

## The Behavioral Ecology of Intermittent Locomotion<sup>1</sup>

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**SYNOPSIS.** Most physiological and ecological approaches to animal locomotion are based on steady state assumptions, yet movements of many animals are interspersed with pauses lasting from milliseconds to minutes. Thus, pauses, along with changes in the duration and speed of moves, form part of a dynamic system of intermittent locomotion by which animals adjust their locomotor behavior to changing circumstances. Intermittent locomotion occurs in a wide array of organisms from protozoans to mammals. It is found in aerial, aquatic and terrestrial locomotion and in many behavioral contexts including search and pursuit of prey, mate search, escape from predators, habitat assessment and general travel. In our survey, animals exhibiting intermittent locomotion paused on average nearly 50% of their locomotion time (range 6–94%). Although intermittent locomotion is usually expected to increase energetic costs as a result of additional expenditure for acceleration and deceleration, a variety of energetic benefits can arise when forward movement continues during pauses. Endurance also can be improved by partial recovery from fatigue during pauses. Perceptual benefits can arise because pauses increase the capacity of the sensory systems to detect relevant stimuli. Several processes, including velocity blur, relative motion detection, foveation, attention and interference between sensory systems are probably involved. In animals that do not pause, alternative mechanisms for stabilizing the perceptual field are often present. Because movement is an important cue for stimulus detection, pauses can also reduce unwanted detection by an organism's predators or prey. Several models have attempted to integrate energetic and perceptual processes, but many challenges remain. Future advances will require improved quantification of the effects of speed on perception.

### INTRODUCTION

Animal locomotion is a topic where the interests of physiologists, functional morphologists, animal behaviorists, ecologists and evolutionary biologists converge. While examining how, why and how much animals move, the majority of previous studies have focused on steady-state locomotion, implicitly assuming that most locomotion occurs at constant speeds or that the variation in speed is unimportant. Yet simply observing the animals around us reveals that moving animals often change speed or stop completely. A robin crosses

the lawn in a series of quick runs separated by motionless periods. Squirrels and chipmunks move through the forest in a similar fashion. A kestrel hovers in one spot over a meadow, then moves on, only to hover again in a new location. Among the grass blades, a cricket walks forward slowly, stops, changes direction and moves forward again. As we walk to the edge of a stream, a stickleback freezes, then darts away in a series of rapid zig-zags punctuated by brief pauses. Although individually brief, lasting only tenths of a second to a few seconds, these pauses are too widespread, too frequent, and take up too much of 'locomotion' time to be ignored.

This symposium reflects a growing interest of biologists from different areas of specialization in the phenomenon known as intermittent locomotion. This interest has extended the range of processes that we now

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recognize as being potentially affected by intermittent as opposed to continuous locomotion. Yet many researchers, while investigating some processes in detail, fail to consider others. Taking into account all relevant costs and benefits is essential to understanding why intermittent locomotion has evolved and to predicting how it will be used in the course of animals' natural activities. Our main purpose here is to provide an overview of the diverse array of processes that could cause the costs and benefits of intermittent and continuous locomotion to differ. First, we define intermittent locomotion, explore its taxonomic, ecological and behavioral distribution, and describe its quantitative diversity. Next, we review each of the mechanisms proposed to provide an advantage to intermittent locomotion. In a final section, we review attempts to develop an integrated framework for these varied mechanisms and suggest some topics for future research.

#### WHAT IS INTERMITTENT LOCOMOTION?

We refer to intermittent locomotion when the force an animal exerts to move itself through space is applied discontinuously and the pauses last longer than the non-powered phase of a single cycle of limb movement. The alternative is continuous locomotion. A terrestrial organism engaged in intermittent locomotion typically comes to a complete stop during the non-powered phase, but in air or water the animal may continue to glide forward so that motion is continuous, though variable in speed, while the application of force is intermittent. Animals supported by wind or flowing water can move with respect to solid substrate when they are not supplying power and, conversely, may require power to maintain a stable position with regard to the substrate. Changes in movement and the relationship of these changes to energy expenditure therefore depend on whether the medium or the substrate is the reference point. Intermittent locomotion does not usually include patterns resulting from changes in the type of activity, for example between search and pursuit of prey or between activity and rest. Intermittent locomotion has also been called stop-go running (Miller,

1979), stop-and-go swimming (Buskey *et al.*, 1993), pause-travel locomotion (Andersson, 1981), and saltatory search (O'Brien *et al.*, 1990).

Figure 1 and Table 1 illustrate intermittent locomotion for a variety of species, including unicellular organisms (ciliates), coelenterates, free-living cercariae of parasitic trematodes, crustaceans, insect larvae and adults, web-building spiders, cephalopods, reptiles, birds and mammals. It also occurs in salticid spiders (Jackson and van Olphen, 1992), anuran amphibians (Lock and Collett, 1979) and marine mammals (Williams *et al.*, 2000). The occurrence of both intermittently and continuously moving species and large interspecific variations in the pattern of intermittent locomotion are recognized in several taxa. These include trematode cercariae (Haas, 1994), parasitoid wasps (Vet and Bakker, 1985), salticid spiders (R. R. Jackson, personal communication), larval and adult fishes (Fuiman and Webb, 1988; O'Brien *et al.*, 1990; Coughlin *et al.*, 1992), lizards (Perry, 1999) and birds (Cody, 1968).

Intermittent locomotion occurs in terrestrial, aquatic and aerial locomotion. Many examples come from food search or unspecified general locomotion, but there are also cases of directed travel toward food hoarding sites (Table 1, 20, 21A), active pursuit of prey (Table 1, 10, 16C; Fig. 1A, B), oriented movement toward potential mates (Table 1, 9B), and habitat assessment (Table 1, 5). It also occurs in water striders holding station in the current (Junger and Varjú, 1990). In viviparous lizards, Avery *et al.* (1987) observed pauses during all behavioral contexts, including general locomotion, active search and pursuit of prey, fleeing from a threatening stimulus and even 'panic' scrabbling movements of animals attempting to escape from a glass jar (Table 1, 16A–16E). In a social spider intermittent locomotion is synchronized among 20 or more individuals attacking a common prey item in the web (Table 1, 10). In diving seals and whales, extended glides occur during the deeper portions of descents (Williams *et al.*, 2000).

Average pause durations typically range from 0.1–1.0 sec, but can last as long as 50

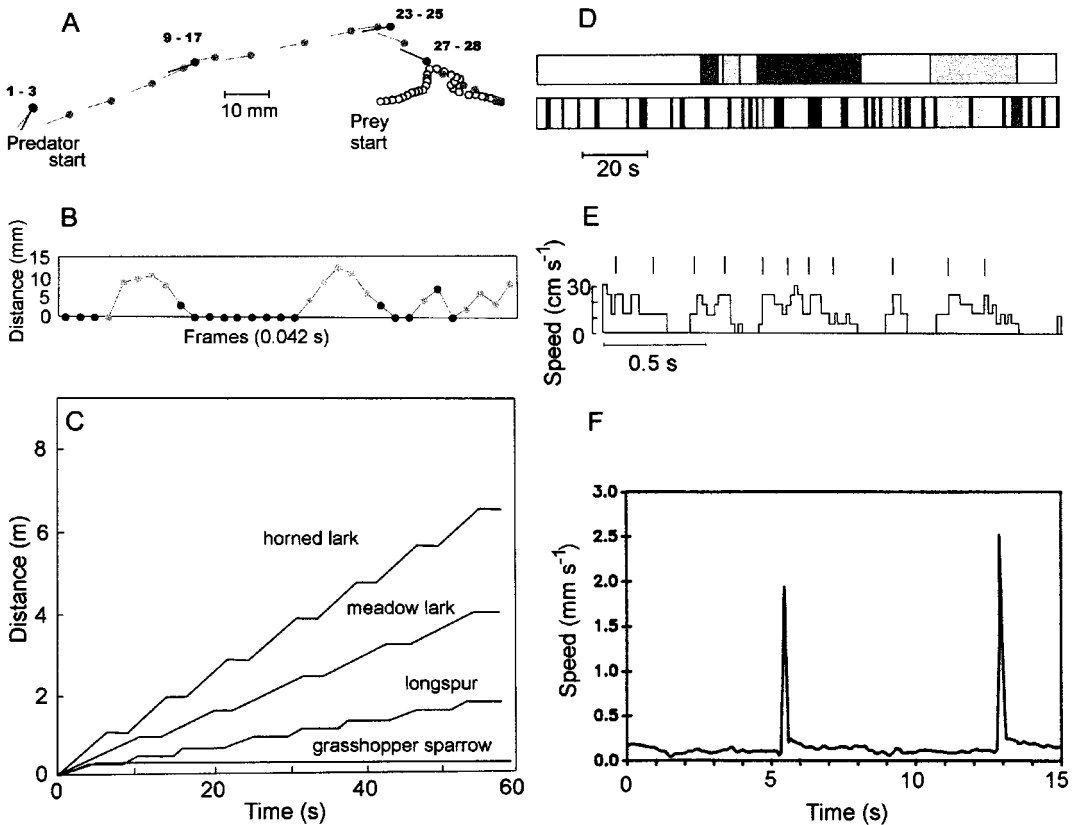


FIG. 1. Examples of intermittent locomotion, illustrating alternative approaches to graphical presentation. A. Successive spatial positions of the head (solid circles) and body axis (lines) of a tiger beetle *Cicindela repanda* pursuing a vestigial-winged fruitfly prey (open circles) in successive frames of a film exposed at 0.042 sec intervals (from Gilbert, 1997, Fig. 1a, with permission of the author and Springer-Verlag©). Solid circles indicate pauses for the frame numbers indicated. B. Distance moved between successive frames in relation to time (frame number) for the tiger beetle illustrated above (Gilbert, 1997, Fig. 1b, with permission of the author and Springer-Verlag©). C. Cumulative distance moved in relation to cumulative time observed for several grassland birds, the horned lark *Otocoris alpestris*, western meadow lark *Sturnella neglecta*, McCown's longspur *Rhynchophanes mccownii* and grasshopper sparrow *Ammodramus saviannarium* (from Cody, 1968, Fig. 2, with permission of The University of Chicago Press©). In this case, mean pause times, move times and distances were used to construct the plot, but values for each move and pause also could have been used. D. Movement speed in relation to time for ghost crabs *Ocypode quadrata* engaged in general locomotion (above) and flight from the observer (below) (from Weinstein, 1995, Fig. 5). Shading represents movement intensity from white (paused) to black (>4 strides sec<sup>-1</sup>). E. Movement speed in relation to time for a viviparous lizard *Lacerta vivipara* in general locomotion (from Avery *et al.*, 1987, Fig. 1a). Height of the bar shows average speed at 0.02 sec intervals, and the vertical line shows the cycle of leg movement by indicating the time that the right foreleg was placed on the ground. F. Movement speed in relation to time for the planktonic marine ciliate *Strobilidium spiralis* (from Buskey *et al.*, 1993, Fig. 5). Line shows average speed calculated at 0.067 sec intervals.

sec and as little as 0.04 sec. For the examples in Table 1, the mean pause duration is 6.1 sec with a median of 1.1 sec. Moves are of similar duration (Table 1, mean = 3.7 sec, median = 1.0 sec), and pause and move durations tend to be correlated (following log-transformation of the data in Table 1,  $r = 0.67$ ). Nevertheless, the percent

time paused can vary greatly among cases, from as little as 6% to as much as 96% (mean = 49.8%, median = 45%). This variation corresponds to a tremendous range in the mean frequency of moving and pausing (0.9–454 moves or pauses/min, mean = 58 moves or pauses/min, median = 22 moves or pauses/min).

TABLE 1. *Examples of intermittent locomotion in a variety of animal species and behavioral situations.*

Type of organism (Genus and species)	Activity	Pause duration <sup>1</sup> (s)	Move duration <sup>1</sup> (s)	Move/pause frequency <sup>2</sup> (No./min)	Time paused <sup>3</sup> (%)	Move speed <sup>4</sup> (cm s <sup>-1</sup> )	Source
1. hydrozoan medusae ( <i>Goni- onemus vertens</i> )	general swimming in aquarium	50	2.2	1.1	96	—	Daniel (1985)
2. trematode cercaria ( <i>Di- plostonum spathaceum</i> )	general swimming/search- ing for host at 26°C	16.7	1.0	3.4	94	0.37	Haas (1969); personal commu- nication W. Haas
3. trematode cercaria ( <i>Trichobilharzia ocellata</i> )	forward swimming/host searching at 25°C	2.9	2.0	12.2	59	0.34	Feiler and Haas (1988); personal communication W. Haas
4. copepod nauplius, stage N2 ( <i>Temora longicornis</i> )	general swimming with food present	1.2	1.7	20.0	42	0.27	van Duren and Videler (1995)
5. barnacle cyprinid larva ( <i>Bal- anus amphitrite</i> )	exploration of substrate prior to settlement	30.7	33.0	0.9	48	—	Walters <i>et al.</i> (1999); personal communication G. Miron
6A. ghost crab ( <i>Ocypode quadrata</i> )	general locomotion	23.4	11.2	1.7	64	7.2	Weinstein (1995)
6B. ghost crab	fleeing observer	7.6	1.4	6.7	77	79.2	Weinstein (1995)
7. fly larva ( <i>Drosophila me- lanogaster</i> )	crawling on non-feeding substrate	6.6	16.1	3.3	29	—	Suster (2000)
8A. phorid fly female ( <i>Puli- ciphora borinquensis</i> )	general locomotion under uncrowded conditions	0.038	0.094	454.5	29	4.0	Miller (1979)
8B. phorid fly female	crowded conditions	0.143	0.048	314.1	75	—	Miller (1979)
9A. cricket female ( <i>Gryllus campestris</i> )	spontaneous walking	1.12	1.38	24	45	4.97	Schmitz <i>et al.</i> (1982)
9B. cricket female	presence of calling male	0.59	2.25	21	21	5.94	Schmitz <i>et al.</i> (1982)
10. social spider ( <i>Anelosimus eximius</i> )	attacking prey captured in web (midpoint of se- quence)	0.60	0.15	80	80	—	Krafft and Pasquet (1991)
11. octopus ( <i>Octopus cyanea</i> )	moving over reef while foraging	7.9	13.5	2.8	37	—	Forsythe and Hanlon (1997); J. Forsythe, personal commu- nication
12. zebrafish larva, 4 mm ( <i>Danio rerio</i> )	general swimming of starved fish	0.9	0.13	58.3	87	1.0	Fuiman and Webb (1988)
13. cod larva ( <i>Gadus morhua</i> )	feeding at low food densi- ty and medium turbu- lence	1.8	0.3	28.6	86	—	MacKenzie and Kjøboe (1985)
14. white crappie fish ( <i>Pomox- is annularis</i> )	food search at 19°C	1.6	0.9	24.0	64	6.3	O'Brien <i>et al.</i> (1986)
15A. arctic grayling ( <i>Thymal- lus arcticus</i> )	food search with small prey	0.3	1.0	46.0	23	6.4	Evans and O'Brien (1988)
15B. arctic grayling	food search with large prey	0.07	0.74	74.1	6	16.2	Evans and O'Brien (1988)

TABLE 1. Continued.

Type of organism (Genus and species)	Activity	Pause duration <sup>1</sup> (s)	Move duration <sup>1</sup> (s)	Move/pause frequency <sup>2</sup> (No./min)	Time paused <sup>3</sup> (%)	Move speed <sup>4</sup> (cm s <sup>-1</sup> )	Source
16A. viviparous lizard adult ( <i>Lacerta vivipara</i> )	moving between ends of a large cage	0.12	0.30	142.8	29	14.6	Avery <i>et al.</i> (1987)
16B. viviparous lizard adult	active search for prey	0.40	0.14	111.1	74	10.3	Avery <i>et al.</i> (1987)
16C. viviparous lizard adult	active pursuit of prey	0.15	0.57	83.3	21	23.9	Avery <i>et al.</i> (1987)
16D. viviparous lizard adult	fleeing	0.18	0.52	85.7	26	54.7	Avery <i>et al.</i> (1987)
16E. viviparous lizard adult	'panic' escape attempts from glass bowl	0.29	0.58	69.0	33	—	Avery <i>et al.</i> (1987)
17. ringed plover ( <i>Charadrius hiaticula</i> )	foraging on beach during day	2.01	0.66	22.5	75	—	Pienkowski (1983)
18. northern wheatear bird ( <i>Oenanthe oenanthe</i> )	foraging on short-grass heath	4.0	0.94	12.1	81	73	Tye (1989)
19A. European kestrel female ( <i>Falco tinnunculus</i> )	windhovering while forag- ing at windspeed of 6 m s <sup>-1</sup>	25	10	1.7	69	—	Videler <i>et al.</i> (1983)
19B. European kestrel male	gliding within windhover- ing bouts at 6 m s <sup>-1</sup>	0.30	1.56	32.3	16	0	Videler <i>et al.</i> (1983)
20. Eastern chipmunk ( <i>Tamias striatus</i> )	returning to burrow with load of seeds (forest habitat)	0.3	3.2	16.2	9	15.3	McAdam and Kramer (1998)
21A. Gray squirrel ( <i>Sciurus carolinensis</i> )	carrying nut to hoarding site in forest habitat	1.40	4.62	10.0	14	141	McAdam and Kramer (1998)
21B. Gray squirrel	approaching food source in open habitat	0.46	2.27	22.0	35	127	McAdam and Kramer (1998)

<sup>1</sup> Mean, median or midpoint of ranges provided by indicated source.

<sup>2</sup> Mean or median value from source or calculated as 60/(move duration + pause duration).

<sup>3</sup> Mean or median value from source or calculated as (100 × pause duration)/(move duration + pause duration).

<sup>4</sup> Estimated mean speed during moves.

Many studies of locomotion lack sufficient precision to record pauses shorter than 1 sec and others ignore longer pauses. The full range of pause durations may be missed in some studies, because distributions are often highly variable and skewed to the right (*e.g.*, Miller, 1979; Moreno, 1984; Evans and O'Brien, 1988; Weinstein, 1995) and because it is a technical challenge to record pauses over two or more orders of magnitude in the same sequence. Different types of pauses may be incorporated into a single locomotor sequence. For example, European kestrels make brief pauses in their flapping flight while windhovering over a specific location (Table 1, 19B) and intersperse bouts of windhovering at a fixed location with glides to a new location (Table 1, 19A). Estimates of pause and move duration depend on decisions regarding how long a pause should be considered a break in a bout of activity and vice versa. Several approaches to the objective definition of bouts have been proposed (Slater and Lester, 1982; Sibly *et al.*, 1990; Collins *et al.*, 1995). However, Cole (1995), who studied activity patterns in *Drosophila* at a time scale that would exclude most intermittent locomotion (shortest pause = 10 sec), concluded that the bouts of activity and inactivity showed a fractal structure such that there was no natural break that could be used for the objective definition of bouts. As a consequence, the percent time inactive increased as the temporal scale of recording became finer. It is not known to what extent Cole's findings may apply to move and pause durations in intermittent locomotion.

Individuals often change their patterns of intermittent locomotion as they change type of behavior or habitat. For example, gray squirrels approaching a food source away from forest cover made 22 pauses  $\text{min}^{-1}$  and spent 35% of their time paused, while those carrying a nut to a site for hoarding in forest cover made 10 pauses  $\text{min}^{-1}$  with 14% of their time paused (Table 1, 21A, B). Viviparous lizards spent 10–55% of their time paused, depending on their activity (Table 1, 16A–3). Intermittent locomotion also changes with developmental stage (*e.g.*, van Duren and Videler, 1995), food

density (MacKenzie and Kiørboe, 1995), food size (Table 1, 15A, B), foraging substrate (Paszowski, 1982), environmental complexity (Avery *et al.*, 1987), enclosure size (Tang and Boisclair, 1993), conspecific density (Miller, 1979) and temperature (O'Brien *et al.*, 1986).

Along with pause duration and move duration, speed while moving is required to characterize intermittent locomotion. Often, move speed changes with move and pause duration. For example, when adult viviparous lizards switched from generalized locomotion to pursuit of prey or fleeing from a threatening stimulus, the percent time pausing remained between 20 and 30%, but the durations of both pauses and moves increased, and the speed while moving increased from 15  $\text{cm sec}^{-1}$  to 24 and 55  $\text{cm sec}^{-1}$  (Table 1, 16). This resulted in an increase in the distance moved per bout from 4 to 14 and 30 cm, respectively. On the other hand, when the lizards actively searched for prey, pauses increased threefold, and move duration and speed while moving both decreased, so that nearly 75% of the time was spent in pauses, and each move took the animal only about 1.4 cm. Ghost crabs fleeing the observer increased their running speed 10-fold over general locomotion and thereby increased their average speed, but at the same time showed an increase in pause frequency and even percent time pausing (Table 1, 6A, B).

#### ENERGETICS

Intermittent locomotion entails more acceleration, more deceleration, and a higher speed while moving than does continuous locomotion at the same average speed. Both acceleration and active deceleration require energy expenditure. Moving at higher speeds may also require more energy expenditure per unit distance. Therefore, intermittent locomotion is expected to increase the energetic costs of moving over those of continuous locomotion under many circumstances (Daniel and Webb, 1987; Alexander, 1989). Several studies of fishes have documented higher costs of spontaneous movements at variable speeds as compared to continuous movement at the same average speed (Webb, 1991; Boisclair



and Tang, 1993; Krohn and Boisclair, 1994). However, intermittent locomotion can also reduce energy costs when forward movement continues during the pauses or when muscles function more efficiently at the higher speeds (Weihs, 1974; Videler and Weihs, 1982; Daniel and Webb, 1987; Rayner, 1985; see also Andersson, 1981). These circumstances are more likely during swimming and flying than during terrestrial locomotion.

In birds, intermittent flight can be energetically superior to continuous flight under some circumstances (Rayner, 1985). Undulating flight, in which the wings are extended to permit gliding during pauses, was predicted to be more economical than continuous flight at slow speeds. A corresponding model predicted that bounding flight, where the wings are held close to the body during pauses, would be energetically more economical than continuous flight at higher speeds and that the advantages would be independent of body size. Available evidence provided circumstantial support for the undulating flight model, but the bounding flight model was rejected because available evidence indicated that bounding flight was most common among small birds flying slowly. Tobalske and Dial (1996), however, supported the model with observations that several bird species in wind tunnel experiments exhibit an increased propensity to bound at faster speeds (Tobalske and Dial, 1994, 1996; Tobalske, 1995). They also suggested that bounding flight is restricted to smaller birds because sustainable flight performance and acceleration ability scale negatively with body mass. Consequently, larger birds may have insufficient power and acceleration ability to counteract the loss of altitude experienced during the pause.

Propulsion by body undulation increases drag relative to that experienced by a rigid body (Daniel and Webb, 1987). Therefore, fish such as cod and pollack can save energy by “burst-coast swimming” for locomotion at higher speeds. The drag while coasting with the body straight has been estimated to be only one third the drag while swimming, reducing energy expenditures by as much as 50% (Videler and Weihs,

1982). The speeds of cod and pollack at the end of the burst and the coast phases were close to those predicted to maximize the gain from intermittent locomotion.

During vertical movements, animals can take advantage of gravity or positive buoyancy to permit unpowered downward or upward locomotion for a longer period. It was recently discovered that whales and seals cease locomotion while continuing to glide downward during the deeper descending portion of dives over 80 m thereby saving considerable energy and reducing their oxygen demands (Williams *et al.*, 2000).

In dolphins and penguins, porpoising also has been modeled as a method of intermittent locomotion whereby animals reduce their energetic expenditure at high speeds by capitalizing on short periods of unpowered movement through the air (Au and Weihs, 1980; Blake, 1983).

For some animals, power production from muscle fibers occurs over a narrow range of contraction speeds (Rayner, 1985; Rome *et al.*, 1990). Intermittent locomotion has been proposed as a way for the animal to adjust overall power output while maintaining power production from muscles at near optimal levels. Rayner (1985) used this idea to explain the tendency for small birds to bound during slow flight (the “simple gear hypothesis”: Tobalske and Dial, 1996). If small size constrains the variety of muscle fiber types (and corresponding range of efficient contraction speeds) of small birds, pauses may allow overall power output to vary while maintaining the power output of muscle within a restricted range.

A related explanation has been proposed to explain the relationship between intermittent locomotion and swimming speed in fishes. A variety of fishes exhibit burst-coast swimming at both slow and fast speeds and continuous swimming at intermediate speeds (Videler and Weihs, 1982; Rome *et al.*, 1990; Johnson *et al.*, 1994; Swanson *et al.*, 1998). Fishes possess two main muscle fiber types: red muscle which is powered aerobically, fatigues slowly, and is used continuously at slow swimming speeds and white muscle which is powered anaerobically, fatigues quickly, and is used

at fast swimming speeds. In a study of carp, Rome *et al.* (1990) argued that the efficiency of red muscle was near maximal when the fish swam steadily at intermediate speeds. The lower power requirements for steady swimming at slower speeds would require muscle contraction speeds and therefore power output to decline. Instead of swimming continuously using muscle contractions at suboptimal speeds, the fish adopt a burst-coast pattern powered intermittently by red muscle operating at maximal power output. At fast speeds, increasing contraction speeds decrease the power output from red muscle. The fish therefore adopt a burst-coast pattern powered by white muscle. The extent to which this explanation applies to other fishes is currently unclear (but see Johnson *et al.*, 1994), and there is evidence that the recruitment of muscle fiber types is likely to be more complex than indicated by this hypothesis (Jayne and Lauder, 1994).

#### RECOVERY FROM FATIGUE

The possibility that pauses during intermittent locomotion permit some recovery from fatigue and thereby increase the total amount of work completed in one bout has been investigated for ghost crabs (Weinstein and Full, 1992) and humans (Åstrand and Rodahl, 1986; Saltin *et al.*, 1976) and suggested for fishes (Videler and Weihs, 1982) and birds (Rayner, 1985). Laboratory studies examining the distance that ghost crabs can run before fatigue provide a well-studied example with application to natural behavior (Weinstein and Full, 1992). At a speed of  $0.3 \text{ m sec}^{-1}$  crabs fatigued after 7.5 min, having covered a distance of 135 m. Individuals alternating between 2-min periods of exercise at  $0.3 \text{ m sec}^{-1}$  and 2-min pauses took more than 10 times as long to fatigue (87 min) and covered nearly 6 times the distance (787 m). These crabs also ran farther before fatiguing than individuals running continuously at the same average speed of  $0.15 \text{ m sec}^{-1}$  (360 m). Lactate accumulated during the exercise periods and was reduced during the pauses. The benefits of intermittent locomotion depended strongly on temperature and the durations of exercise and pause bouts (Weinstein and

Full, 1998). Intermittent locomotion appeared disadvantageous when move and pause bouts were short (5–30 sec) (Weinstein and Full, 1992), even though animals fleeing the experimenter used very short moves (1.4 sec) alternating with only slightly longer pauses (7.6 sec) (Weinstein, 1995).

The physiological mechanisms behind the advantage to pausing are not fully understood and may vary among taxa (Weinstein and Full, 1992, 2000). It is generally hypothesized that the rest period allows high-energy phosphates to be restored and fatigue-producing products (*e.g.*, lactate,  $\text{H}^+$ , inorganic phosphate) to be removed (Weinstein and Full, 1992; Videler and Weihs, 1982; Rayner, 1985). Increased endurance in crabs comes at an energetic cost (Weinstein and Full, 1992). This is believed to result from elevated circulation and ventilation costs during pauses and from non-linear increases in energetic cost per unit time when crabs travel faster than the maximum aerobic speed.

#### STABILIZATION OF THE SENSORY FIELD

Movement is inherently antithetical to the visual recognition of objects in the environment because it produces complex, frequently rapid, movements of the visual field. Self movement causes the visual image to move in the reverse direction over the retinal surface. Different parts of the visual field move at different speeds and directions. There is centrifugal movement away from the point toward which locomotion is directed and more rapid movement of the image of objects that are closer to the eye (Gibson, 1979). Although visual systems compensate wonderfully for these problems, unavoidable constraints remain. Intermittent locomotion may be advantageous, therefore, in providing brief periods of stability of the visual field.

“Velocity blur” or “motion blur” is a reduction in the fineness of detail that can be resolved by the retina when the light reaching a particular photoreceptor fluctuates more rapidly than the response time of that receptor (Carpenter, 1988; Land, 1999). Calculations based on retinal cell acceptance angle and response speed suggest a



threshold for visual blur of about  $1^\circ \text{ sec}^{-1}$  in humans and  $100^\circ \text{ sec}^{-1}$  in insects such as flies and bees, values supported by a few experimental studies (Land, 1999). Humans are more sensitive to blur because of their smaller acceptance angle associated with higher spatial resolution. Pauses reduce blur by stopping movement of the visual field.

Organisms with eyes that can move independently of their bodies can compensate for velocity blur by visual tracking without necessarily ceasing locomotion. Feedback from movement of the visual field or of the head can be used to control eye movements in order to stabilize part of the visual field on the retina (Land, 1999). These stabilizing mechanisms can be experienced by looking at one's outstretched hand and comparing the visual blur from lateral shaking of the hand with that from equivalent shaking of the head (Carpenter, 1988, p. 5). Although most organisms have much more limited capacity for eye movements than humans do, brief stabilizations of the eyes are evident in careful recordings of eye and body positions during turns in a number of different taxa (Land, 1999). Figure 2A illustrates this effect with the eye movements of a goldfish making a turn.

Head movements relative to the body can also stabilize the visual field. Many birds with mobile necks alternately fix the head position and move it rapidly forward while the body moves forward continuously (Fig. 2B). This "intermittent head locomotion," usually referred to as "head bobbing," has been examined most intensively in pigeons and doves, where a series of elegant experimental studies shows that it is related to visual requirements rather than other aspects of locomotion (Friedman, 1975a; Frost, 1978; Davies and Green, 1988). Head bobbing occurs in many other bird species but not all (Dagg, 1977). As movement speeds up, so does the speed of head bobbing. Head bobbing occurs even at higher speeds where precise visual control is required, *e.g.*, landing flight, where it does not make the head stationary but does produce intervals of reduced forward speed (Fig. 2C). The resulting durations of head moves and pauses are very similar to those achieved by intermittent locomotion. For

example, in pigeons the head is stationary about 50% of the time when the body moves at  $20 \text{ cm sec}^{-1}$  and about 5% of the time when the body moves at  $70 \text{ cm sec}^{-1}$  (Davies and Green, 1988).

Movement creates particular challenges for the detection of other moving objects. The design of perceptual systems in many species means that objects are seen more readily if they are moving relative to the background, whether relative motion is elicited by object or observer motion (Kimmerle *et al.*, 1997). Observer motion can either reduce or increase relative motion of an object, depending on the direction of object motion and that of the visual field. The mechanisms by which observer motion is distinguished from object motion are complex and not fully understood (Wertheim, 1994). When object, background and observer are all moving relative to each other, discrimination would seem to be easier if the observer paused and reduced one source of relative motion (Land, 1999). This does indeed seem to be the case. For example, a driver's latency to detect a change in the apparent size of a car ahead on a highway, due to a sudden change in the lead car's relative speed, is much greater than the latency for the equivalent visual task while stationary (Probst *et al.*, 1984). Using tethered flies exposed to a moving background simulating self motion, Kimmerle *et al.* (1997) found that the strength of the turning response toward an object moving against the background (and presumably therefore the fly's ability to detect the object) increased as a function of the object speed and first increased then decreased as a function of background speed (apparent speed of self motion).

For species showing intermittent locomotion, direct evidence of an effect of speed on perception is very limited. Avery (1993) showed that lizards were less likely to detect prey arriving while they were moving, and Friedman (1975b, p. 201) reported similar anecdotal observations of the responses of plovers to small tossed objects. In many species, including birds, toads, fishes, adult and larval insects, moves tend to be relatively straight, with both pursuits of prey and changes of direction initiated

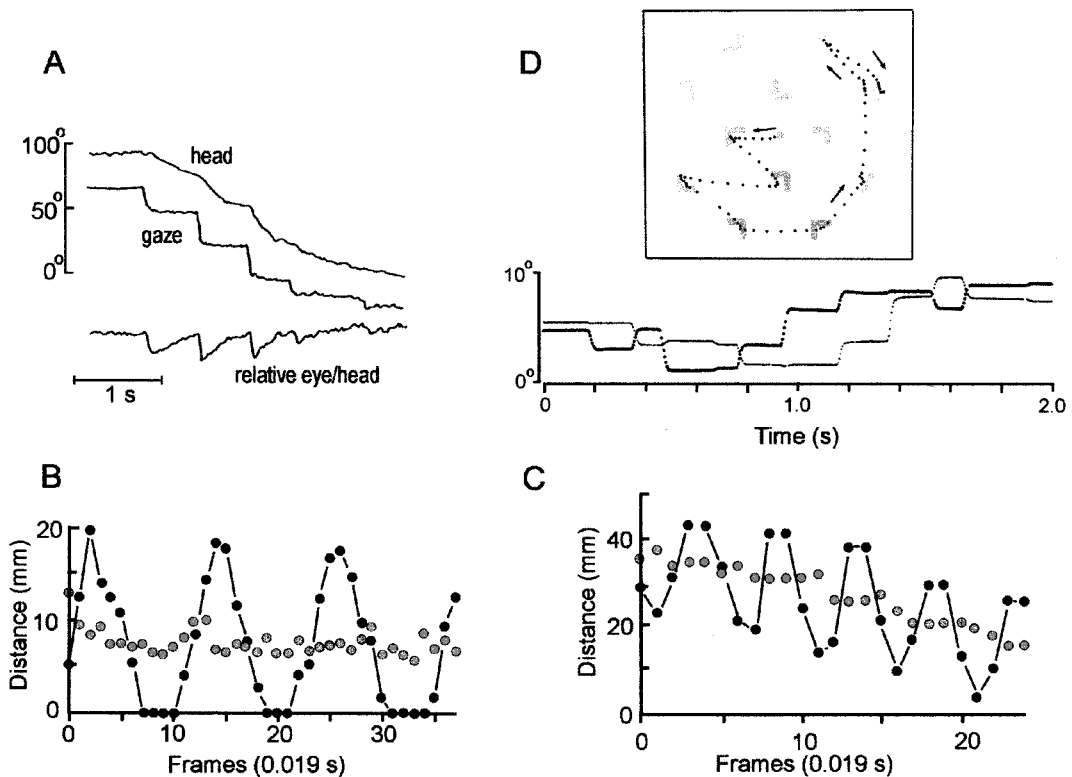


FIG. 2. Alternative methods of stabilizing the visual field. A. As a goldfish turns through  $100^\circ$ , the head makes a smooth turn (top line) while the eye gaze position is stabilized for relatively long intervals separated by rapid shifts (middle line). This is brought about by a series of rapid eye movements in the direction of the turn followed by slower moves in the opposite direction (bottom line) (from Land, 1999, Fig. 2, after Easter *et al.*, 1974, with permission of the authors and Springer-Verlag©). B. Pigeon running, showing distance traveled by the body (gray circles) and head (black circles) between frames (0.019 sec intervals). The head is motionless for several frames in each cycle (from Davies and Green, 1988, Fig. 1). C. Pigeon in landing flight. Symbols are as in (b). Head movements temporarily reduce the forward speed of the head but do not stop it, and body speed is reduced as the bird approaches the perch (from Davies and Green, 1988, Fig. 7). Note difference in scale between (B) and (C). D. Pattern of gaze shifts by a monkey searching for a randomly located letter T in a field of letter Ls. The upper field shows the path followed by the eye. Arrows indicate the direction of movement. The lower field shows the temporal pattern of fixations and saccades. The thick line represents horizontal position and the thin line represents vertical position of the eye (from Schall and Thompson, 1999, Fig. 1, with permission of the author and *The Annual Review of Neuroscience*, Volume 22 ©1999 by Annual Reviews [www.AnnualReviews.org](http://www.AnnualReviews.org)).

mainly following pauses rather than during moves (*e.g.*, Miller, 1979; Lock and Collett, 1979; Evans and O'Brien, 1988; Tye, 1989; Suster, 2000). These observations provide indirect evidence that detection of the stimuli that initiate pursuits and turns occurs primarily during pauses. In fact, studies of doves and toads show that visual input is actually reduced during moves by closing of the eyes (Friedman, 1975*b*; Lock and Collett, 1979).

Although studies comparing perception

of moving and non-moving animals are rare, we have not found any that estimate the probability of detecting either moving or stationary objects as a function of the animal's movement speed. Such studies are important for understanding to what extent perception is possible during moves and whether speed reductions during gliding could provide a perceptual advantage, even if forward motion does not cease. When locomotion produces vertical or lateral as well as forward head movements, as for ex-

ample in many fishes using caudal propulsion, gliding between bouts of propulsion might also improve perception by reducing the complexity of movement of the visual field even if forward movement does not cease (Land, 1999).

We have emphasized vision in considering the effects of self motion on the sensory field because of the extensive amount of work on this system. However, similar effects are likely to occur with other senses. For example, parasitoid wasp species that detect their prey using vibrations in the substrate spend a higher proportion of time motionless than species that use their ovipositors to probe for prey (Vet and Bakker, 1985), suggesting that movement interferes with detection of prey movement. In addition, movement in many environments generates noise that interferes with auditory perception. Humans and other species often stop and listen if they need to detect a faint sound or to make a fine auditory discrimination. Orthopteran insects offer an extreme example. Because the auditory receptors of crickets are located on their forelegs, walking produces excitation of auditory receptors in the absence of sound and suppression of action potentials in response to sounds (Schildberger *et al.*, 1988). Female crickets orienting to a male calling song pause frequently and change direction primarily during pauses (Murphey and Zaretzky, 1972; Bailey and Thomson, 1977; Schmitz *et al.*, 1982). There is evidence that orientation is less effective when the song is heard only during moves than when it is heard only during pauses (Weber *et al.*, 1981; but see Schmitz *et al.*, 1982).

#### ATTENTION TO THE SENSORY FIELD

Several processes involved in the examination of the visual field require time. Motion therefore reduces the probability of detecting important information in a complex scene before that scene changes. In many organisms, part of the retina called the fovea is specialized for high acuity while the rest has higher sensitivity but lower acuity. Examination of the visual field with high acuity requires pointing the fovea successively at areas of potential importance. In humans and some other species, foveation

is not a smooth motion, but takes place in a series of rapid eye movements called saccades interspersed with stable (though not quite motionless) intervals called fixations (Carpenter, 1988; see Fig. 2D). Saccades are extremely rapid, with the eye moving (up to  $700^\circ \text{ sec}^{-1}$ ). They typically last about 40 msec (Carpenter, 1988) and take up about 10% of the total scanning time (Stark and Choi, 1996). During saccades, perception is suppressed (Carpenter, 1988). Perceptual processing of objects in the fovea to ascertain their identity, processing of images in the periphery to locate the target for the next saccade, and programming the next saccade all take place during fixations (Schall and Thompson, 1999). The pattern of fixations and saccades during visual exploration of a scene using only the eyes is strikingly similar to the intermittent locomotion of an animal searching for food in a physical landscape (*e.g.*, Fig. 2D; Carroll *et al.*, 1992).

Detection and recognition of objects in the visual field during fixations depend on cognitive processes in the central nervous system, often grouped under the term 'attention' (Pashler, 1998). Although current authors question whether there is a unitary thing or process that can be called attention and note that the common usage of this term has a variety of meanings, there is no doubt that recognition takes time. In many visual search tasks, the time to locate an item increases with the number of kinds of items being searched for (targets), with the number of non-target items in the field, and with the similarity between non-target and target items. This provides evidence for limited processing capacity and hence competition among potentially perceived objects for representation, analysis or control at one or more points between stimulus input and the animal's response (Desimone and Duncan, 1995). Variation in the magnitude of the effect of other items, from very strong to apparently no effect at all, provides evidence for a bias in the competition (Desimone and Duncan, 1995). When search time does not increase with number of non-target items, some authors conclude that attention is not required. However, Joseph *et al.* (1997) provide evidence that at-

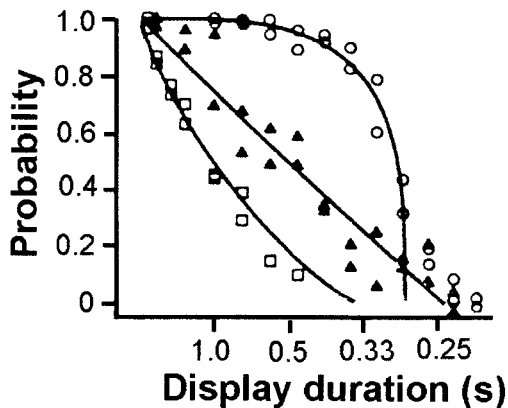


FIG. 3. The effect of display duration and target conspicuousness on the probability that a human subject searching a computer screen will find a target figure (from Gendron and Staddon, 1984, Fig. 3, with permission of The University of Chicago Press©). The graph plots detection probability in relation to the duration of the display for relatively conspicuous (circles, top line), intermediate (triangles, middle line), and cryptic (squares, lower line) figures in relation to the background. Note that longer durations are to the left and that the abscissa is scaled to equal intervals of the inverse of display duration.

tention is still needed because simultaneous presentation of a second task requiring attention does increase the time to locate an object. Search times required to conclude that a target is absent from a field are typically longer than average times to identify the presence of a target and show the capacity for adjustments in response to error rates (Chun and Wolfe, 1996). When search time is fixed, the probability of detection increases as search time increases, with the shape of the curve depending on the similarity between the target object and the background pattern (Gendron and Staddon, 1984; see Fig. 3).

Most work in this area has been carried out in timed searches for relatively simple objects in relatively simple fields on computer screens. It seems likely that attention would play a much larger role when the presence of several different processes are involved (*e.g.*, looking for food, checking for predators and conspecifics, choosing a path to the next site) and when the visual field is very complex. As a response to the temporal demands of foveation and attention, pausing for a longer time may prevent

an animal from missing a prey or coming too close to an obstacle or predator before it has time to take evasive action and may permit it to detect a prey before it is itself detected. Indirect support for the importance of pausing for stimulus detection comes from behavioral changes of animals as the searching environment changes. When prey are more difficult to detect or when environments are visually more complex, foraging pause durations increase and move distances decrease (*e.g.*, Pienkowski, 1983; Gendron, 1986; Avery *et al.*, 1987; Evans and O'Brien, 1988; Ehlinger, 1989; O'Brien *et al.*, 1989; Colishaw and Avery, 1991; Sonerud, 1992). There is some evidence that pausing increases when value of early detection of predators increases (McAdam and Kramer, 1998). Primates pause when moving between trees in the canopy (Cannon and Leighton, 1994). Although called "rests" in the published account, these pauses were usually very brief, on the order of seconds, and likely related to the requirement to identify a route for the next movement sequence (C. H. Cannon, personal communication).

Auditory perception also requires attention, and it is likely that rapid movement may change the auditory field before important sounds are detected. We have not found relevant studies on organisms using other sensory modes. However, observations that tracking dogs move more slowly when faced with a weaker scent or more confounding odors suggest that similar processes may apply (E. D. Bailey, personal communication).

#### INTERFERENCE BETWEEN SENSORY SYSTEMS

In addition to its direct effects on sensory systems, motion may produce interference between perceptual systems. For example, research by Probst *et al.* (1986) revealed that the decrease in motion detection during self motion occurred both when the visual field was stabilized during motion of the observer and when the visual field moved while the observer was stationary. The authors suggested that there is a physiological inhibitory interaction between object-motion and self-motion perception, perhaps as a disadvantageous side effect of the mech-

anisms that stabilize vision during locomotion. There is little information about the magnitude of these effects with natural stimuli and movement speeds.

#### DETECTABILITY

Moving objects create strong visual and mechanical stimuli and sometimes auditory and olfactory stimuli. Conversely, immobility is often required for background matching in both predators and prey (Edmunds, 1974). Movement is, therefore, frequently associated with an increased probability of detection or attack of prey by predators and with an increased probability of detection or flight from predators by prey (Curio, 1976; Wright and O'Brien, 1982; Sokolowski and Turlings, 1987; Martel and Dill, 1995; Yen and Strickler, 1996). Pausing during intermittent locomotion might therefore reduce the probability of detection of both predators and prey. Under many circumstances, however, it seems unlikely that the brief pauses characteristic of much intermittent locomotion would provide a significant advantage over continuous locomotion at the same average speed. A predator that fails to detect a prey while the prey is paused is still likely to be present within the next few seconds when the prey moves again. Similarly, a prey being approached by a predator has lots of moves in which to detect the predator, even if pauses are interspersed. However, intermittent locomotion could provide a greater advantage when moves are timed to coincide with lowered probability of being detected as a result of environmental masking of relevant stimuli or lowered attention. For example, spiders that hunt other spiders on their webs time their movements to coincide with wind-induced movements of the web (Wilcox *et al.*, 1996). Juvenile cuttlefish moving away from predators alternate between motionless cryptic positions on the substrate and movements timed to coincide with the wave-induced passage of clumps of algae and detritus (Hanlon and Messenger, 1996). And carnivores stalking ungulate prey match their moves to moments when the prey's head is down (Curio, 1976).

Pauses may also cause predators to lose contact with prey that they have already be-

gun to pursue. For example, Herzog and Burghardt (1974) observed that yellow-bellied racer snakes lost their orientation and began apparently random search when their cricket prey stopped moving during pursuit. Wilson (1978) briefly described a 'waiting game' between tiger beetles and their prey in which prey stopped moving when approached by the beetles. If the prey then moved first, it was attacked; if the predator moved first, it soon left the area and the prey escaped. Humphries and Driver (1988) proposed that animals use unpredictable movements, especially changes in speed and direction, which they call 'protean behavior' to reduce the ability of predators to anticipate future positions of potential prey. Several species were suggested to incorporate unpredictable pauses in their escape movements, including psychodid flies, fleas evading grooming hosts, and gray squirrels confronted by cars (and presumably natural predators), but no direct measurements of the irregularity of the occurrence and duration of pauses or of their effect on pursuing predators were provided.

#### DISCUSSION

Pausing during bouts of locomotion often adds acceleration and deceleration costs to the energetic demands of movement. It necessitates either increased time to cover a given distance or increased speed while moving, or both. Despite this, our survey shows that intermittent locomotion is widespread, occurring in diverse species and situations. Some of these cases undoubtedly occur in circumstances where the energetic costs of pausing are minimized or reversed, but many others do not. Our review shows that pausing can also assist the recovery from fatigue, improve the detection of prey, predators and travel routes, and reduce detection by other organisms.

Many published studies consider only one or two mechanisms in evaluating intermittent locomotion. In some cases, the assumption that one benefit greatly outweighs the others may be justified. However, this may not always be so. It is worth considering the full range of potential benefits and costs. For example, does burst-glide locomotion improve perception by partially sta-



bilizing the visual field during glides? Does saltatory search improve predator detection or endurance as well as prey detection?

Behavioral ecological models of movement use trade-offs between various costs and benefits to predict the relationship between environmental variables or organismal characteristics and the patterns of locomotion. Most such models have considered only continuous locomotion (Ware, 1975; Pyke, 1981; Gendron and Staddon, 1983; Speakman, 1986; Hedenström and Ålerstam, 1995). However, two have explicitly addressed when intermittent locomotion should be favored over continuous locomotion and how the pattern of pause and move durations should vary with environmental conditions (Andersson, 1981; Anderson *et al.*, 1997). Andersson's (1981) model has been modified by subsequent investigators to apply to a variety of specific taxa, ecological situations and questions (*e.g.*, Ehlinger, 1989; O'Brien *et al.*, 1989; Tye, 1989; Getty and Pulliam, 1991, 1993). These models include both energetic and perceptual variables and consider how movement patterns affect trade-offs 1) between the rate at which the forager comes within potential detection distance (encounter rate) and the probability that encountered prey are actually detected and 2) between encounter rate and the energetic cost of moving. These models predict increased use of intermittent locomotion when the relative cost of moving versus pausing increases, when prey detectability and abundance increase, when prey detectability (or other benefits) decreases at a decreasing rate as speed increases, and when the cost of moving (or other costs) increases at a decreasing rate as speed increases. Pause time is predicted to decrease and move time to increase with increases in detectability and abundance of prey. Although qualitative, such predictions are testable using observational or experimental data on movements from the field and the laboratory (*e.g.*, O'Brien *et al.*, 1989; Tye, 1989; Getty and Pulliam, 1993; Sonnerud, 1992; Anderson *et al.*, 1997).

Research in this area is just beginning and many interesting questions remain unexplored. For example, energetic models of

terrestrial locomotion predict speeds considerably higher than are often observed (Speakman and Bryant, 1993). This suggests that speed while moving is more influenced by perception than energetics, but we currently lack a way to test such a hypothesis. The scarcity of quantitative data on perception in relation to movement speed represents an important challenge for further investigation. Most work on perception during intermittent locomotion has focused on prey detection during foraging pauses. Indeed, it has sometimes been assumed that other perceptual requirements such as scanning for predators take place during moves (O'Brien *et al.*, 1990), but we know very little about how movement will affect different types of visual tasks. Our understanding of the effects of movement on other perceptual systems is even less. The integration of energetics and biomechanics with perceptual physiology and psychology in an ecological framework has the potential to greatly change the way biologists in many disciplines view animal movement.

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