5 Weasels and Martens - Carnivores in Northern Latitudes

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5.1 Introduction

The first mammals were probably nocturnal (McNab 1978; Kemp 1982) and many extant orders of small mammals have retained this trait. This behaviour is presumably due to the measure of protection from predation that darkness provides (Crawford 1934; Falls 1968; Daan and Aschoff 1982). Large, herbivorous mammals are less restricted to the nocturnal phase (e.g. Bunnell and Harestad 1990) and have been classified as `nocturnal-diurnal' (Charles-Dominique 1978). This is either because their large size renders them less vulnerable to predators, because the low energy nature of their folivorous diet demands extended periods of food consumption, or because food search time increases with increasing body size (Harestad and Bunnell 1979; Belovsky and Slade 1986). The carnivorous mammals, however, exhibit a wide diversity and flexibility of activity patterns (Kavanau 1971; Ewer 1973; Curio 1976; Daan 1981; Gittleman 1986). Peak activity times vary among the Carnivora and within individual species studied at different locations or during different seasons. For example, *Mustela erminea* has been described as nocturnal (Figala and Tester 1992), nocturnal in winter but diurnal in summer (Bäumler 1973; Debrot et al. 1985), crepuscular (Müller 1970) and mostly diurnal (Erlinge and Widen 1975; Erlinge 1979).

The activity patterns of mammalian carnivores are influenced by a number of factors, including: diel temperature variation (Schmidt-Nielsen 1983), interference from competitors (Carothers and Jaksic 1984), limitations of the visual system (Walls 1963; Dunstone and Sinclair 1978), risk of predation (King 1975), social behaviour (Ewer 1973; Gittleman 1986), and behavioural thermoregulation (Chappell 1980). However, what makes carnivores unique is the fact that their foods, unlike that of herbivores, have their own circadian cycles of availability and vulnerability (Curio 1976; Zielinski 1986a). The foods of herbivores, although patchy in space, are relatively stable and predictable in time. Perhaps this distinction is the reason why the activity patterns of mammalian carnivores can be described so differently by different authors while the activity patterns of mammalian herbivores tend to be less
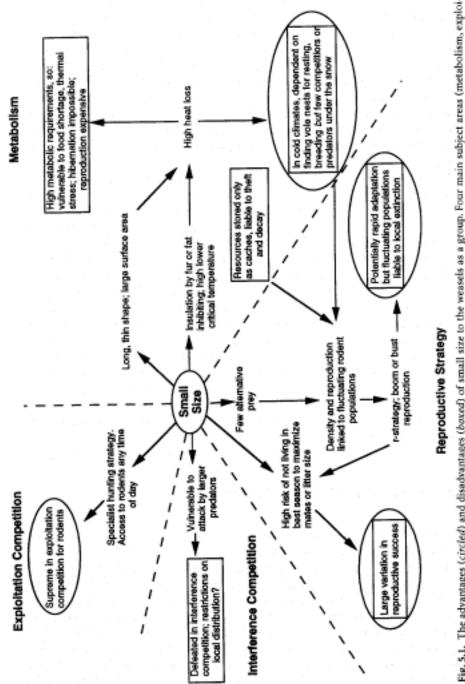
variable. If small carnivores feed on different proportions of prey types in different locales, each with different circadian phases of maximum vulnerability, we would expect considerable intraspecific variation in modal activity times. How the circadian rhythms of prey vulnerability influence predator activity will be a central issue of this review.

   Mustelids are the most ecologically diverse family within the Carnivora (Wozencraft 1989), including dietary specialists and generalists that range from strictly carnivorous to omnivorous. The subfamily Mustelinae (e.g. weasels, mink, polecats, ferrets, martens, sable, fishers) originated in the Miocene (Martin 1989; Anderson 1994) and the earliest forms occupied forest habitats and probably lived in much the same way martens do today. During the Plio-Pleistocene the cooler, drier climate favoured the establishment of grasslands and small mammals, especially voles (*Microtus* spp.), began to radiate into forms that occupied the forest-steppe environment (Webb et al. 1983; Martin 1989*).* Although the genus *Martes* was clearly defined by this time, intermediates between *Martes* and *Mustela* were becoming established (Anderson 1970). The development of the grassland biome provided opportunities for predators that were small enough to pursue voles and lemmings (*Dicrostonyx* spp., *Lemmus* spp.) in their burrows, tolerate the fluctuation in prey numbers typical at northern latitudes, and sustain themselves through the harsh winters (King 1989).

5.2 Metabolic Consequences of Mustelid Size and Shape

Weasels, especially the Holarctic *Mustela nivalis* and *M. erminea,* are a paradoxical group; they occupy some of the coldest regions of the world but manage to do so with short fur, very little fat storage capacity and a surface area/volume ratio that favours heat loss (Brown and Lasiewski 1972; King 1989). Arctic weasels can have a basal metabolic rate two to three times greater than those in Wisconsin (Scholander et al. 1950). Weasels do not migrate, hibernate, or enter torpor during periods of cold or food shortage. They must continually fuel their bodies or die. Long, thin mustelids have basal metabolic rates that can be two to six times higher than that of non-elongate mammals of equivalent weight (Brown and Lasiewski 1972; Iversen 1972; Chappell 1980; Sandell 1985). Least weasels consume from 30 to 40% of their weight in food a day and expend an estimated 21% of the mean average daily metabolic rate on activity; a greater percent than some shrews (Moors 1977; Gillingham 1984). Their elongate body shape and small size impose constraints that influence the ecology of small mustelines in myriad ways (Fig. 5.1).

   Because their activities are focused on confined spaces that are refuges for their prey, weasels must maintain their thin body form, limiting the storage of fat to slight dips in the contours of their body outline (King 1989) and

Fig. 5.1. The advantages (*circled*) and disadvantages (*boxed*) of small size to the weasels as a group. Four main subject areas (metabolism, exploitation competition, interference competition, reproductive strategy) are linked together at various levels. (From King 1989)

minimising the length of their fur (Casey and Casey 1979). They survive with these apparent thermoregulatory disadvantages, particularly during winter, because they can do what no other predator can: hunt small mammals in their narrow burrows and survive on a sparse population when other predators have switched to other prey or dispersed (Fitzgerald 1981). The weasels are a conspicuous exception to Bergman's rule (King 1989); their small size provides them an advantage over larger predators in the exploitation of small rodents in the far north. The energetic disadvantages of their body shape, especially in winter, are partially offset by their habits of hunting under the thermal cover of snow (Kraft 1966; Fitzgerald 1981) and resting in the nests of their prey (Fitzgerald 1977).

Martens (*Martes* spp.), sables (*Martes zibellina*) and fishers (*Martes pennanti)* also experience harsh winter conditions throughout most of their ranges, but they do so in a body with a more economical surface area/volume ratio and with longer fur than the weasels. However, they also consume a large percent of their body weight per day (about 25% in *M. americana,* More 1978), very little of which can be stored as fat (Buskirk and Harlow 1989; Harlow 1994). And like weasels, much of the marten's foraging and resting during winter occurs under the thermal cover of snow (Buskirk et al. 1989; Thompson and Colgan 1994). Mink (*Mustela vision*), ferrets (*Mustela nigripes, M. eversmanni*), and polecats (*M. putorius*) experience less of the extremes of northern climates but their similar body size and shape, and shared ancestry with the weasels suggests that they too experience extreme metabolic demands (Iversen 1972; Harlow 1994). Weasels, however, have a more energy-intensive way of life, more uncertainty in reproductive success, and greater vulnerability to interference from other predators than larger mustelids and therefore are under the most severe energetic constraints (King 1989).

5.3 Proximate and Ultimate Effects on Activity

Locomotor activity is influenced by behavioural responses to environmental events and by endogenous circadian rhythms (Daan and Aschoff 1982). Short-term and unpredictable environmental events can stimulate or inhibit activity, but this generally occurs within a circadian threshold of activity that is governed by the predictable cycle of light and dark. For example, the American mink may be considered `nocturnal' and may be entrained by the LD cycle, but should a mink capture a large prey item at dusk or the weather turn unseasonably cold, nocturnal activity will be suppressed. A recent meal, rain, a full moon, high winds or extremes of heat or cold can all suppress the activity of carnivores (e.g. Ables 1969; Kavanau and Ramos 1972; More 1978; Buskirk et al. 1988; Taylor 1993; Beltran and Delibes 1994).

Ecological factors affect how an animal allocates the energy that is acquired into various activities. Survival and reproduction will presumably be maximised when the amount, duration, and distribution of particular activities are allocated in an optimal fashion (Schoener 1971; Daan and Aschoff 1982). The general activity pattern (i.e., nocturnal, diurnal, crepuscular, ultradian, arhythmic) is a phenotypic expression of the way that environmental constraints, and behavioural responses to them, influence endogenous rhythms. A rhythmic circadian pacemaker may structure the temporal pattern of activity but the ultimate expression is influenced by the physical environment, trophic community interactions, and social factors (Aschoff 1964).

It is important to realise that characterising a species as `nocturnal' simply means that the highest probability of discovering the animal active occurs during the hours of darkness. Any time of an animals' internal day is characterised by its own distribution of probabilities of the occurrence of both spontaneous behaviours and responses to environmental stimuli (Daan 1981). The most common activity time for small mustelids appears to be during the night, followed by crepuscular activity, with diurnal activity much less common (Table 5.1; Gittleman 1986). However, even the phase of the cycle that has the highest probability of activity will include periods of inactivity because foraging and other locomotor activities frequently occur in bouts (e.g. Erlinge 1979; Powell 1979; Thompson and Colgan 1994). Unfortunately, the data on activity patterns in the Mustelidae are few and generally unsuited for quantitative analysis. Rarely is activity the sole focus of a field study of a small mustelid and the activity patterns of captive animals may not be representative of those in the wild (Kavanau 1969; Kavanau et al. 1973; Davidson 1975; Zielinski 1986b). Although the nature of the data make intra-familial comparisons difficult, in this section I examine the variety of reasons that could favour nocturnality in the Mustelidae and also try to explain some of the deviations from this basic pattern.

5.3.1 Foraging Time, Meal Patterning and Digestive Constraints

The metabolic requirements of weasels demand that they eat frequent, energy-rich meals (King 1989). Musteline carnivores are active, on average, about 25% of the 24-h day (Table 5.2, see page 104), ranging from a low of 7 to a high of about 60%. This appears to be somewhat less than is typical for other mammals in the *Mustela* and *Martes* weight categories (Bunnell and Harestad 1990). Outside the breeding season, searching for food probably accounts for most of this activity, if small mustelids are similar to other mammals which engage in `foraging' during 70% of the time they are active (Bunnell and Harestad 1990).

Because the individual prey of weasels and martens can often exceed the amount that can be consumed in a single meal, excess is cached for later consumption (Oksanen et al. 1985; King 1989; Henry et al. 1990). Thus, foraging

Table 5.1. Summary of studies describing musteline activity patterns

Author (year)	Season	Activity pattern[a]	Number (M:F)[b]	Location[c]	Method
Mustela nivalis					
Kavanau (1969)	Summer	Nocturnal/arhythmic[d]	2 (1:1)	Michigan, USA	Captivity
Price (1971)	Summer	Nocturnal	4 (2:2)	Michigan, USA	Captivity
King (1975)	Annual	Diurnal	10 (7:3)	England	Field – trapping
Erdakov (1981)	–	Ultradian	6 (3:3)	Northern Russia	Captivity
Zielinski (1986a)	Summer	Arhythmic	3 (3:0)	Illinois, USA	Captivity
M. erminea					
Robitaille (unpubl.)	Annual	Nocturnal	7 (5:2)	Quebec, Canada	Field – observation
Bäumler (1973)	Winter	Nocturnal	–	Germany	Field – snow tracking
	Summer	Diurnal	–	Germany	Field – observation
Erlinge and Widen (1975)	Fall	Diurnal	7 (3:4)	Sweden	Field – telemetry
Erlinge (1979)	Winter	Nocturnal	4 (4:0)	Sweden	Field – telemetry
	Spring/summer	Diurnal	4 (4:0)	Sweden	Field – telemetry
Nams (1981)	Fall/spring/summer	Nocturnal	–	NWT, Canada	Captivity
Debrot et al. (1985)	Spring/summer/fall	Diurnal	–	Switzerland	Field – trapping
Zielinski (1986b)	Summer	Nocturnal/crepuscular	1 (1:0)	Minnesota, USA	Captivity
Zielinski (1988)	Summer	Nocturnal	3 (3:0)	Minnesota, USA	Captivity
Figala and Tester (1992)	Annual	Nocturnal	1 (0:1)	Germany	Captivity
M. frenata					
Kavanau and Ramos (1975)	Summer	Nocturnal/diurnal	5 (3:2)	Nevada/California, USA	Captivity
M. vison					
Gerell (1969)	Annual	Nocturnal	6 (5:1)	Sweden	Field – telemetry
Melquist et al. (1981)	Fall/winter	Nocturnal/diurnal	6 (–)	Idaho, USA	Field – telemetry
Zielinski (1986b)	Summer	Nocturnal	6 (0:6)	Illinois, USA	Captivity
Zielinski (1988)	Summer	Nocturnal/crepuscular	3 (0:3)	Illinois, USA	Captivity
M. putorius					
Danilow and Rusakow (1969)	–	Nocturnal/diurnal	–	Russia	Field
Bäumler (1973)	Winter	Nocturnal	–	Germany	Field – snow tracking
Blandford (1987)	–	Nocturnal/crepuscular	–	Wales	Field – telemetry
Lode (1995)	Annual	Nocturnal	9 (5:4)	France	Field – telemetry

Table 5.1 (continued)

Reference	Season	Activity type	Number (m:f)	Location	Study type
M. putorius furo (domestic ferret)					
Donovan (1987)	-	Diurnal*	6 (0:6)	-	Captivity
Stockman et al. (1985)	-	Arythmic	12 (6:6)	-	Captivity
M. nigripes					
Henderson et al. (1974)	Annual	Nocturnal	-	South Dakota, USA	Field – observation
Martes americana					
More (1978)	Winter	Diurnal	14 (8:6)	NWT, Canada	Field – telemetry
	Summer	Crepuscular	14 (8:6)	NWT, Canada	Field – telemetry
Hauptman (1979)	Summer	Diurnal/nocturnal	4 (3:1)	Wyoming, USA	Field – telemetry
Zielinski et al. (1983)	Summer	Diurnal/crepuscular	5 (4:1)	California, USA	Field – telemetry
	Winter	Nocturnal/crepuscular	3 (1:2)	California, USA	Field – telemetry
Martin (1987)	Summer	Diurnal/nocturnal	6 (3:3)	California, USA	Field – telemetry
Thompson and Colgan (1994)	Summer	Arhythmic	20 (10:10)	Ontario, Canada	Field – telemetry
	Winter	Diurnal	10 (6:4)	Ontario, Canada	Field – telemetry
M. martes					
Pulliainen and Heikkinen (1980)	Winter	Nocturnal/crepuscular	-	Finland	Field – snow tracking
Clevenger (1993)	Fall/winter	Nocturnal	5 (2:3)	Spain	Field – telemetry
M. pennanti					
Zielinski (unpubl.)	Summer	Crepuscular	10 (2:8)	California, USA	Field – telemetry
Kelly (1977)	Annual	Crepuscular	10 (7:3)	New Hampshire, USA	Field – telemetry
	Summer	Crepuscular/diurnal	10 (7:3)	New Hampshire, USA	Field – telemetry
Powell (1979)	Winter	Crepuscular/diurnal	3 (2:1)	Michigan, USA	Field – telemetry
Johnson (1984)	Annual	Crepuscular	-	Wisconsin, USA	Field – telemetry
Arthur and Krohn (1991)	Annual	Crepuscular	43 (15:28)	Maine, USA	Field – telemetry

a Two activity types are listed when a significant amount of activity is reported during both periods. If a predominant type was mentioned, it is underlined.
b Number of individual animals that contributed to the activity data (males : females).
c Location of field study, or in the case of captive studies, the location where the study animals originated.
d Nocturnal when light/dark transitions are gradual and arhythmic when transitions are abrupt.
e Primary diurnal during anoestrus and increased nocturnal activity during oestrus.

does not necessarily precede the consumption of each meal and the motivation to eat (hunger) can be different from the motivation to find food. Daan (1981) distinguishes two optimisation problems related to feeding: optimisation with respect to the animal's metabolic requirements and optimisation with respect to the fluctuations in food availability. Here I review the data pertinent to the first problem.

Hungry animals actively seek food and sated animals usually rest (de Ruiter 1967). In classic meal pattern studies, large meals are followed by a post-prandial dip in activity proportional to the size of the meal; a phenomenon first demonstrated in captive rats, cats, and dogs (LeMagnen and Devos 1970; Kanarek 1974; Ardisson et al. 1981) but noted in wild and captive mustelids as well (e.g. Müller 1970; Kavanau and Ramos 1975; Thompson and Colgan 1994). Small carnivores that have secured a large prey item may be inactive for a day or two; the movements of American martens are greatest when food is least available (Thompson and Colgan 1990), and fishers are more active when they are provisioning young (Paragi et al.1994). Laboratory evidence also suggests that hunger and locomotor activity are related (Müller 1970; Price 1971; Kavanau and Ramos 1975; Zielinski 1986b, 1988). Price (1971) discovered that total activity exhibited by least weasels was not affected by 8 h of food deprivation, but was nearly doubled in response to 24 h of deprivation. Similarly, Zielinski (1988) demonstrated that the total diel activity of a number of small carnivore species increased significantly when food availability was restricted. Locomotor and feeding behaviour appear closely linked in weasels (Zielinski 1986b,1988; Sandell 1989; Figala and Tester 1992) although they can be easily dissociated in other species (Daan and Aschoff 1982).

Food intake can be extremely limited by digestive constraints in small carnivores. When allowed to feed freely after 16 h of deprivation least weasels could consume no more than an average of 3.1 g of food in an hour and 11.4 g (in 3-4 meals) in 8 h (Gillingham 1984). Meals were consumed about 3 h apart (near the lower limit of food passage time; Short 1961). This occurs despite the fact that least weasels must consume, on average, about 40% of their body weight in food each day (Gillingham 1984). This physiological constraint indicates why optimal meal timing can be very different from optimal foraging. Weasels do not have the option of consuming their daily requirement in 1 or 2 meals, but instead must distribute their feeding among 5-10 meals per day. The rapid processing of food by weasels means they must either stay near cached food and limit long-distance activities or, if cached food is not recovered, to forage every few hours. Martens apparently are not under similar constraints because of significantly slower gut passage times than the weasels (More 1978; Harlow 1994). The least weasel's frequent need to eat may explain the observation by some that they are arrhythmic or exhibit ultradian cycles of activity (Erdakov 1981; Zielinski 1986b), a pattern that also characterises the activity of another energy-demanding taxon, the shrews (Crowcroft 1954). The discontinuous pattern of activity (multiple

short bouts) reported from radiotelemetry studies of some mustelids (Gerell 1969; Erlinge 1979; Powell 1979) could be influenced as much by frequent bouts of eating as by bouts of foraging, behaviours that cannot be distinguished using remote telemetry.

Not all locomotor activity is regulated by the need to replenish an energy deficit. Captive carnivores on ad libitum diets continue to exhibit spontaneous, rhythmic locomotor activity that usually bears some relationship to the LD cycle (Kavanau 1969; Kavanau and Ramos 1975; Zielinski 1986b, 1988; Robitaille and Baron 1987) and is presumed to be under endogenous control. Thus, activity is affected by the history of recent food intake (and other short-term activating or inhibiting events) *and* by cyclic circadian thresholds for activity that are in phase with the light cycle (Kavanau and Ramos 1975; Daan and Aschoff 1982).

In some experiments the circadian variation in food availability and light have been manipulated to understand their relative effects on locomotor activity. When placed in constant dark or constant light, weasels ran for prolonged periods on wheels to anticipate a meal provided with 24-h periodicity (Zielinski 1986b). This response suggested that periodic availability of food could entrain the endogenous rhythm. In a second experiment, weasels and mink were kept in LD 12 : 12 and required to run increasingly longer periods on a running wheel for food during the phase of the LD cycle they preferred, usually the dark (Zielinski 1988). This circumstance tested the animal's `willingness' to abandon the 12 h of the day favoured for activity for the opposing period during which time food was available at a significantly lower energetic cost. Most of the weasels retained their preference for activity during the dark and merely ran the additional distance on the wheel to achieve sufficient food. A modest increase in diurnal activity, and reinforcement, indicated that each animal was aware of the lower cost to foraging during the light phase. Sometimes an order of magnitude of additional effort was expended to acquire food in the preferred phase rather than shift activity to the opposing phase of the LD cycle. This evidence suggests that there is an underlying circadian rhythm of locomotor activation that controls the magnitude of hunger-induced activity. This is similar to the observation that rats deprived of food for equivalent periods of time were more active, and ate more, when deprivation ended during the night (their normal activity time) than during the day (Bellinger and Mendel 1975).

Locomotor activity directed toward foraging is a part of the homeostatic control of food intake. However, animals appear more apt to respond to hunger with activity when the hunger occurs in phase with the underlying endogenous phase of activity. Very little is known about the interaction between the factors that regulate spontaneous activity versus hunger-driven activity in small mustelines, or any other mammal for that matter.

5.3.2 The Visual System

The visual system of most mammalian carnivores is adapted to permit activity at all times of day; many carnivores possess what has been referred to as `the 24-h eye' (Walls 1963; Kavanau and Ramos 1975). Even the eye of primarily nocturnal mammals contains a duplex retina (rod and cone receptors) and adequate pupillary control to permit vision in daylight (Walls 1963). In fact, many carnivores that have eyes generally adapted to function

Table 5.2. Percent of various time periods that mustelids are active

Author (year)	Percent Active[a]	Period of analysis	Season
Mustela nivalis			
Moors (1977)	21.1[b]	24 h	Fall/winter/spring
Buckingham (1979)	20.0	24 h	-
M. erminea			
Erlinge and Widen (1975)	19.0	24 h	Fall
Erlinge (1979)	25.0	24 h	Winter
	18.0	Day	Winter
	32.0	Night	Winter
	38.0	Day	Spring
	29.0	Night	Spring
Robitaille and Baron (1987)	17.8	24 h	Annual
	6.8	24 h	December
	14.4	24 h	September
M. frenata			
Kavanau and Ramos (1975)	70.6	Night	-
	10.0	Day	-
	9.2	24 h	-
M. vison			
Melquist et al. (1981)	50.0	24 h	Fall/winter
M. putorius			
Lode (1995)	31.0	24 h	Annual
M. nigripes			
Powell et al. (1985)	8.5	24 h	Winter
Martes americana			
Thompson and Colgan (1994)	59.2	24 h	Summer
	16.3	24 h	Late winter
M. martes			
Clevenger (1993)	53.0	Night	Fall/winter
	19.0	Day	Fall/winter
	34.0	24 h	Fall/winter
M. pennanti			
Powell and Leonard (1983)	27.0	24 h	Spring

[a] Mean for the period reported, except where otherwise specified.
[b] Percent of average daily metabolic rate, not time.

in darkness will choose the brightest setting when allowed to select among different ambient light levels (Kavanau et al. 1973). Because of the adaptability of the mustelid eye, it is unlikely that the amount of light available is a serious constraint on the choice of activity time.

Kavanau and Ramos (1975) recognised the dual influences of physiology and ecology on the temporal pattern of carnivore activity by contrasting the `visual activity type', the genetically-influenced activity pattern exhibited in the laboratory when food was provided ad libitum, and the `ecological activity type' exhibited in the field. The ecological type was considered a reflection of an animal's response to the times of food availability and threat of predation. The long-tailed weasel's eye appears to be adapted best for dim-light vision, suitable for daytime vision, and least well adapted for vision in very dim light even though the animal was reported to be primarily nocturnal in the field (Kavanau and Ramos 1975). The least weasel had a nocturnal visual type and a reported arrhythmic ecological activity (Kavanau 1969). Both cases suggest that evolution had not yet adjusted the endogenous rhythm to the selective environment.

`Aschoff's Rule' (as described by Pittendrigh 1960) can also be used to assess the genetic, or visual, activity pattern. In Aschoff's original formulation nocturnal animals are characterised by a circadian rhythm with (1) a period (cycle length) that is less than or equal to 24 h in constant dark, (2) a period that is shorter in constant dark than it is in constant light, and (3) an active portion that is greater in constant dark than in constant light. Mink, the only mustelid with adequate data to test the rule, conform to conditions 1 and 2 (Zielinski 1986b), and are nocturnal in the field (Table 5.1), suggesting that their genetic and ecological activity patterns are equivalent.

5.3.3 Temperature and Season

Reduced activity in winter by mammalian carnivores is considered an adaptation to cold stress and has been noted in ursids, procyonids, and mustelids (Ewer 1973). Most mustelids living in northern latitudes are less active during winter than summer and also reduce their activity during extremely cold winter weather (Pulliainen and Heikkinen 1980; Zielinski et al: 1983; Clark et al. 1984; Robitaille and Baron 1987; Buskirk et al. 1988; Arthur and Krohn 1991; Thompson and Colgan 1994; Table 5.2). High winds probably also contribute to reduced activity (Taylor 1993). Thompson and Colgan (1994) observed several martens that were continuously inactive for more than 30 h when the temperature was -25 °C. Given the high energy demands of weasels, especially during winter, reducing activity during winter can yield considerable energy savings. Activity can increase energy consumption up to six times that of the basal metabolic rate in some mustelids (Powell 1979; Karasov 1992). Chappell (1980) found that most Arctic mammals (the least weasel included) could save an average of 30% of thermoregulatory costs if they were diurnal during winter. In contrast, a number of studies on muste-

lines have reported that nocturnal activity actually increases in winter (Bäumler 1973; Zielinski et al. 1983; Debrot et al. 1985), a result that may have more to do with prey availability (see below) than physical factors. The energetic cost of winter nocturnality may not be as great when an animal forages under the snow (Formozov 1946), as is the case for most northern weasels (King 1989) and martens (Buskirk et al. 1988).

Small carnivores that are less active in the winter than the summer must omit some activities during winter that they are normally engaged in during the summer. Obviously the subtraction of activity associated with reproductive behaviour will reduce activity, but some mustelids may exhibit less territorial behaviour as well (Thompson and Colgan 1994). If foraging time is reduced during winter, either the basal metabolic rate is lower in winter than summer (for which there is no evidence), weasels are more efficient at finding the same prey they consume during the summer, or they consume prey of larger average size. With less time available, foraging should be particularly efficient during the winter (Sandell 1985). There is some evidence that this efficiency occurs, at least for martens, by hunting and eating larger-sized prey (Zielinski et al. 1983; Bull and Heater, in press). Anytime large prey are cached near a rest site (Henry et al. 1990), or when the predator resides in the dens of the prey it kills (e.g. Fitzgerald 1977; Powell and Brander 1977; Buskirk et al. 1989; King 1990) the component of activity stimulated by hunger will be reduced. Deep snow also hinders the movements of some mustelids, most notably fishers (Raine 1983; Krohn et al. 1997), but this is unlikely to account entirely for the significant reductions in activity noted.

5.3.4 Competition

Because most mammalian carnivores, mustelids included, are either nocturnal or crepuscular (Table 5.1; Gittleman 1986), the range of activity types does not exist to suggest that these species are either using resources at different times or disassociating because of interference competition. There is no mammalian carnivore equivalent to the extreme partitioning of the temporal niche axis observed in owls and hawks (Jaksic 1982). Considerable overlap is typical among mammalian species in primarily nocturnal and primarily diurnal communities, and between these groups (Daan 1981), though there are some exceptions (e.g. Ziv and Smallwood, Chap. 9). If competition has any role in the evolution of activity pattern it is more likely via interference than exploitation. This is because time is not an independent niche axis, but is dependent on partitioning of either the habitat or food axes (Schoener 1974; Carothers and Jaksic 1984). The same foods can be exploited by many species, no matter how different the activity type.

Larger carnivores are typically dominant over smaller ones (Rosenzweig 1966) and within the Mustelidae there are examples of larger species killing smaller ones (e.g. *Mustela frenata* and *M. nivalis,* Polderboer et al. 1941; *Martes pennanti* and *M. americana,* de Vos 1952; *Martes americana* and

Mustela erminea, Thompson and Colgan 1987). In the southern Sierra Nevada, sympatric fishers and martens exhibit similar crepuscular activity patterns (Zielinski, unpubl. data). There is no evidence that the activity pattern can be influenced by the presence of a potential competitor, unless that competitor is also an important predator (e.g. King 1975).

5.3.5 Predator Avoidance

Predation threats that occur at a particular phase of the LD cycle can influence daily activity patterns in any species where predation is a significant mortality factor (Curio 1976). Predation is considered the reason that most small mammals are nocturnal or crepuscular (Park 1940; Daan and Aschoff 1982). Most of the carnivores considered here are relatively small and as a result are susceptible to predation by avian and larger mammalian predators. If darkness provides some cover from predators, or if predation pressure at night is less than that during the day, nocturnalism may be favoured by selection.

Other small, non-mustelid carnivores (*Genetta genetta, Potos flavus, Bassariscus astutus*) become active very consistently shortly after sunset, a pattern that is attributed in part to avoidance of predators (Kavanau and Ramos 1972). Although least weasels are most typically described as nocturnal (Table 5.1) they are more active by day than by night in Marley Wood, England (King 1975). Although the weasel's prey are nocturnally active, so is a major predator of weasels, the tawny owl (*Strix aluco*). The threat of predation at night is considered the primary reason for the weasel's diurnal activity. Zielinski (1988) found that weasels (*Mustela* spp.) were more reluctant than American mink to shift activity from the nocturnal period, when food was available at a high energetic cost, to the diurnal period were food was available at significantly lower cost. Selection in the significantly smaller weasels may have favoured a stronger association with the nocturnal phase, which provides some cover from predators, than has occurred in the mink. Incidentally, a number of species of carnivores appear to increase their nocturnal activity in the presence of human disturbance, including some mustelids (Lohrl 1972; Rosevear 1974; Curio 1976; Mason and Macdonald 1986). If humans are perceived as a threat the increased nocturnal activity may be an anti-predatory response.

5.3.6 Social and Reproductive Behaviour

Most mustelines are solitary except during the breeding season. Regardless of the season during which reproduction occurs, male activity and movements generally increase when they are searching for mates (Gerell 1970; King 1975; Debrot and Mermod 1983; Sandell 1986; Arthur and Krohn 1991). Presumably the polygynous mating system that is thought to characterise

most mustelids demands that males engage in extensive movements in search of females. Robitaille and Baron (1987) suggest that reproductive behaviour is the dominant activity-generating behaviour of male ermine in midsummer. Female activity is lowest during pregnancy (Gerell 1969; Leonard 1980) and appears to increase, at least in fishers, after parturition (Paragi et al. 1994) and with the age of the kits (Leonard 1980). Amount or intensity of motor activity is not affected by estrous condition or by the administration of estradiol in domestic ferrets (Stockman et al. 1985; Donovan 1987), contrary to the stimulating effect of estrogen on activity in female rats (Blizard 1983). The late winter activity in captive and wild *Martes martes,* previously referred to as `false heat', may instead represent late dispersal of overwintering juveniles (Helldin and Lindström 1995).

The lack of complex social structure in the Mustelinae, compared with some of the viverrids for example, may account in part for the fact that no small mustelids are diurnal. The most social species of viverrids, *Mungo mungo, Helogale parvula,* and *Suricatta suricatta,* are all diurnal (Hinton and Dunn 1967; Rood 1975; Waser 1981; Palomares and Delibes, Chap. 6). Whether diurnalism facilitates the evolution of complex social behaviour, is a consequence of it, or is unrelated, is unknown. However, in an analysis of the correlation between activity pattern and type of social system, 14 of 19 (73.7%) of the social species in the Carnivora were primarily diurnal (Zielinski, unpubl. data).
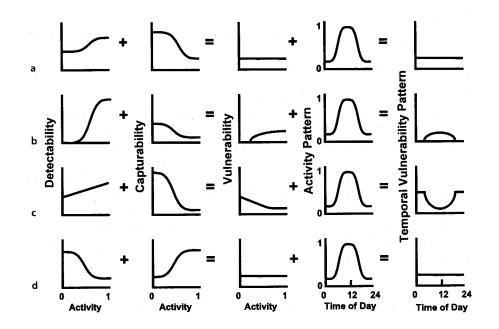
5.3.7 Prey Availability

Foods are distributed patchily in space and time, but the analysis of predator response to spatial variation in food has received considerably more attention than analysis of daily temporal variance in food availability. Predators experience a foraging problem that herbivores do not; their foods are differentially active, and thus differentially available throughout the 24-h period. It is a logical extension of foraging theory to suggest that predators that hunt at the time of day when the probability of prey capture is highest should enjoy greater prey capture success, and at lower cost, than individuals that initiate foraging at random. Although this area has received only modest theoretical consideration (Schoener 1974; Caraco 1980; Williams and Nichols 1984; Zielinski 1986a; Belovsky et al. 1989), empirical evidence of the phenomenon is growing.

In theory, predators should synchronise their activity with the time of day when their prey are most vulnerable. This may be when prey are active, and are producing visual and auditory cues that betray their location, or when prey are resting when they may be more difficult to locate but are easier to catch and subdue (Zielinski 1986a). Two prey species can have the same activity patterns but if they have different detectability and capturability functions (e.g. one rests in inaccessible, and the other in accessible, refugia) each can be most vulnerable to a predator at a different time of day. Whether car-

nivores should forage when prey are active or inactive will depend on the trade-off among these factors. A graphical illustration of the interaction between activity time, detectability, capturability and vulnerability is presented in Fig. 5.2. Prey populations that have the same activity pattern (diurnal in Fig. 5.2) can have sufficient variety in their detectability and capturability functions that they manifest very different vulnerability functions over the 24-h day.

The most thorough studies of this problem have focused on the activity of raptors and their microtine prey (Rijnsdorp et al. 1981; Raptor Group 1982). Small mammals are only available to raptors when they are active and two species of raptors synchronised their flight time with the ultradian pattern of above-ground activity of the voles. Rijnsdorp et al. (1981) estimated that kestrels (*Falco tinnunculus*) that were active in synchrony with the ultradian rhythm of voles could experience sufficient flight-time savings (10-20 kJ per day) to contribute significantly to the number of offspring produced.

Mammalian predators and their prey have not been the subjects of similar studies but we can evaluate their foraging mode and review related literature to help understand the importance of predator-prey synchrony. Because

Fig. 5.2. Relationships between detectability, capturability, vulnerability, and time of day for four hypothetical prey species (**a-d**). **a** Detectability and capturability are increasing and decreasing functions of prey activity, respectively. Relative effects cancel and vulnerability does not vary with time of day. **b** Detectability when active is greater than capturability when inactive, thus vulnerability is greatest during prey activity. **c** Detectability when active is less than capturability when inactive, thus vulnerability is greatest during prey inactivity. **d** Detectability and capturability are decreasing and increasing functions of prey activity, respectively. Relative effects cancel and vulnerability does not vary with time of day

moving prey are easier to detect than inactive prey (Curio 1976; Norrdahl and Korpimäki 1998) predators that hunt primarily using sight and sound should forage during the active phase of their prey; so too should predators that cannot physically enter the resting refugia of their prey. In the least weasel and polecat, vision and olfaction are of equivalent importance in hunting with audition somewhat less important (Murphy 1985), and movement detection is more important than visual acuity in mink and ferrets (Apfelbach and Wester 1977; Dunstone and Sinclair 1978). Audition probably complements the other senses, especially because some small mustelids can hear ultrasound in the range of small mammal vocalisations (Heffner and Heffner 1985; Powell and Zielinski 1989). Thus the sensory modalities of small mustelids suggest that they might benefit from synchrony with the active phase of their prey. However, the smallest predators considered here can enter the burrows of their prey and, unlike raptors or larger predators, are able to locate prey when they are resting. Nams (1981) carefully examined the activity of radio-collared ermine in large enclosures and concluded that prey selection was independent of prey activity. Weasels killed inactive voles more frequently than active voles. Weasels, which can enter burrows and kill rodents when they are inactive, and which can change the activity patterns of their prey (Jedrzejewska and Jedrzejewski 1990), should receive less benefit from timing their foraging to coincide with the activity of their prey than the larger mustelines.

Several studies suggest that mustelids forage with knowledge of their prey's circadian rhythms of vulnerability. Gerell (1969) described the availability of prey as the most significant influence on the activity of mink. The time of maximum activity of their small mammal prey and the `evening rise' of fish coincided with the time of mink activity. Erdakov (1981) suggested that the ultradian rhythms of weasel were coincident with those of its microtine prey, even stating that the fundamental adaptation of the rhythmic cycle of the weasel is not to the LD cycle, but to the availability of its prey. Polecat activity correlated with that of their prey as well (Blandford 1987, Lode 1995). Captive mustelids exhibit increased activity prior to a daily presentation of food (Gerell 1969) even in constant illumination or dark (Zielinski 1986b). And captive mink, but not weasels, substituted diurnal for nocturnal activity when food became more available during the day, indicating that the timing of food availability was capable of producing a 180° shift in activity phase (Zielinski 1988).

Considerable speculation surrounds the functional role of activity time in American martens. In California, martens are primarily diurnal in summer and exhibit a significant increase in nocturnal and crepuscular activity during winter (Zielinski et al. 1983; Martin 1987). This shift at first appears maladaptive because temperatures during the time of peak activity during the summer and winter are above and below thermoneutrality, respectively (Worthen and Kilgore 1981; Buskirk et al. 1988). Zielinski et al. (1983) accounted for the activity change by proposing that the time of maximum vul-

nerability of summer prey was different than that for winter prey, a phenomenon also described for polecats (Lode 1995). Ground-dwelling sciurids (i.e., *Tamias, Spermophilus*) are available only during the summer and then only during the day; martens cannot access them in their burrows at night during the summer nor at all during the winter when they are hibernating. During late fall and winter the crepuscular and nocturnally-active lagomorphs,flying squirrels (*Glaucomys sabrinus*), and voles comprised most of the diet. The energetic benefits accrued to martens by tracking the diel availability of seasonally available prey apparently exceed the thermoregulatory costs for doing so. Hauptman (1979) also found that the activity of American martens in Wyoming was congruent with the activity of their primary prey.

Thompson and Colgan (1994) monitored the activity of American martens in Ontario but did not find evidence for synchrony with prey activity. Martens were arhythmic during summer and diurnal during winter; nearly opposite to that described in California. If synchrony was important martens should have been nocturnal in winter when their snowshoe hare (*Lepus americanus*) and ruffed grouse (*Bonasa umbellus*) prey were active. The authors reasoned that because winter temperatures are so much colder in Ontario than in California that the thermoregulatory benefits of winter diurnality exceeded the foraging advantage of synchrony with prey. More (1978) also believed that winter diurnality was an energy saving behaviour for American martens in Alberta.

Because meal patterning and foraging patterns are driven by different incentives we do not expect that predators will be active every day at the peak of prey activity. Time since the last meal, availability of cached food, and other short-term phenomena will produce only a general synchrony even when environmental conditions favour it. However, this does not discount the potentially large energy savings that can be gained by foraging when probability of success is greatest. Whether these gains can be realised, however, depends on the magnitude of other costs incurred, particularly thermoregulatory costs in northern climates.

5.4 Conclusions

Body size is key to understanding many behaviours (Peters 1983), including the factors that influence the amount and distribution of daily activity. Smaller herbivores spend proportionally more time active and are more nocturnal than large herbivores (Belovsky and Slade 1986); a relationship that may apply to mammalian carnivores as well. In a review of 146 species in the Carnivora, nocturnal species were significantly smaller than those that were not nocturnal, a pattern that was exhibited in the Mustelidae as well (Zielinski, unpubl. data).

The activity patterns of small mustelids, like many other aspects of their ecology, are influenced by their body size and shape and the consequences these have on energetics. Small carnivores must take small prey, need energy-rich and frequent meals, are potentially more vulnerable to predators themselves and are poorer interspecific competitors than large carnivores. The smallest mustelids should be active primarily at night because their prey are usually nocturnal and darkness provides more cover from predators and competitors than daylight. Field and laboratory evidence largely support this prediction. However, their demanding metabolism and limited gut capacity make frequent meals a necessity and some diurnal eating and foraging is necessary. Consequently, weasels have a visual system that permits adequate vison at all natural light levels.

There are fewer incentives for nocturnalism in the larger mustelines (minks, polecats, martens and fishers) and they appear to have a greater diversity of activity patterns. Their diet is not comprised exclusively of small nocturnal rodents and fewer other predators can interfere with their activities or can kill them. Although their larger sizes may make them somewhat less vulnerable to predators than the weasels, they probably experience a sufficient predator threat to find some protection by restricting most of their activity to darkness. However, because their diets change seasonally more than the diets of weasels, we should expect more flexibility in activity patterning in these species than in the smaller, microtine-dependent weasels. The limited data on marten and mink suggest that a more diverse diet and larger size free these larger mustelids from some of the constraints acting on weasels and result in more flexibility in their activity times.

Two factors appear to universally affect the activity of all mustelines; cold weather and reproductive behaviour. Cold suppresses the amount of activity during the winter, especially at night. Martens at the southern limit of their range may be an exception because milder nocturnal temperatures permit them to hunt nocturnally-active prey. During the breeding season the activity of all male mustelines appears to increase. Polygynous mating systems favour multiple matings by males and the increased activity is probably attributable to mate search and the additional foraging needed to support this behaviour.

An understanding of the factors that affect small carnivore activity patterns will require more field and laboratory studies directed toward the study of physical and biotic factors that affect activity. The knowledge of a carnivore's size may explain a considerable amount of variation in its' activity time (Bunnell and Harestad 1990) but more fieldwork on the diel regime of predator and prey behaviours (e.g. Raptor Group 1982) and laboratory work that evaluates the effect of circadian variation in food availability on activity pattern (e.g. Zielinski 1988) are both required before we will understand the roles of exogenous and endogenous factors in the expression of activity patterns. It has been a handicap to the development of the field that activity data are usually collected only incidentally to he primary objective

of a particular research study. These data are usually improperly sampled and uncritically analysed. Using the data available today it is difficult to know, for example, whether the activity patterns of two species differ in some fundamental way or whether methodological differences or unequal sample sizes account for the difference.

The metabolic costs of being small, long and thin are high. Elevated basal metabolic rate, high locomotion costs (especially in winter), and high reproductive costs are difficult to maintain without the ability to store much body fat. Weasels, martens and other small northern carnivores require other adaptations to help balance their energy equation. Reductions in activity during winter and during extreme cold and a generalised visual system that permits foraging at any time of day, are important behavioural and physiological traits that help conserve energy in small predators. The ability to identify and forage during the most vulnerable phase of their prey's activity pattern may be yet another important adaptation that reduces weasel and marten metabolic costs in northern climates.

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