

## Vigilance as a benefit of intermittent locomotion in small mammals

ANDREW G. McADAM & DONALD L. KRAMER

Department of Biology, McGill University

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**Abstract.** In many animal species, locomotion is frequently interrupted by brief pauses. This intermittent locomotion is usually considered a mode of prey search, but other possible functions include reduced detection or attack by predators and improved endurance. We tested the hypothesis that pauses also serve to improve vigilance for predators in two species of sciurid rodent. Videotaping animals travelling between food-collecting and food-hoarding sites revealed that numerous short pauses comprise 5–38% of the time spent 'moving' in grey squirrels, *Sciurus carolinensis*, and 0–41% in eastern chipmunks, *Tamias striatus*. In this situation, search for food items did not occur, and pausing did not reduce the total time spent as a moving stimulus for predators. It also appeared that speed while running was too slow and the pauses too brief to provide an endurance advantage. As predicted by the vigilance hypothesis, both species spent more time pausing when moving away from forest cover (presumably towards areas of higher risk) than when travelling back towards forest cover. In control trials within forest cover, squirrels did not differ in time pausing when approaching and leaving patches, but chipmunks paused more when approaching patches than when leaving them. We conclude that one function of pausing in squirrels is to improve anti-predator vigilance. The occurrence of pausing by chipmunks did not match a priori predictions of the vigilance hypothesis. Because it also failed to match predictions of previous alternative hypotheses, we suggest that studies are needed to examine whether the risk of attacks by conspecifics and predators is higher for chipmunks approaching than leaving food patches in forest habitat.

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Rather than moving continuously through the environment, many animals interrupt their locomotion with frequent brief pauses. Pauses increase the time required to travel a given distance and add costs of acceleration and deceleration to the energetic cost of locomotion. From an adaptationist perspective, pausing should provide benefits that outweigh these costs. One potential benefit of pausing is increased detection of prey, and this form of locomotion is often called pause-travel search, stop-and-go search or saltatory search (Andersson 1981; Gendron & Staddon 1983; O'Brien et al. 1990). Gendron & Staddon (1983) suggested that slower movement speeds improve prey detection by providing more time to scan a given visual field. They summarized indi-

rect evidence for this hypothesis in several studies reporting relatively slow speeds or long pauses by predators foraging for relatively small or cryptic prey. More direct evidence in support of this hypothesis is that human subjects searching for hidden objects in computer screen images have lower detection rates when scanning time is reduced (Gendron & Staddon 1984) and that lizards, *Lacerta vivipara*, are more likely to attack prey that appear when they are pausing than those that appear when they are moving (Avery 1993).

A second potential benefit of pausing is reduced attack rate by predators. Many predators are more likely to attack moving prey, perhaps because such prey is more easily detected or recognized (Curio 1976; Martel & Dill 1995). Motionlessness ('freezing') is therefore a widespread response by prey that detect a predator (Lima & Dill 1990) and may also provide an advantage even if predators are not detected. For pausing to provide a benefit by reducing detection or attack by predators, the total time

Correspondence: D. L. Kramer, Department of Biology, McGill University, 1205 Docteur Penfield Avenue, Montreal, Quebec H3A 1B1, Canada (email: don\_kramer@maclean.mcgill.ca). A. G. McAdam is now at the Department of Zoology, University of Western Ontario, London, Ontario N6A 5B7, Canada.

spent moving must be reduced. When animals travel a fixed distance, however, pausing increases only the duration of the trip without affecting the total amount of movement required and therefore should not be advantageous.

A third potential benefit of pausing is increased endurance. For animals moving faster than their aerobically sustainable speeds, the maximum distance run can be increased by a series of pauses (Åstrand & Rodahl 1986; Weinstein & Full 1992). These pauses appear to reduce lactate build-up by allowing more of the energy demand to be met aerobically (Åstrand & Rodahl 1986) or by permitting more of the lactate to be cleared from the muscles (Weinstein & Full 1992).

We hypothesize that pausing during locomotion improves detection of predators. Feeding animals spend as much as 60% of their time with their heads raised to scan for predators (Caraco et al. 1980; Underwood 1982), and this type of vigilance has been widely studied (Elgar 1989). The form and requirements of vigilance in moving animals seem to have been ignored, however. Pausing could assist moving animals to detect predators in several ways. Visual acuity should be greater if the visual field is stationary than if it is moving (Probst et al. 1986). If selecting a route on a complex substrate requires focusing on nearby objects, scanning more distant regions of the visual field for predators may depend upon cessation of forward movement. In tall vegetation or fallen leaves, pauses may permit listening for sounds generated by predators' movements, without the auditory interference generated by the animal's own movement. O'Brien et al. (1990) proposed that vigilance for predators in saltatory searchers would take place during the moving phase because of the conflict between scanning for prey and scanning for predators. If motion interferes with visual perception, however, both types of scanning may be more effective during pauses.

The purpose of the present study was to document the time spent pausing during locomotion in two species of diurnal, sciurid rodents, the grey squirrel, *Sciurus carolinensis*, and the eastern chipmunk, *Tamias striatus*, and to test the hypothesis that one function of pausing is improved vigilance. We predicted that if vigilance were a function of pausing, animals would pause even when not searching for food, when pausing would not reduce the overall amount of movement, and when travelling below their aerobic limit. We

also predicted that pausing would increase in situations where more vigilance was required.

When presented with a concentrated, storable food source, both grey squirrels and chipmunks make repeated hoarding trips. Like other members of the genus *Sciurus*, grey squirrels scatter-hoard individual nuts, burying them at variable distances and directions from the patch (Vander Wall 1990). Chipmunks typically larder-hoard, carrying multiple-seed loads to their burrow (Elliott 1978; Vander Wall 1990). Although searching for seeds occurs in the patch and squirrels may search for locations in which to scatter-hoard, searching is unlikely to provide a benefit for pausing during locomotion between the patch and hoarding sites in either species. Furthermore, pausing during locomotion between a patch and hoarding sites is unlikely to reduce overall detection or attack rate by predators, because the same amount of locomotion is required to cover the distance. A more effective tactic to reduce detection would be to minimize the time spent in exposed areas and then retreat to the greater safety of dens or burrows.

Squirrels and chipmunks are forest-dwelling species. When attacked by predators, squirrels typically climb trees (Temple 1987; Dill & Houtman 1989), whereas chipmunks seek cover in holes, under logs or brush, or occasionally by climbing trees (Clarke et al. 1993; Bonenfant 1996). For both species, therefore, moving into open areas is likely to increase predation risk because of increased distance from suitable refuges. Both species adjust their foraging behaviour to their distance from trees in ways that would be expected if predation risk increased with distance from cover (e.g. squirrels: Lima & Valone 1986; Brown et al. 1992; chipmunks: Bowers & Ellis 1993; Bowers et al. 1993). For animals leaving cover, vigilance achieved by pausing would delay travel into progressively more dangerous locations while determining whether predators are in the vicinity. In contrast, for animals returning to cover, pausing would provide earlier predator detection at a cost of delaying the return to a safer environment. The vigilance hypothesis therefore predicts that squirrels and chipmunks should pause more when leaving cover to collect food from a patch in the open than when returning to the forest with food items to hoard. A parallel set of observations within forest cover controlled for other effects on pausing of movement to and from a patch.

## MATERIALS AND METHODS

We carried out the first experiment with squirrels during winter (January–March) 1995. To be certain that the observed patterns did not apply only to snow-covered ground, we carried out a second experiment with squirrels the following summer (July–August). In both experiments, we selected open patch sites in urban parks of Montreal such that a stand of mature trees was available at a distance of 15 m in at least one direction. In the same parks, we selected forest patch sites that had a relatively homogeneous distribution of mature deciduous trees with a continuous canopy. To ensure that each trial involved a different individual, sites were more than 100 m from each other, and only one trial was performed per site, except in a few cases where identifying marks ensured that different individuals were being tested.

In preparation for a trial, we identified the centre of the patch site by a tent peg and flagging tape. Two circles of 1- and 15-m radius around the centre of the patch were marked by tent pegs and thin yellow cord or by packing down snow. We positioned a video-camera at the edge of the 15-m circle. For open trials, the camera was situated on a line perpendicular to the direction of the forest; for forest trials, the camera was situated in the direction providing the least obstructed view.

To start a trial, we placed whole hazelnuts, *Corylus* sp., in the 1-m circle to attract squirrels. Once a squirrel started making regular trips, we placed 600 g of hazelnuts in the patch, and distracted potential competitors using additional patches away from the experimental area. The observer, positioned at the edge of the 15-m circle, videotaped the trial until the squirrel had completed one uninterrupted trip between the patch and refuge trees in each direction. Recorded trips to and from the patch were not necessarily sequential. To avoid including pauses that could be explained by other benefits, we excluded trips if there was a disturbance due to the approach of humans or dogs, *Canis familiaris*, if there was an aggressive interaction between the focal squirrel and a conspecific, or if the focal individual stopped within the 15-m circle to reposition the nut in its mouth, to groom, to scatter-hoard or to search for a hoarding site. Searching for a scatter-hoarding site was indicated when the squirrel's head pointed towards the substrate rather than along the horizontal plane. We completed 14 trials

in open sites and 13 trials in forest sites in the winter, and 14 trials in each type of site in the summer.

The chipmunk experiment was carried out in a deciduous forest in the public area of the McGill University Field Station at Mont St Hilaire, 35 km southeast of Montreal, during July and August 1995. We conducted 10 open and 10 forest site trials, using a design similar to that used for the squirrels. The substrate in open areas consisted of either grass or unpaved roadways. Patches consisted of 400 ml of whole sunflower, *Helianthus* sp., seeds mixed with 1500 ml of vermiculite in a tray, 38 × 15 × 4.5 cm, placed in the centre of a circle with a 0.5-m radius. The distance from forest cover to patches in open trials was reduced to 5.5 m, because it was very difficult to induce chipmunks to forage at greater distances. Because individuals could be identified unambiguously by the location of their burrows, different chipmunks were often tested at the same site. The shorter distances and individual identification permitted us to obtain five complete and undisturbed trips in each direction for each individual.

In the laboratory, a continuous running time record was superimposed on the videotaped trials using a time-date generator. We then viewed the tapes frame by frame to determine (to the nearest 0.01 s) the duration of each trip, defined as the difference between the times at which the animal's nose crossed the inner and outer circles (14 m for squirrels, 5 m for chipmunks), the number of pauses and the length of each pause. Pauses were sequences in which the animal was in the same location in successive frames. For each individual, we calculated the total and the per cent time pausing, the median pause duration and the speed while running. For squirrels, there was only one trip per individual. For chipmunks, the median pause duration was calculated from all pauses occurring during the five trips in each direction. The other measures were based on the median of the five trips. Because many of the data were not normally distributed, non-parametric tests were used, and data are presented as medians ± interquartile range (Zar 1996). The effect of travel direction was examined with the Wilcoxon signed-ranks test (Siegel 1956) using data matched by individual. We used one-tailed probabilities to test for effects of travel direction at sites in the open because we had an a priori prediction, but used two-tailed probabilities for tests at forest sites.

Our alpha level was 0.05 (readers preferring the Bonferroni correction should use an alpha of 0.01 for interpreting our results, because there are five main dependent variables in each experiment). To reduce the probability of incorrectly rejecting one or more null hypotheses as a result of multiple tests, we applied the sequential Bonferroni test (Rice 1989) to each of our experiments.

## RESULTS

Squirrels often paused while travelling to and from patches in both open and forest sites, spending 5–38% of their travel time pausing (Table I). All four feet usually remained on the ground during pauses and there were no obvious scanning movements of the head, but squirrels occasionally adopted an upright or forward-leaning posture with the front feet raised. The distribution of pause lengths was strongly skewed to the right with many pauses under 1 s and few long pauses. As predicted by the vigilance hypothesis, total time spent pausing in the open was greater for trips to the patch than for trips from the patch back to forest cover (Table I). This was true in both winter and summer experiments. Total time pausing did not differ between trips to and from the patch in forest sites. The significantly greater time pausing on trips to the patch than on trips from the patch in the open appeared to be due primarily to an increase in the number of pauses per trip. The number of pauses per trip differed significantly in both winter and summer, but median pause durations did not differ and the trends were in opposite directions. Because some squirrels did not pause, sample sizes for pause duration were reduced (winter: open;  $N=10$ , forest;  $N=9$ ; summer: open;  $N=12$ , forest;  $N=9$ ). Squirrel speeds while running ranged from about 1.3 to 1.8 m/s and were influenced by direction only in the summer when animals approaching sites in the open had a significantly lower running speed than animals heading back towards cover.

Chipmunks paused frequently under most conditions, spending up to 41% of their time motionless (Table II). Like squirrels, they usually kept all four feet on the ground during pauses and did not show head movements. The distribution of pause durations was also skewed to the right. As predicted by the vigilance hypothesis, the total time pausing was greater for trips to patches in the

open than for trips returning to the forest. Indeed, chipmunks almost never paused while heading towards cover (Table II). Unlike squirrels, however, chipmunks also paused more when approaching than when leaving patches at forest sites. In both habitats, the difference in amount of pausing appeared to be due primarily to changes in the number of pauses per trip which showed a highly significant difference in both cases. (In the open, so few chipmunks paused that statistical comparison of pause durations was not possible; in the forest, sample size was reduced to  $N=8$ .) Chipmunks' speeds while running were lower while approaching than while leaving patches in both open and forest sites (Table II). They also ran more slowly in the forest than in the open (Mann-Whitney  $U$ -tests,  $P<0.005$  for both directions). The interacting effects of running speed and per cent time pausing resulted in a nearly four-fold effect of direction and habitat on the average time for chipmunks to travel 5 m (1.98 s leaving patches in the open; 7.86 s approaching patches in the forest).

## DISCUSSION

Our observations showed that both squirrels and chipmunks pause frequently during locomotion, even when they are not searching for food. Pausing adds significantly to the travel times of foraging squirrels and chipmunks. Depending on the season, habitat and direction of movement, squirrels averaged 5–38% of their travel time motionless. Within the forest, which is their normal habitat, they averaged 13% of their time pausing. For chipmunks, pausing occupied on average 0–41% of their travel time, with a mean of 21% in their normal forest habitat. There are few other data on pause times of animals not searching for food, but Avery et al. (1987) showed that viviparous lizards spent 30% of their locomotion time in pauses that averaged well under 1 s. For squirrels and chipmunks, fitness is likely to be positively related to the rate at which they can sequester food during periods of abundance. Thus, it is unlikely that animals would repeatedly pause during foraging travel unless these interruptions provided a strong benefit.

Food search cannot explain the frequent pauses. The recording procedure in our study excluded search in the immediate vicinity of the

**Table 1.** Characteristics of intermittent locomotion by grey squirrels running to and from food patches in open and forest habitat during winter and summer observations

	Food patch in open			Food patch in forest		
	To the patch	From the patch	P (one-tailed)	To the patch	From the patch	P (two-tailed)
(a) Winter						
Number of individuals	14	14		13	13	
Total time per 14-m trip (s)	12.70 ± 3.72	8.59 ± 1.51	***	11.73 ± 4.41	11.72 ± 4.51	NS
Total time pausing (s)	4.51 ± 3.35	0.56 ± 0.51	***	2.69 ± 2.89	1.40 ± 1.39	NS
Number of pauses per trip	3.5 ± 1.5	1.0 ± 1.0	***	2.0 ± 1.5	4.0 ± 2.3	NS
Median pause duration (s)	0.59 ± 0.65	0.44 ± 0.32	NS	0.75 ± 0.82	0.39 ± 0.21	NS
Pause time (%)	37.9 ± 14.8	6.5 ± 6.9	***	20.6 ± 14.7	12.9 ± 7.0	NS
Speed while running (m/s)	1.80 ± 0.19	1.76 ± 0.21	NS	1.47 ± 0.37	1.45 ± 0.35	NS
(b) Summer						
Number of individuals	14	14		14	14	
Total time per 14-m trip (s)	15.5 ± 5.97	12.23 ± 2.01	**	10.43 ± 1.86	11.56 ± 2.18	NS
Total time pausing (s)	5.29 ± 3.16	2.28 ± 1.45	**	0.49 ± 1.05	2.31 ± 0.87	NS
Number of pauses per trip	4.5 ± 3.5	2.0 ± 1.5	***	1.0 ± 1.0	2.0 ± 0.5	NS
Median pause duration (s)	0.46 ± 0.41	0.67 ± 0.66	NS	0.28 ± 0.68	1.40 ± 0.43	NS
Pause time (%)	35.4 ± 8.3	17.6 ± 9.4	**	5.3 ± 7.8	14.1 ± 9.0	NS
Speed while running (m/s)	1.27 ± 0.25	1.45 ± 0.14	*	1.42 ± 0.23	1.41 ± 0.32	NS

Values show medians ± quartile deviation.

Wilcoxon signed-ranks test: \* $P \leq 0.05$ ; \*\* $P \leq 0.01$ ; \*\*\* $P \leq 0.005$ .

All comparisons significant at  $P \leq 0.01$  remained significant after the sequential Bonferroni correction.

**Table II.** Characteristics of intermittent locomotion by chipmunks running to and from food patches in open and forest habitat in the summer

	Food patch in open			Food patch in forest		
	To the patch	From the patch	P (one-tailed)	To the patch	From the patch	P (two-tailed)
Number of individuals	10	10		10	10	
Total time per 5-m trip (s)	4.52 ± 1.30	1.98 ± 0.19	***	7.71 ± 2.13	3.71 ± 1.08	***
Total time pausing (s)	1.92 ± 1.07	0.00 ± 0.00	***	2.35 ± 0.34	0.46 ± 0.37	***
Number of pauses per trip	2.0 ± 0.0	0.0 ± 0.0	***	3.5 ± 1.0	1.0 ± 1.0	***
Median pause duration (s)	0.97 ± 0.41	0.00 ± 0.00	NT	0.44 ± 0.13	0.30 ± 0.16	NS
Pause time (%)	40.9 ± 10.7	0.0 ± 0.0	***	33.9 ± 9.7	9.0 ± 9.4	***
Speed while running (m/s)	1.81 ± 0.15	2.53 ± 0.26	***	1.13 ± 0.38	1.53 ± 0.26	**

Values show medians ± quartile deviation.

Wilcoxon signed-ranks test: \* $P \leq 0.05$ ; \*\* $P \leq 0.01$ ; \*\*\* $P \leq 0.005$ .

NT: no test possible because of small number of individuals that paused.

All significant tests remained so after the sequential Bonferroni correction.

food patch. Animals farther away from patches were unlikely to be engaged in food search: animals were recorded only after they had made several visits to the patch, and their direct approach suggested that there was no uncertainty about where the food was. Furthermore, except for chipmunks in the open, animals continued to pause when they were leaving the patch and could not collect additional food items even if they discovered them. It is also unlikely that the pauses were related to searching for hoarding sites. For squirrels, the transition from travel to the general vicinity of a scatter-hoarding site to localized search for a place in which to bury a nut seemed clear. Chipmunks use the same burrow for long periods (Elliott 1978; Wishner 1982), and their direct approach to it on hoarding trips suggested that no search was required.

The frequent pausing by squirrels and chipmunks is unlikely to be explained by an advantage of reduced detection or attack rates by predators. Since the animals were making repeated trips between the sites of food availability and food storage, pausing during trips could not have reduced the total time spent in motion except by reducing the total number of trips performed. If the animals were to reduce the total number of trips, it would seem less dangerous to have spent the remaining time in safer areas rather than pausing in the course of travel. Our procedure eliminated pauses that could have been explained by animals freezing in response to obvious disturbances from humans, dogs or conspecifics. Although we cannot rule out the possibility of freezing in relation to small disturbances that we failed to recognize, it is unlikely that the numerous very short pauses could be explained in this way.

The hypothesis that pausing provides short rest periods during locomotion also fails to explain our observations. Although there are few studies of the energetics of intermittent running, short rests appear to benefit endurance only when the speed is above the aerobic maximum and when the pauses are considerably longer than those observed in the present study (Åstrand & Rodahl 1986; Weinstein & Full 1992). Running speeds of squirrels in this study averaged 1.3–1.8 m/s, which is well below their maximum speed of 8.3 m/s (Garland et al. 1988) and probably below their maximum aerobic speed. In another sciurid, the golden-mantled ground squirrel, *Spermophilus saturatus*, maximum aerobic speed (3.0 m/s) is

about half the maximum running speed (>6 m/s, Hoyt & Kenagy 1988; Kenagy & Hoyt 1989). The running speeds of chipmunks ranged from 1.1 to 2.5 m/s, generally below the maximum aerobic speed of 2.6 m/s (Seeherman et al. 1981) and well below the maximum of about 4.8 m/s (Layne & Benton 1954; Seeherman et al. 1981; Biewener 1983). Thus, squirrels and chipmunks pause frequently during locomotion in situations that cannot be explained by the previous hypotheses of improved food search, reduced detection by predators or increased endurance.

The difference in pausing behaviour of squirrels and chipmunks going to and from patches in the open is consistent with the hypothesis that one function of pause-travel locomotion is vigilance for predators. We assumed that animals moving into situations of higher risk would have higher levels of vigilance than animals returning towards safety, and both squirrels and chipmunks showed patterns of pausing that conformed to the hypothesis that this vigilance was achieved by pausing. Lima & Valone (1986) also reported longer travel times and more frequent pauses when grey squirrels were moving towards a patch in the open than when they were returning to cover. For squirrels in the summer and for chipmunks, speed while running was lower for animals leaving cover to approach patches in the open than for animals returning to cover. If vigilance is affected by running speed, animals may modulate both pausing and speed while running according to risk and the need for vigilance.

We had assumed that going to and from patches within the forest habitat would not be associated with changes in predation risk and therefore used this as a control for other effects of movement direction on pausing behaviour. Squirrels did not show a significant effect of travel direction on pause time in the forest, and the trends were in the opposite direction in summer and winter. However, chipmunks showed almost as much difference in pausing between trips to and from the patch in the forest as they did in the open. This result implies that the difference in pausing between trips to and from the patch in the open is not a response to a difference in the benefits of vigilance or that there is some danger associated with approaching patches in both open and forest that can be reduced by increased vigilance. One possible benefit of vigilance would be to reduce the risk of attack from conspecifics

already at the patch. Chipmunks at a feeding patch often freeze upon detecting an approaching conspecific, then suddenly initiate a chase (Elliott 1978; A. G. McAdam & D. L. Kramer, personal observations). A motionless chipmunk is difficult for humans to detect and may be so for chipmunks. Another possibility is that if chipmunks survey the area for predators while approaching the patch and while collecting a load, a predator would be unlikely to get close enough to pose a serious threat as the animal traverses the first 5 m while leaving the patch. Additional studies are therefore required to examine the extent to which pause-travel locomotion can be explained by the vigilance hypothesis in chipmunks.

In studies of both vigilance and locomotion, investigators have tended to ignore the problem of watching for predators while moving. Direct tests of the effect of movement on the detection of visual and auditory stimuli are needed. Reduced ability to detect predators as a result of movement is an additional mechanism for the fundamental trade-off between foraging activity and survival proposed by Werner & Anholt (1993). Conflicts between vigilance and locomotion could help to explain animal movement patterns. The most appropriate anti-predator tactics for animals that are moving are not necessarily the same as those for animals that are feeding or preening as in the majority of previous investigations of vigilance. For example, pausing may increase in unfamiliar locations or visually complex habitats and decrease with repeated experience of the same area. Pauses may occur close to refuges and before crossing high-risk areas. Routes may be selected for their visual advantage or for their ability to reveal stalking predators (Underwood 1982). Recognizing pauses as a form of vigilance should facilitate the development and testing of such hypotheses.

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