

Factors regulating mustelid populations

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The c. 70 species of mustelids are widely distributed, and vary greatly in body size, habitat adaptation, and means of population control. The variation in the family is illustrated by examples representing the large, equilibrium species (*Meles meles*, *Taxidea taxus*, *Lutra lutra*, *L. canadensis*, *Martes pennanti*, *M. zibellina* and *M. americana*); the small, opportunistic species (*Mustela nivalis* and *M. erminea*); and the intermediate species (*Mustela vison* and *M. putorius*). Different manipulations of productivity and mortality determine density in equilibrium compared with opportunistic species.

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1. Introduction

The family Mustelidae contains 5 sub-families and 60—70 species, distributed throughout the world except in Australia and Antarctica. A brief review can merely select a few recent studies of the better known (mainly Holarctic) species to represent the variation in population dynamics (not structure) found in the family.

Mustelids vary widely in body size and in habitat adaptations. The larger species (mostly 1—10 kg; *Enhydra* and *Gulo* to over 30 kg) are generalised searching predators, unlike in morphology because of their advanced adaptation to different habitats (e.g. badgers fossorial; martens arboreal; otters aquatic). At the other extreme are the size-graded set of co-existing *Mustela* species (most ≤ 1 kg), specialised searching predators which share habitat and similar morphology, but partition prey resources by size.

Body size, habitat, and their interaction, profoundly influence population dynamics. Size affects energy requirements, metabolic rate, generation time and rate of increase (r_m) (McNab 1980), and hence influences home range size and population density. Habitat (the part of the total environment available to the individual for foraging) determines the distribution, density and reliability of prey. A very important character of a habitat is its duration stability, the relationship between the species' generation time (T) and the length of time that the habitat remains favourable (H) (Southwood 1976). Body size is one of several important characters governing T/H , and hence, the scale and permanence of an individual's habitat. For example, a patch of long grass containing many fieldvoles is a temporary habitat for a weasel, which its young, if any, will probably have to leave (T/H is relatively high); by contrast, the whole

district may be a stable and permanent habitat for generations of badgers (T/H is low). Mustelids of different sizes therefore must have different population dynamics even when sympatric.

Small mustelids living in very variable habitats with short duration stability have the characters attributed to opportunistic species, or "r-strategists", as summarised by Southwood (1976); large mustelids living in less variable habitats with long duration stability have those of equilibrium species, or "K-strategists"; others are intermediate. King & Moors (1979a) showed that the British mustelid fauna could be ranged along the so-called r-K spectrum, from weasels and stoats at the r-end, through polecats to pine martens, otters and badgers at the K-end, with associated characters as predicted by r-K theory (e.g. more stable populations and decreased reproductive effort in K-strategists), although this observation neither confirms nor denies that theory.

2. Population regulation

Any aspect of the complex environment of a population, or any interaction between its members, may be identified as a "regulating factor", on two conditions. It must be responsive to, and itself influenced by, changes in the density of the population; and its action must increase in at least direct proportion with any increase in population density. Various factors, internal and external to the population, are responsive to density, but not all density-dependent factors exercise regulation. The minimum data required to understand the variation in any population include complete age-specific birth and death schedules, and knowledge of

how these vary with environmental conditions and with population density. These details are hard to get and seldom all available together.

Terms used by different authors have here been standardised as follows: *Fecundity*: ova shed/female/year. *Fertility*: embryos or newborn young/female/year. *Pregnancy rate*: proportion of females fertile/population/year. *Productivity*: juveniles produced/population/year.

2.1. Population regulation in equilibrium species

Meles meles (10–11 kg). Unlike most other mustelids, European badgers are sociable, living in clans of mutually tolerant individuals sharing a territory and its large permanent underground sett(s). They forage at night, usually alone, on a variety of foods but especially on earthworms (Kruuk 1978a). Intraspecific aggression between members of neighbouring clans influences the spacing-out of territories (Kruuk 1978b); the availability of food, mediated through social interaction within a clan, is perhaps the factor limiting clan size. In Sweden, populations are recorded long into the period of delay in implantation; over 95 % of adult and about 50 % of yearlings conceive 2–4 young every year (Ahnlund 1980a). However, mortality of small juveniles is at least 50–60 % (Ahnlund 1980b) and Kruuk (1978b) noted that, in one closely observed high-density population, usually only one female per clan had cubs. Ahnlund (1980a) suggests that the prolonged season of sexual activity may have a secondary, social function, especially in young females seeking admission to or status within a group. Hence, pregnancy rate is constantly high, but the actual productivity of a local population each year is probably determined largely by density-dependent social interaction, in turn determined by the distribution of food supplies (Kruuk & Parish 1982).

Taxidea taxus (6–7 kg). The North American badger, unlike *Meles*, is a non-sociable predator of small mammals, especially ground squirrels. In an Idaho population described by Messick & Hornocker (1981), density decreased from 1975 to 1977, apparently due to increasing mortality of adults caused mainly by man. Through the same three years, the proportion of productive (fecund or fertile) females increased (0.33, 0.54, 0.58) and so did the number of female births per female (0.3, 0.6, 0.7). In 1977 the population of ground squirrels (*Spermophilus townsendi*) declined; adult badgers survived well on other food and pregnancy rate remained high, but the actual productivity in 1978 is unknown. The precise details of how fecundity, fertility and pregnancy rate interacted, between themselves and with food supplies, to achieve the observed increase in productivity, are unclear.

Lutra sp. Undisturbed populations of the Eurasian otter (*L. lutra*, 7–10 kg) are relatively stable. Home ranges are shared by an adult male and two or more females, which apparently breed in succession, each keeping her cubs for a year or more (Erlinge 1967, 1968, Jenkins 1980). Adults are fertile at all seasons and implantation is direct. Cubs can be reared successfully,

all year round in mild climates, but young cubs seldom survive hard winters. There is great flexibility of social organisation, ranging from strict territoriality to mutual avoidance. The habitat of otters is vulnerable to human interference, especially water pollution by toxic agricultural and industrial chemicals (Erlinge 1972, Chanin & Jefferies 1978), which are probably the main cause of general declines in the otter populations of Sweden and Britain since the 1950s. By contrast, the related Nearctic otter, *L. canadensis* (8–13 kg) has delayed implantation and, since the introduction of strict hunting regulations, populations vigorous enough to allow sustained-yield cropping. For example, in northern New York state (52 000 km²) the annual harvest averaged 570 pelts through the late 1970s (M.K. Brown, pers. comm.). It is ironic that man's actions have had opposite results for *lutra* and *canadensis*.

Martes sp. All martens are valuable furbearers, of modest fecundity, and very sensitive to over-harvesting. For example, when Ontario harvest quotas for fisher (*M. pennanti*, 2–5 kg) were set too high in 1972–73, the catch increased to a peak of 5.4 fisher/100 km² in 1973–74, but comprised many adult females and few juveniles, and the next two years' catches were reduced (Strickland & Douglas 1981). When the quotas were reduced in 1976–77, fewer females and more juveniles were caught, and since then the harvest has slowly increased. The effects of variations in fertility and food supplies on this recovery are not stated. The Russian sable (*M. zibellina*, 0.8–1.4 kg) shows pronounced geographic variation in density (0.1–18.0 sable/10 km²), fecundity (2.96–4.03 corpora lutea/♀), and yield (0.08–7.0 skins/10 km²), related to habitat (Bakayev & Monakhov 1970). In one area the difference between fecundity and productivity varied from < 12 % in good years to 78 % in hungry ones. A local population decline in 1953–56 of *M. americana* (0.6–1.0 kg), characterised by a disappearance of adults (especially females), reduction in productivity, and dispersal of juveniles, followed a decline in small forest rodents (Weckwerth & Hawley 1962). Martens at low density were in good condition, and recovered their numbers when rodents increased in 1956–57.

2.2. Population regulation in opportunist species

Mustela nivalis (50–130 g). Two recent studies (Tapper 1979, King 1980) investigated in different ways the unstable populations of weasels on British game estates. Weasels are well adapted, physically and demographically, to dependence on small rodents, especially *Microtus*. Variations in the distribution, density and breeding rates of weasels and *Microtus* are closely correlated. In *Microtus* peak years, adult female weasels produce an extra summer litter (doubling their fecundity for the year) and the spring-born young females also breed in summer. However, such population peaks are short-lived; the mean mortality rate after independence is about 0.75–0.80 and the mean lifespan < 1 year. In poor years, the pregnancy rate is drastically reduced, and weasel density declines. Variation in the reproductive success of weasels is

certainly controlled mainly by independent variations in food supplies, and is therefore not necessarily density-dependent, although Tapper found some density-dependence in the relationship between the weasels and the *Microtus*.

Mustela erminea (200—350 g). In cold and snowy climates stoats are as dependent on small rodents as are weasels, and have populations equally unstable (Nasimovich 1949). In New Zealand beech (*Nothofagus* spp.) forest, stoat populations follow fluctuations in feral *Mus musculus* and *Rattus rattus*, correlated with 3—5 year falls of beech seed. Virtually all female stoats of all ages breed every year, and mean fecundity (8—10 corpora lutea per female) is relatively constant between years and habitats (King 1981). In the summer after a mouse peak, productivity is 3—5 times higher than average, and is correlated with density of mice during the period of implantation. In the following summer, when the mice have disappeared, the production of young stoats is often nil, although all females are pregnant as usual. (The same constantly high pregnancy rate, with variable success, is found in *Meles*, but for a different reason.)

Elsewhere in New Zealand and in Britain, stoats eat many rabbits (*Oryctolagus cuniculus*): removal of rabbits, by myxomatosis or poisoning, causes drastic declines in stoats (King & Moors 1979b, and unpubl.). In European Russia, Aspisov & Popov (1940) found a close correlation between the annual harvests of pelts of ermine and of water vole (*Arvicola amphibius*) ($r = 0.71 \pm 0.09$, $n = 34$).

In stable habitats, food and density may interact in some way to limit the total numbers of young surviving to establish a breeding territory (Simms 1979). For resident adults, however, distribution and abundance of favoured prey adequately explain differences in average productivity of females, e.g. between years in New Zealand (King 1981) and between habitats in Sweden (Erlinge 1981) and Canada (Raymond & Bergeron 1982).

2.3. Population regulation in intermediate species

Mustela vison (0.6—1.3 kg). The American mink has a spectacular history of invasion and spread over Europe this century. In Britain, over 7 000 were caught in 10 years before the official eradication campaign was abandoned as hopeless in 1970 (Corbet & Southern 1977). No demographic analysis of this abundant material has been published, so the details of the expansion phase of that invasion are presumably now lost. Mink colonised all Sweden, except the northern mountains, in about 35 years; a semi-log plot of the annual catch shows an almost perfect sigmoid curve, levelling out at about 60 000 mink killed per year (Gerell 1971). A population analysis of mink in Scania, done with livetraps, gave no age-specific fecundity or

mortality data. Litter size was 3—6, but not every female bred every year; population turnover was rather high (only 3 of 20 mink marked in autumn 1968 remained in spring 1970). Gerell concluded that mink increase rapidly where free of hunting, and are then regulated by enforced dispersal of juveniles, a form of density-dependent behaviour that would certainly assist rapid colonisation of a new country.

Mustela putorius (0.6—1.0 kg). The polecat is similar to the mink in size, shape and population characters (one litter a year, normally of 5—8 young, both sexes mature at one year old, life expectancy 8 months mean, 4—5 years maximum: Corbet & Southern 1977). The contrast is in their response to direct persecution by man. In England, control measures exterminated the polecat in the nineteenth century (Langley & Yalden 1977), but failed to prevent the spread of mink in the twentieth. The reason for this difference is unknown.

3. Conclusions

1. Demographic analyses are available only for species which are regularly harvested for fur or sport, or as pests, which provide the motive and the opportunity to collect large samples of normally scarce carnivores. Rare or protected species (e.g. European otter, polecat) can be observed only as live animals in the field, and their population biology is largely unknown.

2. Variation in natural population density increases from opportunistic through intermediate to equilibrium species. This generalisation is illustrated by the density data for one of each kind through a population peak of *Microtus arvalis* on Polish farmland in 1970—72 (Ryszkowski et al. 1973). In the winter of 1970—71, *Microtus* was low; the peak was in summer 1971 and the decline started in winter 1971—72. During this time the density of *Mustela nivalis* varied threefold, between 15 and 46 ha/individual. The density of *Martes* sp. varied twofold, between 221 and 443 ha/individual, and that of *Meles meles* remained at 510 ha/individual throughout.

3. This review suggests that different manipulations of productivity and mortality determine density in equilibrium species compared with opportunistic species. The starting point, mean fecundity, varies from 2—3 ova/♀/year in *Meles* and *Lutra* to 8—10 ova/♀/year in *Mustela erminea*, but, except in *M. nivalis*, fecundity seldom varies as much as do the later stages of reproduction, or as does mortality. Actual productivity is apparently controlled by density-dependent variation in fertility in *Meles* and in pregnancy rate in *Taxidea*; by food-dependent variation in fertility in *Mustela erminea*, and additional litters in *M. nivalis*; and by food/?density dependent variation in fertility and pregnancy rate in *Martes*. Mortality is affected mainly by man and by social interactions (influenced by food supplies) in the equilibrium species, and almost solely by food in the opportunists.

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