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The influence of daily variation in foraging cost on the activity of small carnivores

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Abstract. The daily activity of some predators is correlated with the activity pattern of their prey. If capture efficiency varies as a function of prey activity, a predator that synchronizes its foraging activity with the time of day that prey are most vulnerable should capture more prey, and at lower cost, than a predator that initiates foraging at random. Mink, *Mustela vison*, and weasels, *M. erminea* and *M. nivalis*, were presented with an opportunity to maximize their intake in similar circumstances in the laboratory. An animal's ability to synchronize its foraging activity with the time of day when food was most available was tested. Energy costs (wheel revolutions) were varied to encourage an animal to redistribute its activity from a preferred 12-h phase of the light–dark cycle to the other phase, and then back again. The degree to which activity changed to coincide with the most economical phase was analysed for each individual, and weasels were compared to mink. The activity of six (of seven) animals shifted in response to modified foraging costs, but only two animals (both mink) approached the 180° redistribution of activity expected of an energy-maximizing forager. In general, all animals were active during a favoured phase (usually dark) of the light–dark cycle and relatively large variations in foraging cost during this cycle had only modest effects on activity.

The food of carnivores, unlike that of herbivores, often exhibits a daily cycle of activity (i.e. prey can be nocturnal, diurnal, crepuscular, or arhythmic). If capture efficiency varies as a function of prey activity, a predator that synchronizes its foraging activity with the time of day that the prey are most vulnerable should experience greater success than a predator that forages at random (Daan 1981). Indeed, the activity patterns of predators can be correlated with, and change in response to, the active period of their primary prey (Mikkola 1970; Schuh et al. 1971; Erdakov 1981; Rijnsdorp et al. 1981; Estes et al. 1982; Raptor Group 1982; Zielinski et al. 1983). Prey are easier to detect when active (Fox 1969; Eisenberg & Leyhausen 1972; Rasa 1973; Kaufman 1974; Curio 1976; Davies 1976; Davies & Green 1976), so it is possible that synchronizing predator activity with prey activity could reduce search costs. However, prey are easier to capture and subdue if detected while resting, so synchronizing predator activity with prey inactivity could reduce capture costs. Regardless of the reason, if foraging costs change as a function of prey activity, foraging theory (Pyke et al. 1977; Pyke 1984) suggests that predators should distribute their activity patterns to maximize net foraging benefit.

Because carnivore activity is flexible enough to respond to changing within-day availability of food, as well as other factors, it is not surprising that the activity pattern of a species differs from study to study. The mustelids are a case in point. Least weasels, *Mustela nivalis*, have been reported as exclusively nocturnal in the laboratory (Kavanau 1969; Erdakov 1981) but diurnal during a field study (King 1975). The activity of short-tailed weasels, *M. erminea*, in the wild has been described as nocturnal during winter and diurnal during summer (Baumler 1973; Erlinge 1980; Debrot et al. 1985) and mostly diurnal (Erlinge & Widen 1975). Mink (*M. vison*) are primarily nocturnal in the wild and the laboratory, but diurnal activity can be common (Gerell 1969; Melquist et al. 1981; Zielinski 1986). The activity rhythms of some mustelid predators appear to be correlated with feeding opportunities in the field (Gerell 1969; Zielinski et al. 1983) and captive mustelids exhibit increased activity prior to a daily presentation of food, even in constant illumination or dark (Zielinski 1986). However, the responses of these animals to within-day variation in foraging cost has not been studied directly.

I tested mink and weasels in laboratory environments where foraging cost varied with the time of day and level of illumination. Animals were encouraged to redistribute their activity from a

preferred 12-h phase of the light–dark cycle to the other phase when the foraging cost in the former was increased. The disparity in costs necessary to induce a change measured the influence that diel variation in foraging cost had on circadian rhythms primarily influenced by the light cycle. Fixed-ratio operant schedules (Ferster & Skinner 1957) that varied with the light cycle were used to establish diel variation in foraging cost. These schedules simulated the variation in foraging costs thought to occur in nature as predators hunt prey that exhibit a daily cycle of availability.

METHODS

Animals and Test Chambers

Three female mink and four male weasels (one least and three short-tailed) were used in the experiment. The mink were ranch animals purchased from Vail's Fur Farm (Crystal Lake, Illinois, 60014) and were approximately 1·5 years old when the experiment began. All short-tailed weasels were captive-born at the Minnesota Zoological Gardens to wild-caught females and were at least 10 months old at the beginning of the experiment. The least weasel was wild-caught in Illinois and acquired through the Department of Ecology, Ethology and Evolution at the University of Illinois, Champaign. When not involved in experiments, the animals were housed in wire-mesh cages in a building exposed to outdoor ambient temperature and photoperiod.

During the experiment each animal lived in a wire cage within a light-tight wooden box that served as an operant conditioning chamber. The weasels were housed in a smaller chamber ($76{\cdot}2 \times 43{\cdot}2 \times 38{\cdot}1$ cm) than the mink ($91{\cdot}4 \times 55{\cdot}9 \times 38{\cdot}1$ cm). The wire cage was suspended 6 cm above an aluminium tray filled with cat litter to collect the urine and faeces. Air was circulated through two light-proof vents by the action of a small exhaust fan. Lighting was provided by two small incandescent bulbs (Sylvania No. 1819) that provided an average illumination of 13 lux and 6 lux in the weasel and mink chambers, respectively. The light:dark cycle was 12:12 h with lights off at 1500 hours Eastern Standard Time. Ambient temperature was relatively constant at 20 ± 1°C. Both cages contained running wheels constructed of 9-mm hardware cloth, and in the weasel chamber the wheel was also covered with window screen. Mink and weasel chambers had running wheels that were 39·2 cm and 30·6 cm in diameter respectively. Water was provided ad libitum.

Food delivery was contingent upon wheel running. The animals earned canned cat food (Zupreme, Riviana Foods, Topeka, Kansas 66601) in pellets of 2–4 g (weasels) or 6–8 g (mink). The pellets were arranged around the circumference of a large funnel located on top of the chamber. Each pellet was placed between the funnel lip and one of 24 small, 24-V DC solenoids (Universal Manufacturing Corporation, Paterson, NJ 07509) which propelled the food into the funnel after a required number of wheel revolutions. Operation of each solenoid was controlled by a Predetermining Counter and Stepper (Gerbrands Corporation, Arlington, Massachusetts 02174) that interfaced with a wheel-operated microswitch. Earned pellets travelled from the funnel, down a plastic tube and into an aluminium tray on the cage floor. The food was lightly coated with corn meal to prevent adherence to the equipment.

Continuous locomotor activity was recorded by signals sent from a microswitch operated by the wheel to an Esterline-Angus event recorder. This record was cut into 24-h strips which were pasted one below the other to produce an actogram for each individual. In addition, the number of revolutions executed and reinforcements earned (pellets) were tallied for 2-h intervals on 24-V DC electromagnetic counters (Gerbrands Corporation). All of the schedule-control and recording equipment was located outside the experimental room. The information from the counters was recorded at the time of lights off, after which the equipment was reset. The food dispenser was usually refilled at this time, but occasionally it was refilled more or less frequently, as an animal's running behaviour varied.

Experimental Protocol

Each animal was trained to associate wheel running with food delivery by gradually increasing the number of revolutions required per pellet from one up to a baseline value. The number of revolutions per pellet and the food pellet weight that generated this baseline value were not the same for all individuals. Since weasels and mink will run on wheels without being rewarded (Zielinski 1986), the number of revolutions had to be set above the

number of revolutions that would be run spontaneously. Consequently, a combination of the number of revolutions per pellet and pellet weight values was selected for each animal that could keep it adequately fed without exhausting the food dispenser.

After a baseline combination of the number of revolutions per pellet and pellet weight was established, each animal was subjected to a sequence of four test periods. During period 1, the number of revolutions per pellet was maintained at an individual animal's baseline value (250–550 for mink, and 550–1500 for weasels) for both lights on and lights off. This was continued until a preference for either nocturnal or diurnal activity was illustrated. Preference was determined by inspection when an activity pattern was obvious and by statistical evaluation of wheel revolution distribution in the rare case when preference was not obvious. Then in period 2, the costs (number of revolutions per pellet) were increased during the 12-h phase of the light–dark cycle during which the animal preferred to run (Preferred phase) while costs in the Non-preferred phase remained at baseline. At first, the number of revolutions per pellet were increased by 100 to 500 revolutions per pellet per day or on some occasions every 2 days. However, after realizing that the greatest effects were generated with larger, less frequent step-wise increments, the number of increases in costs were decreased and their magnitude increased. The animals appeared insensitive to small, daily increases and many such increases prolonged the experiment without enhancing the results.

After approximately 3 weeks of period 2, the diurnal and nocturnal costs were held at their most disparate values for 1–3 weeks (period 3). The difference between nocturnal and diurnal costs in period 3 varied from 6·0-fold to 12·6-fold among individuals since costs were increased only to the point where an animal's intake fell to approximately 75% of its ad libitum daily intake (measured in an earlier experiment, Zielinski 1986). I did not monitor body weight as an index of food stress because the handling and disturbance necessary for weighing can profoundly influence activity (personal observation). During period 4 the conditions were returned to those of period 1 where the number of revolutions per pellet was equal for night and day. This occurred in all experiments except when weasel 02 and mink 04 were involved, where the experiment was terminated at the end of period 3 due to equipment failure.

Most of the animals (four of seven) were tested during their non-reproductive season. Two of the weasels (14 and 18) and one mink (01) were tested during the late spring to early summer period when they may be found breeding in the wild (Jackson 1961). In addition, while oestradiol can increase activity in rats (Gerall et al. 1973) it has no effect on the locomotor activity of female ferrets, *Mustela furo* (Stockman et al. 1985), and therefore, even if reproductive hormones varied during the experiment I assumed that they had little influence on activity.

Analyses

During the course of the experiment, I sought evidence for a shift in an animal's activity from its preferred 12-h phase of the light–dark cycle to the other 12-h phase. If a shift occurred, the difference between the nocturnal and diurnal costs at the time indicated the disparity necessary to induce a change. If a shift did not occur, and period 3 was ended because an animal's daily intake fell below 75% ad libitum, the difference in costs measured an animal's reluctance to be active during a non-preferred light level.

Mean daily values of reinforcements earned and wheel revolutions executed were determined for periods 1, 3 and 4 for each animal. Comparisons made between periods 1 and 3 measured activity and pellet delivery differences when foraging costs were very different. Comparisons made between periods 1 and 4 determined whether an animal's activity returned to its original pattern after the treatment was applied in period 3. Mean values were compared using *t*-tests which were corrected for autocorrelation (Durbin & Watson 1951). Proportions were arcsine transformed for analysis (Sokal & Rohlf 1981).

RESULTS

All animals except mink 04 and weasel 17 demonstrated a strong preference for being active during darkness (Figs 1 and 2; Table I). Mink 04 overwhelmingly preferred the light phase, but weasel 17 showed no preference so the light phase was arbitrarily chosen as its Preferred phase.

The distribution of activity of all animals (except weasel 17) changed in response to the experimental

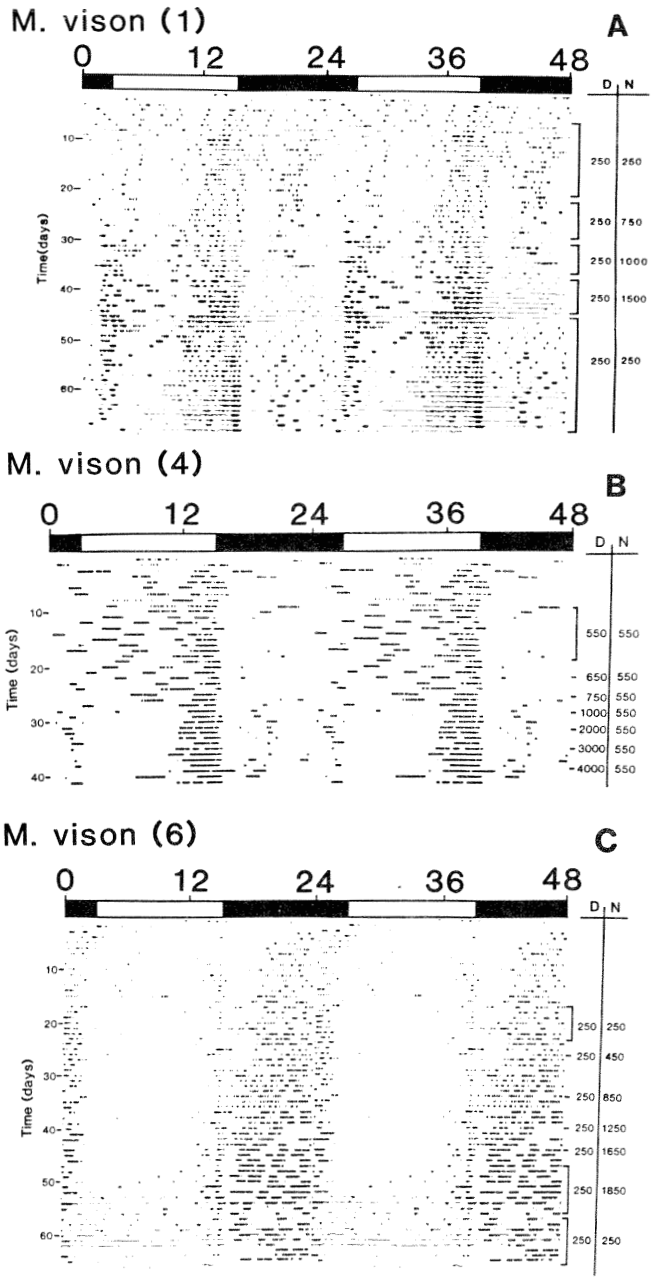

Figure 1. Mink activity actograms. A, B and C represent different animals. The data are double-plotted for continuity and the alternating light and dark bars along the top indicate the diurnal and nocturnal periods. Numbers along the right margin indicate the revolutions required per pellet during the diurnal (D) and nocturnal (N) phases of the light cycle.

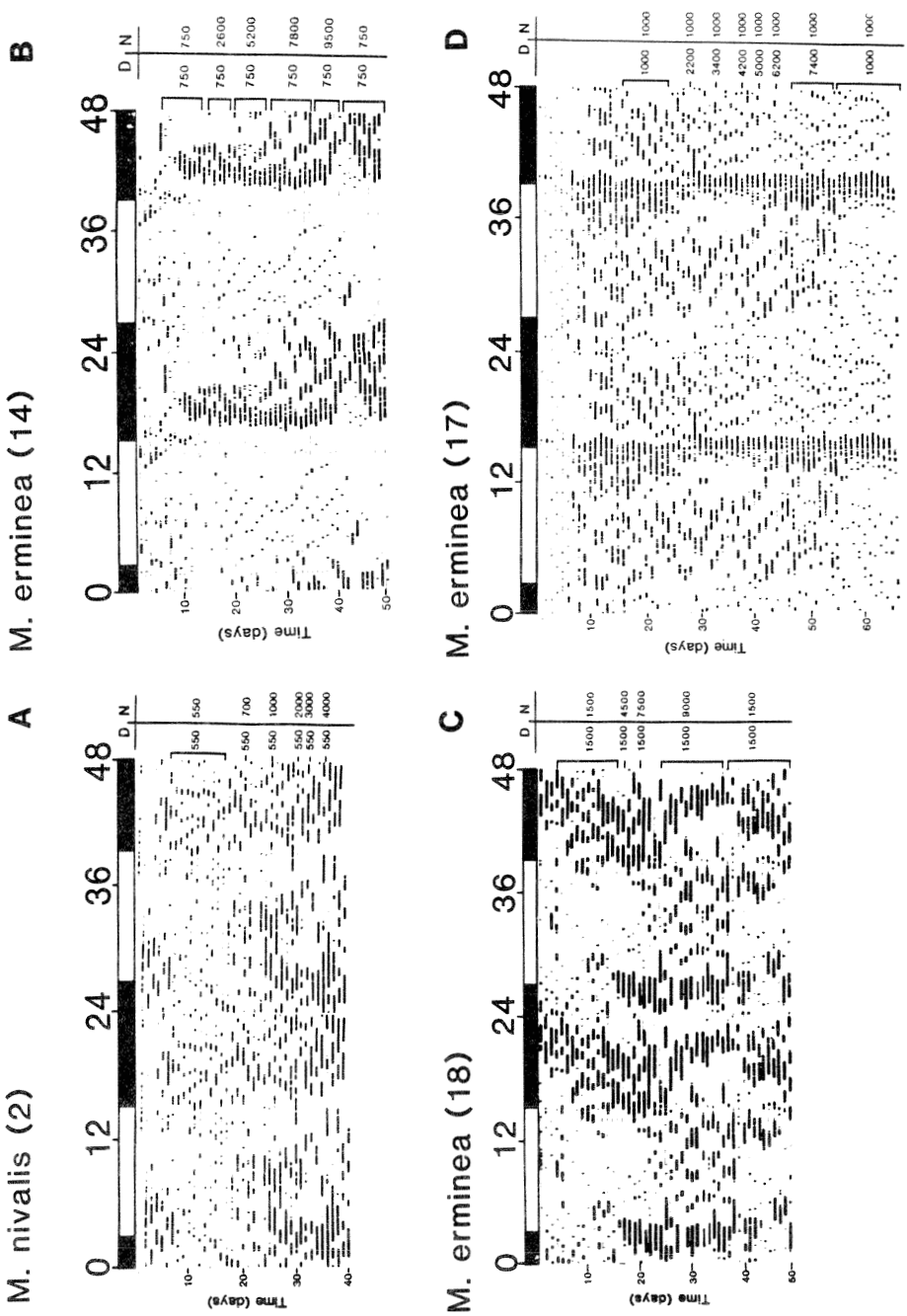

Figure 2. Weasel activity actograms. A, B, C and D represent different animals. See Fig. 1 for details.

Table I. Mean number of reinforcements (pellets) earned per day during periods 1, 3 and 4 for each animal's Non-preferred and Preferred phase

Animal	Period 1	Period 3	Period 4
Non-preferred phase			
M01	3·7	11·0*	0·6*
M04	3·1	9·6*	—
M06	0·4	4·4*	1·1
W02	4·8	25·0*	—
W14	1·1	3·4*	2·1
W17	12·1	11·6	10·2
W18	2·2	11·8*	3·6
Preferred phase			
M01	4·3	2·4*	7·9*
M04	16·1	1·2*	—
M06	22·0	4·7*	21·0
W02	16·7	7·6*	—
W14	9·4	2·8*	36·3*
W17	12·1	1·4*	4·4*
W18	13·6	2·5*	11·3

* Significantly different ($P<0·05$) from period 1; t-test corrected for autocorrelation (Durbin & Watson 1951).

Table II. Mean number of wheel revolutions run per day during periods 1, 3 and 4 for each animal's Non-preferred and Preferred phase

Animal	Period 1	Period 3	Period 4
Non-preferred phase			
M01	939·1	2865·8*	1505·3*
M04	2980·3	5293·2*	—
M06	189·7	1127·9*	332·6
W02	2777·3	14001·9*	—
W14	1138·2	2641·3*	1761·1
W17	12757·3	11448·1	10263·0*
W18	3871·3	18042·8*	6071·8
Preferred phase			
M01	1189·9	606·4*†	2001·7*
M04	8954·3	6626·4*†	—
M06	4731·7	9832·9*‡	5178·0
W02	9314·3	28333·3*‡	—
W14	7569·1	25907·3*‡	27357·2*
W17	12871·0	13643·2	4887·5*
W18	19092·2	25004·7*‡	18510·4

* Significantly different ($P<0·05$) from period 1; t-test corrected for autocorrelation (Durbin & Watson 1951).
† Significantly less than period 1.
‡ Significantly greater than period 1.

treatment. The change in activity was measured by several criteria. The animals earned more food pellets in their Non-preferred phase (Table I), earned fewer pellets in their Preferred phases (Table I), and ran more in their Non-preferred phase (Table II) when period-3 and period-1 values were compared. However, satisfying these three criteria indicate only a statistical shift in activity, not a complete switch from one phase of the light cycle to the other. Most animals did not alter their modal activity time (Figs 1 and 2), and when costs in the Preferred phase were increased they seemed to run only enough in their Non-preferred phase to satisfy their immediate hunger.

However, two of three mink satisfied criteria that suggested a more complete activity switch. For these animals most activity in the Preferred phase was abandoned in favour of easier foraging in the Non-preferred phase. Mink 01 and 04 not only increased wheel running in their Non-preferred Phase but also decreased activity in their Preferred phase during period 3 (Table II). This indicates that they not only expanded their active phase to include the Non-preferred phase but correspondingly decreased activity during the time of day they had previously preferred to run. Mink 01 was the only animal to respond with a complete statistical switch: the ratio of its total daily wheel revolutions executed per food pellet earned did not change when period 1 was compared with period 3 (Table III, Fig. 1A). This ratio is a measure of the ability of an animal to maintain the same energetic foraging efficiency in period 3 as was demonstrated in period 1 and is perhaps the most stringent criteria by which to measure an animal's activity switch.

Table III. Mean ratio of total revolutions/total reinforcements per day for periods 1, 3 and 4

Animal	Period 1	Period 3	Period 4
M01	271·2	259·8	470·2*
M04	624·0	1151·6*	—
M06	232·7	1290·1*	261·2
W02	565·4	1313·6*	—
W14	832·5	4676·2*	755·2
W17	1063·8	1921·8*	1045·3
W18	1450·1	2729·2*	1758·2

* Significantly different ($P<0·05$) from period 1; t-test corrected for autocorrelation (Durbin & Watson 1951).

No weasel satisfied the last two criteria, perhaps indicating that they have less flexible activity patterns than do mink. This apparent difference

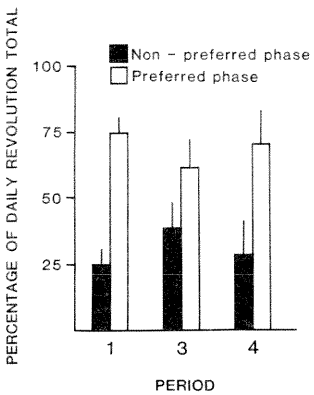

Figure 3. Mean percentage of daily wheel revolution total run in Preferred and Non-preferred phases for all animals. Period 1 is compared with periods 3 and 4. Vertical line indicates 1 SE.

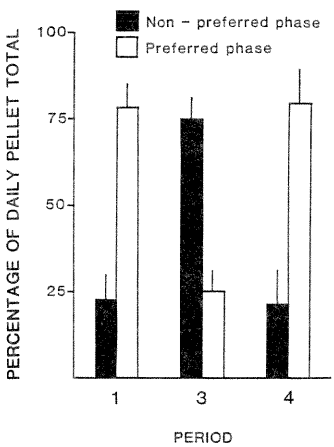

Figure 4. Mean percentage of daily pellet total obtained within the Preferred and Non-preferred phases for all animals. Period 1 is compared with periods 3 and 4. Vertical line indicates 1 SE.

between weasels and mink was not due to any difference in the disparity between the costs in their Preferred and Non-preferred phases because the average ratio of costs in period 3 was actually higher for weasels (8·7) than for mink (7·1). Thus, even though the experimental conditions were more favourable for a switch to occur in weasels, it did not.

Despite the apparent flexibility in several mink, it is important to note that, like all other animals tested, they basically maintained a modal activity peak at the same time of day throughout the entire experiment (Fig. 1). This pattern of general inflexibility in activity is especially apparent when data from all animals are pooled. The absence of a 180° switch in activity pattern for most animals is clear when the percentage of total revolutions is analysed for each phase (Fig. 3). Although the mean percentage of revolutions in the Non-preferred phase was higher in period 3 than period 1, the change was not significant ($t=2{\cdot}27$, $P=0{\cdot}064$, $N=7$). However, the percentage of daily total food pellets earned during the Non-preferred phase increased significantly during period 3 compared with period 1 ($t=9{\cdot}79$, $P<0{\cdot}05$, $N=7$; Fig. 4), but this was expected given the difficulty of earning pellets during the Preferred phase in period 3.

For both reinforcements and revolutions, period-4 and period-1 values were indistinguishable for the Preferred phase and Non-preferred phase (Figs 3 and 4). This provides evidence that any changes in behaviour seen during period 3 were due to differences in foraging costs and were not an artefact of other, uncontrolled experimental conditions.

All of the animals that did not demonstrate a switch (the weasels and mink 06; Table II Preferred phase, Table III) responded to increasing costs during period 2 in a characteristic manner. This pattern is best illustrated by the behaviour of weasel 14 (Fig. 2B). As period 2 began, the first response of these animals was to increase the intensity of their running during the time of day they originally preferred to be active. The running rate (normally about 100 and 50 revolutions per min for weasels and mink respectively) increased when food was not being delivered on the schedule to which an animal had become accustomed (personal observation). After several days to a week of this behaviour, the duration of activity began to increase but activity remained within the Preferred phase. This resulted in an increase in total hours of activity, but because activity remained restricted to the Preferred phase, food was still earned with great difficulty. Finally, the activity distribution began, perhaps by chance, to include a portion of the Non-preferred phase. At this point most of the weasels and mink 06 did not continue to switch, but merely maintained this pattern until conditions returned to baseline in period 4.

The animals that exhibited the most complete switch (mink 01 and 04) responded differently

(Fig. 1A, B). Shortly after the beginning of period 2 these animals began to abandon portions of their Preferred phase. For these animals the switch began when the ratio of costs (Preferred phase/Non-preferred phase) was approximately 3·0 and 1·5 respectively.

DISCUSSION

The activity distribution of six of seven animals shifted in response to changing diel foraging costs. However, only in two mink did the activity pattern switch enough for the increase of activity in the Non-preferred phase to be compensated for by a decrease in activity in the Preferred phase. The activity shifts probably occurred as a result of hunger-induced activity expansion. As noted earlier, an animal's typical response when failing to receive food during its Preferred phase was to increase its running rate during that phase and then increase its running bout length or frequency. This change effectively distributed an animal's activity over a larger portion of the 24-h day than in period 1. Price (1971) also demonstrated that wheel running increased in response to food deprivation in least weasels. As a result of activity expansion, the mink probably began to run enough during their Non-preferred phase to learn that food was now more available in this phase than their original Preferred phase. This explanation is more parsimonious than assuming that an animal could detect foraging costs a priori, via sampling, and then decide upon the optimal time of day to forage.

Given the extremely high energy requirement of weasels (Brown & Lasiewski 1972) and the benefits that would accrue to them if they switched, it is puzzling that the weasels did not show a more complete activity switch. All but one weasel originally preferred the dark phase of the illuminance cycle (the exception showed no preference), but illuminance in the light phase should not have inhibited activity. The illuminance level used was within the range considered most stimulatory for long-tailed weasels (Kavanau & Ramos 1975). In fact, total darkness inhibited activity in these same weasels. Kavanau (1969) found that least weasels were entirely nocturnal, but the dark phase in the experiment was slightly illuminated. It does not seem likely that the weasels in the present experiment would avoid the light phase on the basis of illuminance level alone.

Because two of three mink showed evidence of switching, and the switch occurred at a cost disparity lower than that used for any weasel, the mink appeared more sensitive to the experimental conditions. It could be argued that the differences are sexual since the mink were female and the weasels were male, but the majority of animals were tested during their non-reproductive season, minimizing differences in activity that could be due to the effects of reproductive hormones. The interspecific differences in plasticity may instead have an ecological basis. The mink diet in the wild is extremely diverse; it includes mammals, birds, amphibians, crustaceans, insects and plant material (Hamilton 1936; Cowan & Reilly 1973; Eberhardt & Sargeant 1975). Conversely, weasels are specialists on vole species (Day 1968; Simms 1979; Erlinge 1981) which are largely nocturnal or crepuscular (Davis 1936; Erkinaro 1961; Herman 1977). Generalists that forage on a diverse prey base probably experience a complex milieu of daily periods of vulnerability of their prey (e.g. prey exhibit a variety of activity rhythms and are differentially vulnerable at different phases of their rhythm). Flexibility in activity would thus be more beneficial to generalists then specialists. A specialist that has evolved dependence on one or a few similar prey species, each of which are most vulnerable at the same phase of the light–dark cycle, does not experience much unpredictable variation in prey availability. If change occurs, it is seasonal and therefore expected, or occurs over evolutionary time. Because weasels are inseparably linked to the largely nocturnal voles as food, they would not be likely to shift activity from a phase of the light cycle that has been associated with prey vulnerability over evolutionary time. Historical predation by diurnal raptors on weasels (Craighead & Craighead 1956; Powell 1982) may also have contributed to the weasels' reluctance to be active during the light phase. Perhaps the absolute level of illumination in each 12-h phase is unimportant and the weasels restricted their activity to the relatively darker of the two choices because darkness is usually associated with prey and with cover from predation.

Alternatively, the general lack of flexibility in the mustelids tested may be because the foraging environment in the operant chamber did not provide enough cues for some of the animals to learn about changing foraging conditions. During period 1 the revolutions per pellet remained con-

stant and similar for day and night long enough for most animals to anticipate pellet delivery. Typically, an animal would run continuously at first, and then as the target number of revolutions approached would jump off the wheel and check the delivery tube more and more frequently. However, during the course of period 2, the revolutions per pellet were increased frequently, preventing the animals from acquiring a sense of the running time (or effort) necessary to earn a pellet. If conditions change frequently the animals become aware that food delivery is imminent only when the solenoid is activated. Perhaps an animal's activity pattern would be more flexible if more cues about the availability of food were available. Reinforcement of a foraging behaviour in the wild may occur via several related stimuli. Foraging consists of a chain of stimuli and responses, each leading to the next, until food is consumed (Collier et al. 1972). Prey capture may be the strongest cue that predators use to learn vulnerable times but they can also learn about prey behaviour through unsuccessful capture attempts and observations. Pellet delivery is functionally analogous to the last event in the chain and was the only pre-capture stimulus available to the weasels in this experiment. Intermediate responses, especially those late in the chain, may tell the animal nearly as much as obtaining food because they provide more information than obtaining nothing at all (Cherfas 1980). Future experiments should provide more meal-associated cues.

In conclusion, the majority of animals did not behave as optimal foragers. The majority constrained their activity to the least economical, but darkest, of the two 12-h illumination phases. This occurred at an obvious energy cost in the laboratory situation presented here, but whether this would occur in analogous situations in the wild is unknown. Even if this response occurred in the wild the cost incurred may be negated by other savings. It is clear from previous work that it is shortsighted to describe one behavioural response as suboptimal without considering other fitness inputs (Krebs et al. 1978; Milinski & Heller 1978; Westoby 1978; Sih 1980; Crowder & Magnuson 1983; Mangel & Clark 1986) or time scale (Katz 1974; Staddon et al. 1981). Certainly, the weasels would have been more efficient foragers if they had shifted all their activity into their Non-preferred phase during period 3. However, this behaviour in the wild may not be without risk. Unless diel variation in food availability is great, synchrony with peaks in prey vulnerability may cost the weasels more in terms of predatory risk or lost synchrony with conspecifics of the opposite sex than they can gain. Fitness is influenced by a lifetime of events, of which net foraging gain may not always be the most important. The experiments presented here indicate that small carnivores can be sensitive to within-day variation in foraging cost, but it is not the only criterion that influences activity patterns.

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