grass.

## Factors Influencing Body Size in Contemporary Weasels

The consequences of small size to mammals in general have often been reviewed (e.g., Bourlière 1975; Panteleev 1981; Clutton-Brock and Harvey 1983; Peters 1983; Schmidt-Nielsen 1984; Gittleman 1985). When weasels are considered alone, only a certain subset of factors need be listed (Figure 11.2):

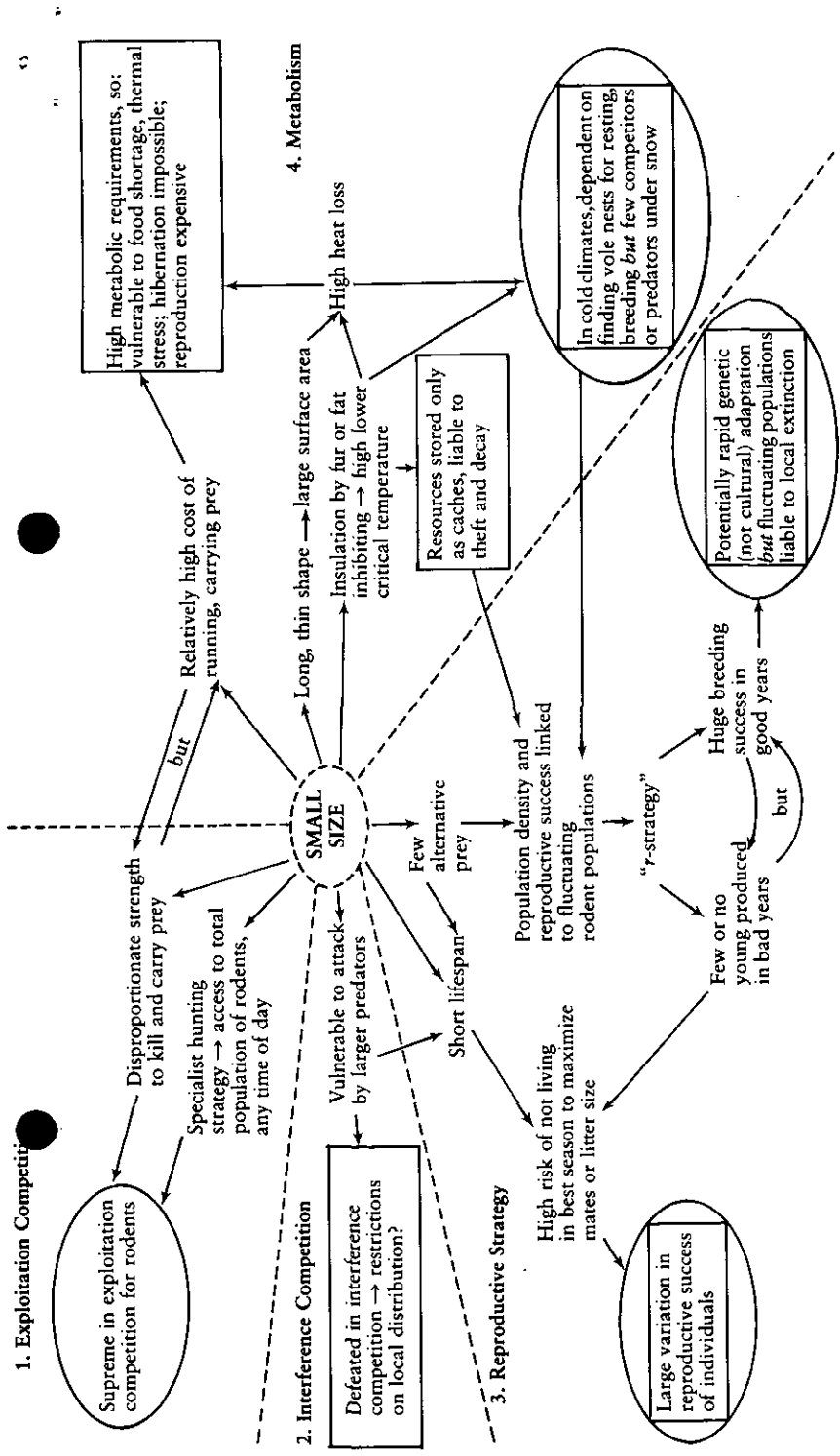


Figure 11.2. The advantages (circled) and disadvantages (boxed) of small size to the weasels as a group. There are four main subject areas, linked together at various levels. The advantage in exploitation competition (area 1) is balanced by the disadvantage in interference competition (area 2); in reproductive strategy (area 3) there is a net balance at both individual and population levels; only in metabolism (area 4) are the advantages outweighed by the disadvantages. It seems likely that ecological energetics is especially significant in determining body size in weasels, and/or the advantage in foraging efficiency is important enough to compensate.

hunting strategy and exploitation competition, predation and interference competition, metabolism, and reproductive strategy.

The interplay of profit and loss can be understood on three levels. First and most obviously, there are the advantages and disadvantages of small size to weasels as a group compared with other mammalian carnivores. However, although all weasels may be considered small by comparison with other carnivores, not all are equally small; there are degrees of smallness within the group, caused by substantial interspecific and sexual variation. Hence, we may look at the same list of advantages and disadvantages of *relative smallness* as applied, second, to the species of weasels separately, and third, to the sexes within each species.

### Hunting Strategy and Exploitation Competition

A predator has first to find a suitable prey and then to kill and process it without incurring a net loss in energy. The size of the predator strongly influences both the energy equations and the risks involved, in different ways according to the size of the prey.

Small rodents are relatively easy to kill but often hard to find. Weasels observed in enclosures can easily overpower mice or voles exposed in the open, although even in such artificial conditions they do not always catch every one (Erlinge et al. 1974; Nams 1981). Rodents familiar with the enclosure can often detect a hunting weasel first (Jamison 1975); failing that, they may escape by freezing or by rapid flight along known routes, deliberately dodging through dense cover and around obstacles to throw off the pursuer (Metzgar 1967; King 1985). In the wild, where rodents are free to hide in or escape to much larger areas of more complex cover than can be provided in any enclosure, the work of hunting must greatly increase, especially during the periodic population declines of voles, or in habitats where small rodents are generally scarce. For example, each male *nivalis* living in a deciduous woodland observed in England must have had to search through miles of tunnels on its large home range (7–15 ha) in order to find, every day, enough of the 21–39 rodents hidden on each hectare (King 1980a). Smaller ranges would not have been viable, and, as it was, the resident weasels were often seriously undernourished. When the density of rodents dropped lower still, all weasels disappeared from the area (Hayward 1983).

Weasels therefore run a greater risk of failing to find a prey than of being injured while attempting to capture it. Their optimum hunting strategy is to maximize their ability to search through the burrows and runway systems of rodents and lagomorphs, and through all kinds of cover into which these prey could escape. Because the senses of weasels are adapted to function either in full sunlight or underground (Gewalt 1959), they are able to hunt at any time of day and to reach a far higher proportion of the prey population (including

nestlings) than is available to larger predators. The smallest weasels (*M. n. nivalis*) can go wherever a vole can go, even into its own nest; in cold climates they are very efficient at hunting under snow (Formosov 1946) and regularly take over the nests of their most recent prey (McLean et al. 1974; Madison et al. 1984). Larger weasels (*erminea* and *frenata*) can still follow voles into thick cover (log piles, tumbled rocks) that would exclude a fox or cat, and can enter the burrows of watervoles (*Arvicola* spp.) and rabbits. They will take a variety of mammals up to sciurid/lagomorph size, as well as birds; but changes in the numbers of small rodents still influence their density and population dynamics (Edson 1933; Erlinge 1983; King 1983b, 1983c).

Unfortunately, although weasels are the world experts at finding rodents, their ultimate dependence on rodents may, in some temperate habitats, put weasels at a long-term disadvantage in exploitation competition with larger predators. A varied fauna of generalist predators with other prey available can sometimes exert a very strong collective pressure on small rodents, enough to hold their populations low all the year round and reduce the breeding success of female weasels (Erlinge 1983). Weasels come into their own in the far north, where they can continue to survive on a sparse population of voles or lemmings long after other predators have turned to hunt other prey or moved elsewhere (Fitzgerald 1981).

Hunters small enough to enter rodent runways must still not be too small to execute a kill; weasels therefore make up extra size in length rather than girth, and use it by wrapping their long bodies around a catch, which helps to contain its struggles (as described by, e.g., Heidt 1972). They do not have to sacrifice muscular strength for size, since the force that an individual muscle can exert is the same, per unit of cross-sectional area, in mammals of any size (Schmidt-Nielsen 1984:163). On the contrary, weasels appear to be relatively stronger than larger predators; no lion can run at speed carrying a carcass of half its own weight. The difference is a simple result of scaling. With decreasing size, the mass of an animal decreases in proportion to the third power of its length ( $L^3$ ), but the cross-sectional area of its muscles (which determines the force they can exert) decreases only as the square of their length ( $L^2$ ). Hence, the force exerted by muscles, relative to mass, increases in proportion to the decrease in body size. This apparently disproportionate strength of weasels is one of the mechanical advantages of small size, and there are others. For example, although the incremental cost of moving one unit of body weight over one unit of vertical distance is independent of size (about 1.36 ml  $O_2$  per kg per vertical meter: Schmidt-Nielsen 1984:175), the increase in metabolic rate attributable to the vertical component, relative to the resting rate, is much smaller in lighter animals. It makes little difference to a weasel whether it is running straight, up, or down; climbing trees or steep mountainsides takes hardly any extra effort.

The economics of hunting also have some particular disadvantages for a small predator. The energy cost of running is relatively high in small animals,

because they have to take many more steps to move one unit of body mass over one unit of distance, each step requiring work in proportion to mass. Hence, the foraging range of weasels is limited, even though they depend entirely on fresh meat, a scarce food resource, and therefore need relatively large home ranges (Gittleman and Harvey 1982). For the same reason, when local food supplies fail, long-distance migration is not a feasible option for weasels. Another problem is that the energy cost of carrying prey, to a safe place or to the young, increases in direct proportion to the added load: for example, if the load is 50% of the body mass, oxygen consumption increases by 50% (Schmidt-Nielsen 1984:176). Weasels routinely carry prey at least that heavy; even the smallest of them have the strength, but the cost is high. Finally, the prey resources in any local community are nested; whatever is food for the smaller predators is also food for the larger, and weasels cannot defend the stocks of live prey on their home ranges against larger competitors. Sometimes they can be seriously affected by this competition (Erlinge 1983). Oksanen et al. (1985) suggest that the weasels' habit of making caches of dead prey in inaccessible places (Rubina 1960; Parovshchikov 1963) is not a consequence of "surplus killing" but a positive strategy for the smaller members of a predator guild competing with larger ones for access to unpredictable resources.

### Predators and Interference Competition

Weasels are small enough to be vulnerable to attack by almost any other predator. Most species of raptors and larger carnivores have been recorded as killing weasels occasionally, although the victim is not always eaten; Macdonald (1977) reported that a red fox (*Vulpes vulpes*) appeared to find weasel carcasses distasteful. Weasels caught too far from cover have little defense except extreme pugnacity. In a face-to-face encounter with a larger carnivore, a determined weasel with its sharp, explosive bark, bared teeth, fearless attitude, and powerful anal scent glands can sometimes effectively deter an attack; but a swooping raptor is a more dangerous enemy. If the raptor's talons do not pierce the weasel's body at once, it might twist around in the raptor's grasp and attack the bird's throat, perhaps forcing it to release its hold (Seton 1929; Burnham 1970). A better defense is the black tail tip of the two larger weasel species, which Powell (1982) has shown to be a classic predator-deflection spot. A stooping hawk may be confused into grasping at the end of the weasel's thin tail and missing its body. The smallest species, *nivalis*, has no spot because, Powell suggests, it has too short a tail. This does not explain why it does not have a longer tail, which would presumably allow it to have a spot too. Powell suggests that *nivalis* has a short tail for reasons of heat conservation, and I would add that it may be less vulnerable to raptors because it spends relatively more time under snow, thick cover, or underground.

The vulnerability of weasels to predation may, perhaps, restrict their dis-

tribution (e.g., they avoid open spaces: Musgrove 1951), and it gives them a distinct disadvantage in interference competition with the many larger predators that also feed on small mammals; it does not, however, necessarily mean that the body size, population density, or dynamics of weasels is controlled by interaction with or predation by larger predators. Powell's (1973) model was based on a number of assumptions (e.g., that weasel populations are not limited by food) that now appear unlikely (Delattre 1983; Erlinge 1983; King 1983b), so it is not acceptable itself even though it led directly to Powell's (1982) elegant experiments. Likewise, Ralls and Harvey (1985) have thrown doubt on the validity of character displacement as a factor controlling body size in North American weasels, as once advocated by McNab (1971).

### Metabolism

Three features of the weasel's hunting strategy have important consequences for their physiology: (1) their long, thin shape exposes a relatively large surface area to the air (Brown and Lasiewski 1972); (2) their unique niche depends on their ability to search through narrow runways and dense cover to find hidden rodents not available to other predators, and this active technique is very expensive in energy (see above); and (3) their ability to move through confined spaces would be compromised by heavy body insulation, so their fur must be relatively short (Freuchen and Salomonsen 1959; Casey and Casey 1979) and any subcutaneous fat confined to dips in the body outline (Appendix 11.1).

Weasels therefore suffer a very high rate of loss of body heat. Their lower critical temperatures are so high that they almost never reach a state of thermoneutrality (Casey and Casey 1979). The resting metabolism of a weasel depends on ambient temperature; in cold climates, throughout most of the weasels' range, the energy cost of thermoregulation for an inactive weasel may be up to three (Sandell 1985) to six times BMR (Chappell 1980). Arctic weasels can avoid this huge expenditure only by resting in a borrowed nest (Casey and Casey 1979; Chappell 1980), especially if they improve its insulating properties by lining the inside with rodent fur (McLean et al. 1974).

Weasels cannot, of course, stay in the shelter of their nests indefinitely, but opinions are divided as to whether low temperatures restrict their movements when they are actively hunting. Casey and Casey (1979:162) point out that, if the arctic weasels have to generate up to six times BMR merely to maintain body temperature, they "might have little capacity in reserve for energy generation during activity," especially as "heat loss should be even greater in active animals due to forced convection." If this is so, we would expect the arctic weasels to keep to the shelter of the snow cover even when they are active. Tracking studies in USSR report that weasels do not venture above the snow when the air temperature falls below a certain minimum, measured at  $-13^{\circ}\text{C}$  in western Siberia by Kraft (1966). Formosov (1946:79) found that "common

voles which ran onto the snow to escape an ermine, which had dug into their nest, froze in a distance of 3–4 meters from their snow hole” when the temperature was  $-12^{\circ}$  to  $-15^{\circ}\text{C}$ .

A contrary view is expressed by Sandell (1985). He estimates that weasels do not need to generate more than three times BMR even when the ambient temperature is  $-30^{\circ}\text{C}$ , and that, since 75% of the energy expended during activity is released as heat, a running animal does not need to spend energy on thermoregulation. Sandell concludes from this that active weasels are, in practice, almost independent of ambient temperature; in Sweden he has snow-tracked *erminea* after nights with temperatures down to  $-25^{\circ}\text{C}$ , and at the same time seen tracks of voles running for tens of meters above the snow (M. Sandell, pers. comm.). Casey and Casey (1979) and Sandell (1985) worked in habitats differing in important conditions (e.g., permafrost, light regime), and calculated the energy requirements of weasels from different models, so it is not clear whether this disagreement is real or technical. Much depends on the estimated rate of loss of body heat during activity at low ambient temperatures. Nevertheless, it is still clear that the northern weasels are absolutely dependent on insulated rodent nests when they are resting or breeding; and presumably they might often choose to hunt under the snow when it is less cold there than on the surface.

The physiological consequences of small size for weasels in general are practically all seriously disadvantageous, and the northern weasels survive at what appears to be the limit of their metabolic capacity (Casey and Casey 1979). Their constant need for shelter and frequent meals is a handicap in years when rodent populations are low and winter nests few; they can store resources only as caches, liable to theft and decay, not as fat; they are vulnerable to temporary food shortages, but hibernation, torpor (at least in adults), and migration are all impossible; and the additional energy required for reproduction may be hard to find except in years when rodents are abundant. These are all serious problems for small homeotherms living in a cold climate. Weasels do have the incidental advantage that the subnivean habitat is relatively free of competitors and predators, but those hazards are much less serious than the constant danger of chilling and starvation.

### Reproductive Strategy

All mammals live for roughly the same length of physiological time, that is, about 200–250 million breaths and about 800–1200 million heartbeats (Peters 1983:122; Schmidt-Nielsen 1984:146). The pulse of a weasel runs at about 400–500 beats per minute (measured by Tumanov and Levin 1974 on male and female *nivalis* and *erminea*), which gives it a physiological lifespan of about 3–6 years. In captivity both those species can live that long, but in the wild, very few indeed; the average age at death of *nivalis* is  $<1$  year, and of

*erminea* <1.5 years, and the maximum age attained (infrequently) 3+ and 8 years, respectively (King 1980b; Erlinge 1983; Debrot 1984; Grue and King 1984).

Lifespan is therefore scaled to size, so that small animals "must rush to complete their life histories in the face of an early expiration date" (Calder 1983:217). This introduces a new, acute problem for weasels, as regards timing. For all temperate and northern mammals the resources vital for reproductive success are seasonal, linked to a fixed annual cycle of plant growth; but for weasels the ordinary annual cycle is overlain by multi-annual fluctuations in the abundance of their key resource. The northern weasels are supreme specialists in the exploitation of unstable populations of small rodents, and for that they must be small; but small size automatically speeds up their physiology and reduces their lifespan to the extent that the periods of most favorable conditions for breeding (the peaks in rodent numbers every three or four years) are longer apart than the average weasel's expectation of life at birth.

Weasels in general are, relative to the larger carnivores, typical "*r*-strategists" (King and Moors 1979a) and this is a high risk-high reward policy, with advantages and disadvantages at both the individual and the population levels. In a cold or stressful environment individuals may not always be able to provide enough energy both for normal metabolism and for reproduction at the same time. Yet all weasels must seize every possible opportunity to breed, and some must manage to produce a few young even in poor years; but their full potential productivity can be achieved only when food is not limiting (i.e., at rodent peaks). Small rodents are the ideal prey for breeding weasels throughout their range, and the reproductive output of weasel populations is strongly correlated with the distribution and density of rodents even where other prey are available (Erlinge 1981; King 1983b, 1983c).

Individuals living at a time of peak rodent numbers are likely to achieve high reproductive success. King (1981, 1983c) documented the changes in fecundity and productivity of the *erminea* living in New Zealand beech forests through two population irruptions of rodents (feral *Mus musculus* and, to a lesser extent, *Rattus rattus*). The unusual breeding success of the post-seedfall years was certainly measurable in terms of increased numbers of young reared by the adult females, and the equivalent statistic (not measured) would presumably be increased numbers of matings for males. But both males and females are short-lived on average and run a high risk of missing the best season. When the density of weasels is low, males have a lesser chance of finding several mates, or even one; when the density of rodents is low, females have a lesser chance of producing their full potential number of young, or even any at all (Tapper 1979; King 1983a, 1983b). Over the general population, then, there is always a large variation in the breeding success of individuals. For the adults, the rewards are great in the years when the chances of success are high, but the losses disastrous in all other years. For the young, growth is rapid and hunting instinctive (i.e., they do not need the extended apprenticeship required to learn

the complex hunting skills of larger carnivores: Bekoff et al. 1984), so they can leave the family and disperse with minimum delay; but very few will survive the following winter.

At the population level, the rapid production of young, high population turnover, and huge rate of increase in good years are advantages in that weasels have great potential for rapid genetic adaptation; but these are also disadvantages, because weasel populations fluctuate a great deal and are very liable to local (though not to total) extinction (King and Moors 1979a, 1979b). The short contact between the generations also means that weasels are confined to a somewhat conservative way of life, in contrast to the elaborate and flexible social patterns developed by some of the larger carnivores (Bourlière 1975).

### Body Size in Relation to Species and Sex

The general advantages and disadvantages of small size in the weasels as a group (Figure 11.2) also apply, to different degrees, to individual weasels of each sex and species. There are also additional considerations, not entered into Figure 11.2, that apply only to relationships between sexes or species; for example, small size is probably a disadvantage to males in competition for mates. The balance of profit and loss in relation to local resources is therefore different for each of up to six size classes of weasels living in a given place. This adjustable relationship may help to explain two important puzzles about weasels: the coexistence of similar species within the weasel set, and their strong sexual dimorphism.

#### Coexistence of Similar Species

The problem of the nearly universal coexistence of at least two species of weasels throughout the northern Holarctic, despite the extensive overlap in their ecological requirements, has frequently been discussed. Rosenzweig (1966) concluded that it must depend on predation of the smaller by the larger species; Powell and Zielinski (1983) invested much thought and computer time in the question and concluded that, in theory, it ought not to be possible except by continual local extinction and recolonization. King and Moors (1979b) suggested that coexistence might be permitted by an unstable balance of the different size-related advantages enjoyed by each species, as determined by the environment. For example, in Europe *nivalis* is superior to *erminea* in the exploitation of small rodents and is able to respond to vole peaks immediately by producing extra summer litters but is more vulnerable to local extinction; *erminea* is superior in interference and is able to exploit larger prey but is restricted by obligatory delayed implantation to producing only one

litter a year. In a patchy environment of sufficient size, each species can find, at least locally and temporarily, conditions that suit its strategy; *nivalis* can avoid confrontations with *erminea*, and *erminea* can avoid dependence on a single prey resource.

The assumptions on which this idea was based have since been checked by field work. Pounds (1981) confirmed that *nivalis* is much more efficient in hunting small rodents, and Erlinge and Sandell (1985) confirmed that *erminea* does dominate *nivalis* in the field. That does not prove the idea correct; nevertheless, any significant change in the size distribution of prey does have differential results explicable, at least in part, as consequences of a shift in a dynamic balance of opposing forces. For example, the removal of rabbits by myxomatosis in Britain in 1953–55 put *erminea* at a disadvantage in competition both with *nivalis* and, perhaps, also with larger predators (Erlinge 1983), whereas *nivalis* greatly increased. Conversely, when both were transported to New Zealand, *nivalis* was disadvantaged by the absence there of voles, whereas *erminea* thrived (King and Moors 1979b).

Obviously, no such simple proposition could provide the whole answer. The net relative effect of close competitors of different sizes on each other involves a whole suite of spatial, temporal, and other components even more difficult to quantify than body size, prey size, and dominance (Hespenheide 1973). We can observe that these two species do coexist, at least partly because they are of different sizes, although it is clear that interspecific competition plays no *direct* role in determining the local mean body size in either species (Ralls and Harvey 1985; Harvey and Ralls 1985). They do deal in totally different ways with the same problem, that of adjusting reproductive effort to wildly variable probabilities of success (King 1981). No further conclusions are possible at present.

### Sexual Dimorphism

Male and female weasels have in common the goal of minimizing the chances of leaving no young, given that their expectation of life is short and their chances of successful breeding vary greatly from year to year. However, there the similarity ends, because each sex has evolved different breeding strategies, and they cooperate as little as possible. For both sexes, body size is one of the most important factors involved, but for different reasons.

Females invariably bring up their young alone (Erlinge 1979), and in order to maximize the number of weaned young surviving at the end of each attempt, they must value foraging efficiency above all things, for two reasons. First, the energy demands of solo parenthood are enormous. During lactation the female's own food requirements increase by a massive 80–100% even in a temperate climate (East and Lockie 1964; Hayward 1983), and later, until they are fully independent, she has to supply dead prey for her young as well. Her requirements may amount to a total of 500–600% above normal (Sandell

1985). The female can accomplish this best when rodents are abundant, since rodents are the ideal resource on which to rear young weasels; they pose no risk for the mother to kill, are rapidly replaced, are not too heavy to carry (but see above on strength and loading), are not too big to be taken into a nest or cache whole, and are supplied in a convenient waterproof skin that helps to retard decay. Females therefore are always under strong pressure to stay small enough to be maximally efficient rodent hunters (Simms 1979; Pounds 1981). They can still kill larger prey, aided by the "shock effect" described by Hewson and Healing (1971), but this takes more energy and risk and so is less efficient as a means of feeding the young than concentrating on rodents if they are available. Incidentally, the argument that females stay small so as to minimize their own energy requirements for maintenance and thereby are able to channel more of their catch into their young (Moors 1980) is valid only "if smaller and larger females were equally efficient hunters, which may not be the case . . . nothing is known about the relationship between weasel size and hunting efficiency" (Ralls and Harvey 1985:162). It is worth pointing out, though, that the energy costs of running and carrying loads are inversely related to size (see above); I wonder whether females hunting prey of a given size, available at a given density, might even have to expend relatively more energy than males to search for, kill, and carry home each meal; the advantage of their smaller appetites, if it is one, might soon be canceled out. It would be interesting to see this prediction tested.

The second reason why females must maximize foraging efficiency is that small young (less than 5–7 weeks old in the case of *erminea*) are unable to maintain their body temperature when left in the nest alone. While the female is out hunting, the young huddle together, and if the nest temperature falls below 10–12°C, they will enter into a reversible cold rigor, with reduced sensitivity, cardiac and respiratory function (Segal 1975). Full homiothermy at environmental temperatures down to 0°C is achieved only when their fur is fully grown, at the age of about two months. This mechanism is an advantage to the young, which can channel all their energy into rapid growth during the periods that the female is present. But from the female's point of view it is a strong reason to minimize the time she is away from the nest during that first few weeks, since the young in torpor are not growing and are also vulnerable to interference or predation. The breeding female should therefore maximize her total hunting efficiency by starting with a time-minimizing strategy when the young are very small, and changing gradually to an energy-maximizing one when they are older. This idea is not supported by evidence, but, again, it could be tested.

Males, by contrast, are polygynous or promiscuous, and attempt to maximize the number of matings they can achieve each season. Large size is a positive advantage in competition for females, because it is a reliable indicator of fighting ability, and this is important even if damaging fights are usually avoided. Larger size is also often correlated with age and, by implication, with

willingness to escalate a confrontation (Erlinge 1977; Sandell 1986). In very cold climates the advantage to a dominant male of larger size during the very brief breeding season must be (at least above a certain limit) counteracted by other penalties jeopardizing survival through the much longer nonbreeding season.

If large size is really so vital for reproductive success in males, the question arises as to why male size should be so extremely variable. One possible answer is that males may often fail to reach their full potential size (Ralls and Harvey 1985; R. A. Powell, pers. comm.). Whatever the genetic heritage of an individual male, his actual size at maturity may be set by whether or not he is well fed by his mother. Weasels in captivity commonly reach much higher weights than in the wild, especially the males (East and Lockie 1964; Hayward 1983); and local patterns of sexual dimorphism are variable and sometimes conflicting (Ralls and Harvey 1985). A simple way to test this idea would be to compare the degree of sexual dimorphism in cohorts of weasels born in years of good and bad supplies of small rodents. This requires year-class age determination of adults, which has only recently been proved reliable (Grue and King 1984), and then the analysis of a large sample of weasels collected in both good and bad years (Kopein, 1969; Powell and King, in preparation).

### Geographical Variation in the Body Size of Weasels

Size in mammals is affected by many factors, some synergistic, some interacting, and some opposing; the observed phenotype is always a compromise between them. Eventually it may be possible to construct a model to explain body size in weasels, but we do not have enough data at present, either on the actual variation in their body size (especially in Eurasia) or on their ecological requirements, to do that. However, it is possible to make a few suggestions.

#### The Northern Hemisphere Continents

The patterns of geographical variation in the separate species of *Mustela* are complex and contradictory; for example, the smallest local races of *erminea* in Eurasia are found in the north and east, whereas the smallest in North America are in the southwest. However, in weasels in general, the continental-scale pattern is the same in both the Old and the New Worlds; the largest or only local species is relatively small in the far north (mean male condylobasal lengths in *erminea*, always the largest species in the north, not exceeding 43–46 mm right around the Pole), and relatively large in the south (*frenata* in the southern United States, and *nivalis* in Egypt, reach 50–53 mm or more) (Kratovichil 1977a, 1977b; Osborn and Helmy 1980; Ralls and Harvey 1985).

The first and most obvious explanation to check is Bergmann's Rule, which

states that mammals living in very cold climates tend to be larger than related mammals of similar habits living in milder conditions (McNab 1971; Gittleman 1985; Erlinge 1987). Weasels ought to be prime examples of this generalization, because they are so extremely sensitive to thermal stress; their metabolic inefficiency is costly in the northern parts (the great majority) of their range. In fact, as in the order Carnivora in general (Gittleman 1985), Bergmann's Rule fails to explain the observed variation, either in individual species or in the weasels as a group (Ralls and Harvey 1985). Only the *erminea* in North America are substantially larger in the north (Figure 11.3C), and then only by comparison with their exceptionally small relatives farther south in that continent; they are not larger than the *erminea* living at the same latitudes in Eurasia. The *nivalis* of Europe are just as substantially larger in the south (Figure 11.3A). Within defined areas spanning a range of climates, Bergmann's Rule does not explain the observed variation among local populations of *erminea* in the USSR (Petrov 1962), New Zealand (King and Moody 1982), or Europe (Erlinge 1987).

There are two critical assumptions behind Bergmann's Rule: that latitude and temperature are correlated, and that all the species being compared are equally exposed to ambient air temperature. Ralls and Harvey (1985) found that the skull lengths of North American weasels were, indeed, about as well correlated with temperature as with latitude; but in Eurasia the simple latitude-temperature correlation is confused by low-latitude ranges of high mountains, on which some exceptionally small weasels live (Reichstein 1957; Morosova-Turova 1965; Heptner et al. 1967). A direct correlation between weasel size and local temperature shows that both sexes of both species of Eurasian weasels are smaller in colder climates—the opposite of Bergmann's prediction (Table 11.1). But this does not mean that weasels disprove the rule. The smaller, cold-climate weasels sheltering under snow are not directly exposed to ambient temperature, as their southern and lowland relatives are, so it is logically invalid to apply the rule to weasels anyway. Besides, the relationship between size and temperature cannot be crucial, since there is usually at least as great a difference between the males and the females living in one place as there is between the northern and the southern members of either sex. We need, then, to explain in other terms the general north-south variation in body size of the largest or only local weasel species.

Sandell (1985) has proposed a model predicting the optimal body size in male and female *erminea* in terms of ecological energetics and sexual selection. His basic assumption is that the total energy budget of any animal, expressed as a multiple of BMR, is limited. This seems reasonable, especially for weasels, which often have to operate their energy budgets with little to spare. Sandell assumes that, in winter, both sexes will be under pressure to minimize their daily energy expenditure, and that the best way to do that is to increase foraging efficiency, thereby reducing the total time out of the nest. Hence, for any combination of values for foraging efficiency and ambient temperature,

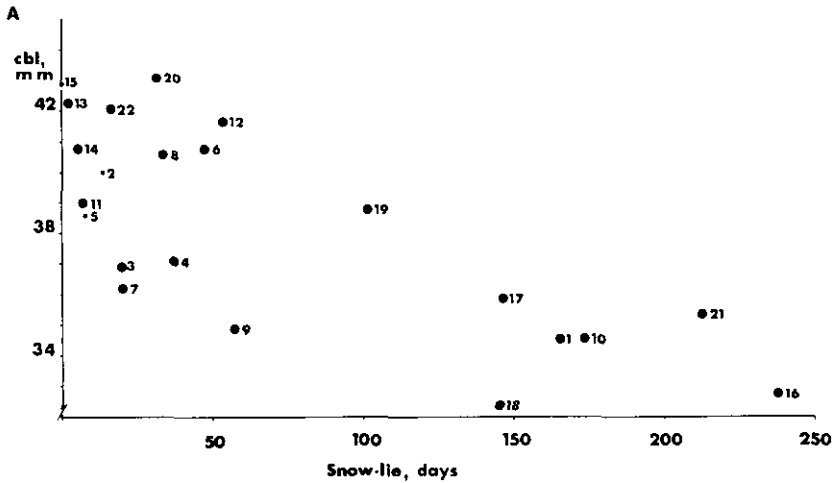


Figure 11.3. Geographical variation in skull size (condylobasal length in A and B; basal length of Hall [1951] in C and D) of male weasels with duration of snow-lie. Smaller symbols refer to island populations. A. Eurasian *mivalis* (N.B.: in Egypt, mean condyloincisive length of males is 50 mm: Osborn and Helmy 1980). B. Eurasian *erminea*. C. North American *erminea*. D. *frenata*.

Key to sources and locations:

#### Eurasia

1. Scandinavia (Stroganov 1962; Reichstein 1957)
2. Scotland (King 1977; King and Moody 1982)
3. Denmark (Fog 1969)
4. Northern Germany (Reichstein 1957)
5. England (King 1977; King and Moody 1982)
6. Poland (Reichstein 1957)
7. Central Germany (Reichstein 1957)
8. Czechoslovakia (Kratochvil 1977a, 1977b)
9. Southern Germany (Reichstein 1957)
10. Switzerland (Reichstein 1957)
11. Western France (Beaucournu and Grulich 1968)
12. Roumania (Barbu 1968)
13. Italy (Miller 1912)
14. Spain (Reichstein 1957)
15. Sardinia (Beaucournu and Grulich 1968)
16. Northern Siberia (Stroganov 1962)
17. Central European Russia (Morozova-Turova 1965; Heptner et al. 1967)
18. Transbaikal (Morozova-Turova 1965; Stroganov 1962)
19. Southern European Russia (Morozova-Turova 1965)
20. Turkmenia (Morozova-Turova 1965)
21. Tien Shan Mountains (Morozova-Turova 1965; Heptner et al. 1967)
22. Trans-Caucasus (Morozova-Turova 1965)
23. Islay Island (off western Scotland) (Miller 1912)
- 24N. Northern Ireland (Fairley 1981)
- 24S. Southern Ireland (Fairley 1981)
25. Terschelling Island (off Holland) (van Soest et al. 1972)
26. Holland (van Soest et al. 1972)
27. Eastern Siberia (Stroganov 1962)
28. Karaginski Island (off Kamchatka) (Stroganov 1962)
29. Western Siberia (Stroganov 1962)
30. Kamchatka (Vershinin 1972)
31. Shantar Island (Sea of Okhotsk) (Petrov 1956)

32. Altai Mountains (Stroganov 1962)

33. Northern Caucasus (Heptner et al. 1967)

#### North America

All the points plotted are local means taken from Hall (1951), and some are based on small samples. The data analyzed by Ralls and Harvey (1985) are much more detailed, comprehensive, and accurate but not available to be plotted against snow-lie in the same way as the Eurasian data.

34. Greenland
35. Point Barrow, Alaska
36. Southampton Island
37. Great Slave Lake
38. Southeastern Alaska
39. Admiralty Island, Alaska
40. Queen Charlotte Island
41. Vancouver Island
42. Newfoundland
43. Vancouver district
44. Olympic Peninsula
45. Cascade Mountains
46. Minnesota
47. Idaho
48. New York and Pennsylvania
49. Coastal Oregon
50. Colorado
51. Southeastern British Columbia
52. Southern Alberta
53. Maine
54. Massachusetts
55. Northwestern California
56. Southwestern California
57. San Joaquin Valley
58. Los Angeles
59. Arkansas
60. Georgia
61. Southern Texas

(continued)

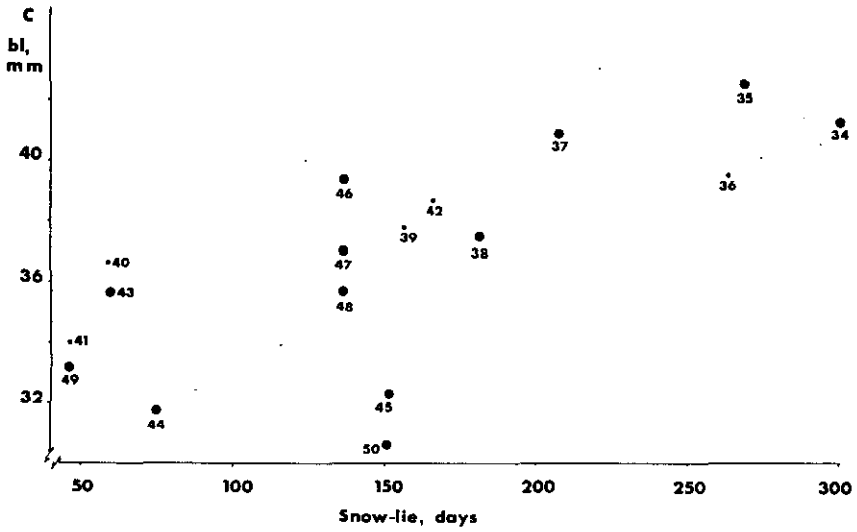
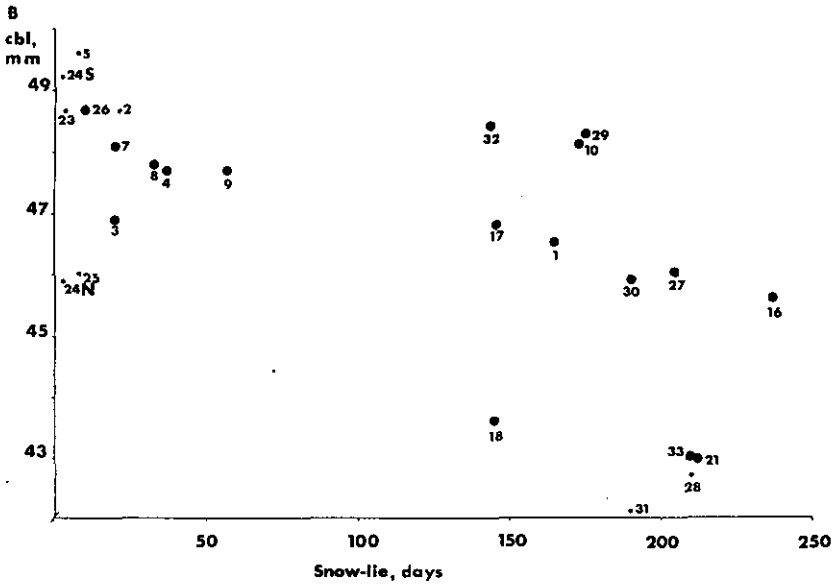


Fig. 11.3 (continued)

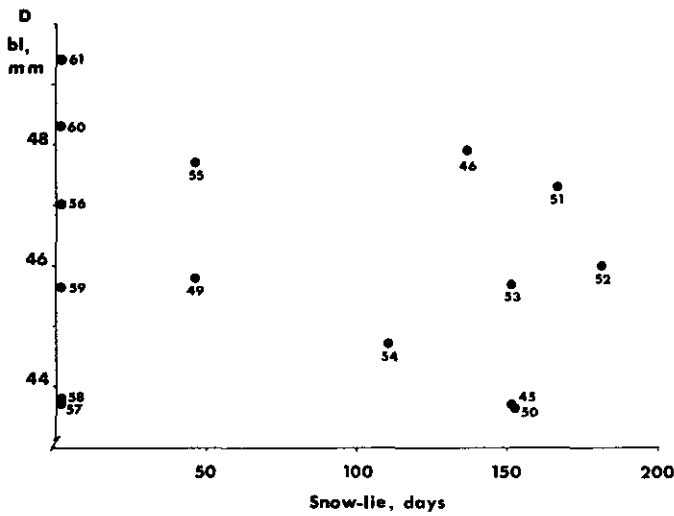


Fig. 11.3 (continued)

Table 11.1. Geographical variation in northern hemisphere mainland weasels (condylobasal length) with respect to latitude and climate

		Spearman rank correlation coefficients <sup>a</sup>		
		<i>nivalis</i>	<i>erminea</i>	<i>frenata</i>
<b>Males</b>				
Eurasia	Latitude	-0.63	n.s.	—
	Temperature <sup>b</sup>	0.87	0.60	—
	Snow-lie <sup>c</sup>	-0.77	-0.69	—
North America	Latitude	n.s.	0.67	n.s.
	Temperature	n.s.	-0.69	n.s.
<b>Females</b>				
Eurasia	Latitude	-0.45	n.s.	—
	Temperature	0.67	0.68	—
	Snow-lie	-0.62	-0.67	—
North America	Latitude	-0.44	0.67	0.16
	Temperature	n.s.	-0.64	n.s.

<sup>a</sup>Coefficients given are significant at  $P < 0.05$  or better. n.s. = not significant.

<sup>b</sup>Mean annual dry bulb temperature recorded at one or several meteorological stations representing the areas sampled. Eurasian data collected by C. M. King (unpublished), North American by Ralls and Harvey 1985.

<sup>c</sup>Analyzed as the number of days per year of stable snowcover over 2.5 cm thick. No snow-lie analysis given by Ralls and Harvey; but the weasels that live in regions of heavy snow cover (*nivalis* and *erminea* in Canada and Alaska) are much smaller than those that live in the snow-free south (*frenata* in southern U.S.A.). The correlation between snow cover and size in five samples of European *erminea* reappears in fig. 1 of Erlinge (1987).

there will be an optimum body size, which in winter will be the same for both males and females. In the breeding season, however, the equations leading to success are different: intense sexual selection favors a larger size in males than in females. The actual body size observed is a compromise between the different seasonal optima.

Sandell confined his model to *erminea* living in the conditions he had studied in Sweden. I propose the following hypothesis, an extension of Sandell's model, to explain the general, continental-scale southward increase in the body size of the largest or only local weasel species.

My balance sheet of the profits and losses associated with small size (Figure 11.2), is not exhaustive and cannot assign relative values to the factors identified. Nevertheless, it confirms Sandell's assumption that ecological energetics is one of the most important considerations—more specifically, the effect of ambient temperature on metabolism and foraging efficiency. In arctic and alpine regions environmental conditions above the snow are severe (Pruitt 1978), and the ability to escape them is the condition for survival of small mammals there (Formosov 1946). When the air temperature is mild and the wind-chill factor low, weasels may emerge onto the surface, and their tracks are often seen (Teplov 1948; Nyholm 1959; Fitzgerald 1977); but they are still absolutely dependent on subnivean nests and prey. Therefore, the primary needs to avoid exposure to ambient temperature and to retain access to rodent tunnels and nests impose an upper limit to the size of arctic and alpine weasels. This overrides all other considerations, such as the reproductive advantage of larger size to males. The same restrictions apply to the small mammals hunted by the weasels. Hence, the advantages of avoiding thermal stress and of maximizing foraging efficiency reinforce each other in favoring small size in northern weasels.

By contrast, in the milder climates of lowland southern United States and southwestern Europe, the lesser need to avoid exposure to the air relaxes the restraints on sexual selection favoring larger size in males. Dawkins and Krebs (1979) point out that competition favors males that are slightly larger than the current population mode, whatever the current mode may be; hence, a general increase in the mean body size of both sexes (female size is "dragged upwards" by selection for increased male size, for reasons explained by Lande 1980) may be expected, if permitted by the net balance of energy economy as outlined by Sandell (1985). Moreover, in the south there are various larger prey such as lagomorphs and sciurids whose populations are more stable than those of small rodents, and which could more easily be caught by larger weasels. It is true that small rodent populations are relatively more stable in the south (Hansson and Henttonen 1985); but they are still capable of pronounced fluctuations over the long term (Southern and Lowe 1982), and they also serve as staple prey for a variety of generalist predators (Erlinge 1983). These considerations would make small size and extreme specialization on small prey

less viable strategies in the south than in the north, and reinforce sexual selection in favoring larger size in southern weasels.

If this hypothesis is correct, parallel southward increases in the body sizes of the largest or only local weasel species and in its prey would be expected. However, since correlation does not necessarily imply causation, this is merely an observation, not an explanation. For example, it is not possible to predict in advance whether the northern weasels are small because their prey are small or because both are constrained by the same environmental hazards. As Erlinge (1987) pointed out, "The correlation between stoat body size and prey availability . . . can be interpreted either as a causal relationship or as an effect of an alternative process of adaptation."

I propose that this combination of energetics, size of available prey, and sexual selection (in unknown proportions) explains why the niche for a weasel-shaped carnivore allows only smaller individuals in severe climates, but larger ones in milder climates. In Eurasia the mean body sizes of both sexes in local populations of *nivalis* and *erminea* are inversely correlated with the mean number of days of snow cover per year (Figure 11.3A, B; Table 11.1). In North America neither *nivalis* nor *erminea* is larger in the south; the niche for a large southern weasel with relatively generalist food habits was already occupied by *frenata* (and presumably also by its predecessor and possible ancestor, *rexroadensis*) by the time the ancestors of the present *erminea* crossed the Bering bridge from Siberia in the middle Pleistocene or before (Kurtén and Anderson 1980). Of course, *frenata* can travel across snow and burrow into it (Fitzgerald 1977); its southern niche is determined more by prey diversity than by the snow cover itself (Gamble 1981, cf. Simms 1979).

The basic idea presented here was suggested by the size distribution of the living species; but there is some other evidence that small size actually is advantageous to cold-climate weasels, both in the Pleistocene and now. First, fossil *M. palerminea* (the direct ancestor of the contemporary *erminea*) from the cold phases of the middle Pleistocene are smaller than those from the warm phases (Kurtén 1960); and fossil *nivalis* from Polish caves dated to the Eemian (last) interglacial period resemble modern Polish *nivalis vulgaris*, whereas fossil *nivalis* dated to the following Weichselian glacial period are smaller, like the modern boreal *nivalis nivalis*, which no longer lives as far south as Poland (Wojcik 1974). Second, among > 4000 skulls of *erminea* collected north of Tjumen (57°N, 65°E) over the years 1959–64, there was a progressive decrease with age in mean condylobasal length in every annual cohort, in both sexes; and the smaller animals were fatter. To Kopein (1969) these were signs that the smaller individuals were better adapted, and lived longer, in that severe environment than did the larger ones.

It is important to note that this idea is a generalization and applies only to the largest weasel species in a local set (or to the only one, if only one is present). Like all other generalizations, ranging from simple verbal hypotheses

to complex mathematical models, it is not entirely true but may have value as "a lie which makes you see the truth" (R. H. MacArthur, as quoted by Crowell 1986:59). It does not apply to the smaller species, except indirectly as follows. Where two species of weasels are sympatric, the smaller one is always the more strongly specialized on small rodents (King and Moors 1979b). If this strategy is less successful in the south (for reasons suggested above), it may explain why the smaller species do not extend as far south as the larger ones.

Most generalizations are difficult to test, and this one will be too, for several reasons. First, the key concept in Sandell's model, foraging efficiency, is hard to define. There is an almost endless list of variables that might contribute to it, and practically nothing is known about what determines it in weasels. Second, the hypothesis includes two other considerations, ecological energetics and sexual selection, and all three must be taken into account if we are to determine which is cause and which effect. Simple correlations dealing with only one variable at a time tend to be inadequate. For example, of the five hypotheses on geographic variation in North American weasels tested by Harvey and Ralls (1985), all except prey-size distribution were rejected. There is indeed a simple general relationship between body size of weasels and their prey (Moors 1980; Erlinge 1987), but certainly the equations that govern the dynamics of hunting must include many other characters of the prey besides body size. For example, the relationship between body size in weasels and the average size of the local voles and their tunnels is closer in females than in males (Simms 1979; Pounds 1981), which implies that males and females are differentially sensitive to some other factor(s) besides prey size. Ecological energetics and sexual selection are both powerful forces whose consequences for body size must affect males and females differently. It seems unlikely that any single-factor hypothesis will suffice to explain body size, which is inevitably a compromise between a range of possible optima.

### The Northern Hemisphere Islands

Permanent populations of weasels can live only on large islands: off the coast of Britain the lower limit is approximately 60 km<sup>2</sup> (King and Moors 1979b). Data on body size in island weasels are sparse and statistically inadequate, and the origin and date of colonization is seldom known. However, island weasels are often at least slightly different from those of the nearest mainland, either larger or smaller, and *erminea* in Ireland has been wrongly quoted as an example of a theoretical generalization (Hutchinson 1959).

For many years the only measurements of Irish weasels available were from the northern part of the island, where *M. erminea hibernica* (Figure 11.3B, point 24N) is roughly intermediate in size between mainland British *M. e. erminea* (points 2, England, and 5, Scotland) and *M. nivalis*. These small

northern animals were assumed to represent all Irish *erminea*; this assumption was linked with the absence of *nivalis* from Ireland, and the conclusion was drawn that *erminea* in Ireland must be one of the classic examples of character displacement (Hutchinson 1959; Williamson 1972:117). This explanation has been decisively quashed by Fairley's (1981) data, showing that, although *erminea* in the north of Ireland is indeed much smaller than in Britain, only 250 km away in the south it is as large or larger (point 24S). Hutchinson also took the very large *nivalis* living in the Mediterranean, in the absence of *erminea*, as the reverse example, but that is disputable too. There is a clear north-south increase in the size of *nivalis* in Europe, with (on present data) no clear step past the southern limit of *erminea*; all the Mediterranean races of *nivalis* are large, both on the mainland (Figure 11.3A, points 13, Italy, and 14, Spain) and on islands (point 15, Sardinia).

A special explanation was offered by van Soest et al. (1972) to account for the relatively small size of the *erminea* living on the island of Terschelling, off the coast of Holland (Figure 11.3B, points 25, 26). These weasels are very heavily infested with *Skrjabinoglyus nasicola*, a damaging cranial parasite (91%, cf. 23% on the nearby mainland coast), which van Soest et al. suggest may stunt their growth. However, the size differences were not tested, and there is no evidence of the same effect elsewhere (King 1977; King and Moody 1982).

The real explanation for the variation in size of weasels in Ireland, Terschelling, and other islands is still unknown. My guess is that the mean body size of the weasels on any island will drift toward whatever gives them, in the local conditions, the best year-round, long-term compromise between the advantages of small size (Figure 11.2) and the upward pull of sexual selection; and the point of balance will be related, in some way we do not yet understand, both to the climate and to the size distribution of the prey. Unfortunately, we have no precise data on the size ranges and relative abundance of prey available on any of the northern hemisphere islands occupied by weasels, or even any certainty as to what characteristics of the prey fauna to measure. It is not necessarily a simple correlation between the body sizes of predator and prey, or of the diameters of weasel bodies and rodent tunnels (Simms 1979), since there is a well-documented tendency for rodents to be larger on islands (Lomolino 1985), whereas weasels seem to be either smaller or larger (Figure 11.3). If the observed size of the weasels on each island is a unique local compromise, no generalized theoretical model will explain the whole pattern unless it includes detailed information on the ecology of the weasels living in all the island habitats, how long they have been there, and where they came from. But there is one group of islands, the New Zealand archipelago, where some at least of the required information is available, and any attempt to devise a general explanation of what determine body size in weasels must take account of what is happening there.

### New Zealand

Both *nivalis* and *erminea* were introduced into New Zealand over the 20 or so years after 1884 (King and Moors 1979b; King 1984b). Both were relatively large, since they came from British stock, among the largest in western Europe (Figure 11.3A, B; Kratochvil 1977a, 1979b). They found in New Zealand an environment radically different from home, with a wider range of climates (warmer in the north, colder in the high mountains) and a fauna of potential prey which was (and is) completely different in size distribution (King and Moors 1979b). There were no voles, and feral house mice (*Mus musculus*) were the only rodents under 50 g; on the other hand, there were Norway and ship rats (*Rattus norvegicus*, *R. rattus*) and European rabbits (*Oryctolagus cuniculus*), all in great numbers, as well as (at that time) still considerable numbers of large and unwary native birds. There were also numerous species of large (3 g) flightless native insects (Orthoptera), collectively known by their Maori name *weta*. These have been called "invertebrate mice" or "insect rodents" (Stevens 1980:255) because they to some extent held the niche occupied by small rodents elsewhere in the world.

In the 100 years since their arrival in the alpine beech forests of New Zealand, *erminea* of both sexes have become, on average, slightly larger than their British ancestors (assumed to have remained the same); in the lower-altitude mixed podocarp forests females are larger but males are not (Figure 11.4). This shift in mean size is precisely dated and consistent at all ages and even on small local scales (King and Moody 1982). The male *erminea* living in the foothills of the Southern Alps are probably the largest in the world, and near the top of the range for male *frenata*; the females are larger than any Eurasian female *erminea*, and near the middle of the range for female *frenata*. This pattern has not yet been shown to be genetic; but even simple phenetic changes, if as consistent as that, may be taken as evidence of adaptation in the broadest sense (Clutton-Brock and Harvey 1979), if only as indicating some change in the conditions of life for *erminea* in New Zealand. It seems most likely that the key factor is the size distribution and local abundance of the prey available. For example, it is no longer profitable for females to remain small so as to specialize on rodents. Perhaps this is the reason why they have become larger in all habitats. They still take what small rodents there are more often than do males (King and Moody 1982:63) and the abundant *weta*; but they also catch large prey (rats and lagomorphs) as often as do males (King and Moody 1982:68). However, there is no simple correlation between the body sizes of New Zealand *erminea* in general and their prey. If there were, we would expect to be able to predict the position of a point for New Zealand on the plot neatly relating prey size and body weight in *erminea* given by Erlinge (1987). But when this is done (from the list of prey items given by King and Moody 1982) according to the formula and prey weight loadings given by Erlinge (1987), the

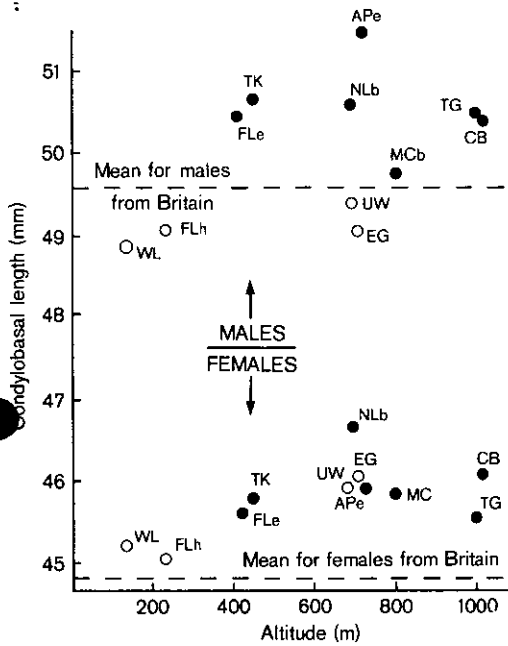


Figure 11.4. Mean condylobasal length of adult male and female *erminea* in New Zealand. ○ = mixed native podocarp and hardwood forests; ● = southern beech (*Nothofagus* spp.) forests and tussock grassland. Key to localities, further information, and statistics in King and Moody (1982). The mean condylobasal lengths of adult *erminea* from Britain (ages classified by the same criteria) are shown by the dotted lines. (Courtesy *New Zealand Journal of Zoology*.)

- Key to abbreviations:
- APe Arthur's Pass (eastern side)
  - CB Craigieburn
  - EG Egmont
  - FLe Fiordland (Eglinton Valley)
  - FLh Fiordland (Hollyford Valley)
  - MC Mount Cook
  - MCb Mount Cook (Ball Hut Road)
  - NLb Nelson Lakes (beech forest)
  - TG Tangariro
  - TK Takaro
  - UW Urewera
  - WL Westland

mean prey size of *erminea* in New Zealand works out at about the same figure as for the much smaller *erminea* in northern Sweden.

There are two reasons for this. One is that the formula requires the frequencies of occurrences of prey items eaten to be loaded according to prey body weight. The results are hugely influenced by the weight assigned to the large prey species, which depends on some assessment of the age of the individuals taken and the number of meals eaten from each carcass. The other reason is that *erminea* in New Zealand take large numbers of insects, especially *weta*, whereas the diet analyses of European *erminea* quoted by Erlinge reported only vertebrates. The high frequencies of insects distort the relative values for vertebrate prey. Yet we have shown, using a different logic and loading system (King and Moody 1982:71), that although insects were frequently found in our samples (in 41% of all guts containing food), they contributed only a small proportion (<10%) of the biomass of food eaten. New Zealand *erminea* depend for most of their sustenance (>50%) on large prey (lagomorphs, possums, and rats). If insects are omitted and the data recalculated from the frequencies of vertebrate prey alone, the prey size index works out, as one would expect, at about the same as for *erminea* from Britain.

Whether or not it is valid to omit the numerous but nutritionally unproductive insects in such comparisons depends on the foraging strategy of *erminea* in New Zealand. Nothing is known about how they hunt insects, or whether they

pick them up only in passing or deliberately search them out, so this intriguing problem remains unresolved. Neither is there any simple correlation between local variations in the body size of *erminea* and the local distribution of any particularly favored large mammalian prey. For example, the size distribution of local populations shown in Figure 11.4 is positively correlated in both sexes with the distribution of rabbits. The larger, beech forest-tussock grassland *erminea* tend to eat relatively more rabbits than the smaller ones living in the podocarp-hardwood forests ( $r_3 = 0.57$ ,  $P < 0.05$  in males;  $r_3 = 0.22$ ,  $P > 0.05$  in females). But we cannot thereby conclude that the male alpine New Zealand *erminea* have become larger than their British ancestors in order to exploit rabbits more efficiently, because they generally eat rabbits less often than do British *erminea* (King and Moody 1982). Overall, they take as many large mammalian prey as do their relatives in Britain, by making up the total with possums and rats; but these are more common on the podocarp-hardwood forests. New Zealand would be a fertile field for further study on the ecology and economics of hunting by weasels.

## Conclusions

The natural history of the weasels is very largely the story of how these adaptable little carnivores profit from the advantages, and cope with the disadvantages, of their diminutive stature. Almost every aspect of their lives is controlled by their small size, but, in the four most important ones (Figure 11.2), the list of the advantages and disadvantages seems to be more or less balanced in all respects except that of physiology. In competitive relationships the weasels' supremacy in exploitation, compared with the larger carnivores and raptors, is countered by their vulnerability to interference. In reproductive strategy the gains and losses that follow from being small roughly cancel each other out at both individual and population levels. Only with respect to metabolism are the pluses far outweighed by the minuses, the more so the colder the climate. Of course, none of the factors identified in Figure 11.2 can be quantified; they are most unlikely to be equal, of if they were, the way of life of a weasel would be impossible, especially in the Arctic. As Bergmann recognized long ago, for most mammals small size is most demanding and dangerous in cold climates. Paradoxically, the weasels have turned this argument on its head; for them it is their small size that provides a passport to survival and an unassailable advantage over larger predators in the exploitation of small rodents in the Arctic.

Weasels, like most carnivores, are not easy to study; they are scarcer, more intelligent, and more wide-ranging than mice and voles, and the literature on weasels is only just beginning to get past the straight descriptive stage that students of small rodents left behind years ago. Anyone who has pitted wits

against weasels in the field knows, all too well, that it can be difficult to obtain large quantities of statistically respectable data from them. Weasel populations are also very unstable, and many conscientious field workers who deserved better have been disappointed when the weasels they expected to study declined to cooperate. On the other hand, weasels are certainly more abundant than larger carnivores, potentially able to supply large samples; and with the development in recent years of many new field techniques, they are beginning to provide some good opportunities to test theoretical ideas (Sandell 1985; Sandell, this volume). This review suggests a considerable list of ideas that could be tested and questions that might be answered by future field observers and modelers. The great difficulties will be in deciding how to identify and define the critical parameters, especially foraging efficiency and size distribution of *available* prey, and how to determine their effects on body size without falling into circular arguments. For example, the difficulty of interpreting the body size of *erminea* in New Zealand in terms of the most acceptable current hypothesis (Erlinge 1987) underlines (1) the need to understand the comparison between the sizes of predator and prey in terms of foraging strategy rather than simple morphometrics, and (2) the possibility that other factors besides prey size may be important. Erlinge (1987:37) concluded that "since alternative explanations for size variation in the small mustelids are not supported by existing data, evidence suggests that size variation in the stoat [*erminea*] is caused primarily by regional differences in the size frequency distribution of their available prey." Perhaps it is time to cease relying on existing data, to collect new information that could test alternative or additional ideas, and to design some critical experiments capable of distinguishing between or ranking competing explanations.

How far does the above discussion apply to other small carnivores, such as *Martes* species (the martens and fishers) and the viverrids? Some of it certainly does. All carnivores have to balance the energy equations of hunting, though not all take the risks that weasels do; metabolic restraints presumably apply in some form to all mammals. On the other hand, only weasels have the *combination* of (1) such an extremely stressful, energy-intensive way of life (the net result of inefficient heat conservation, active hunting technique, and wide distribution in cold climates); (2) such great uncertainty in reproductive success (the net result of a short average lifespan and dependence on fluctuating prey resources for maximum productivity); (3) such vulnerability to interference from so many other predators. *Martes* species also live in cold climates but are well protected against heat loss by their thick fur. The reproductive success of some martens is also strongly affected by the population fluctuations of voles (Bayevsky 1956; Weckwerth and Hawley 1962), but established adults probably have more chance of living to the next breeding season than adult weasels do. Viverrids (civets, genets, and mongooses), native to the tropics and subtropics of Africa and Asia, tend to be omnivorous; all are much larger and longer lived than weasels. Weasels alone have perfected the danger-

ous art of being the smallest carnivore of all, in the most challenging environment in the world.

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### Appendix 11.1: Distribution of Adipose Tissue in Weasels

In the course of dissecting many hundreds of weasels (*M. nivalis* in Britain and *M. erminea* in New Zealand: King 1977; King and Moody 1982:100), I observed that adipose tissue was stored only in a few discrete sites, and that fat was laid down in these in a certain order and withdrawn in the reverse order. If there was any fat present at all, it was first deposited along the spine and around the kidneys. The abdominal mesenteries were used next, although deposition there was moderate until the later stages. With increasing fatness, sites outside the body cavity were used, filling in the dips in the body outline from the posterior forward; beginning under the tail, around the testes and in the loins, and then in the angles of the hind legs, in the brachial pit and the angles of the forelegs. As deposition progressed, the first sites were still being used: a weasel that had reached the stage of using the front limb sites had a relatively greater amount in the body cavity. This pattern ensures that even a grossly fat weasel has the same streamlined profile characteristic of the species and does not become too rotund to enter rodent tunnels and nests.

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