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Vigilance as a benefit of intermittent locomotion in small mammals

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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.

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 indirect 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

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