



Dissecting the effects of behaviour and habitat on the locomotion of a lizard (*Urosaurus ornatus*)

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(Received 26 April 2006; initial acceptance 1 June 2006;
final acceptance 31 August 2006; published online 8 January 2007; MS. number: A10431R)

Locomotion is one way that organisms interface with their environment, and this relationship can be affected by the structural habitat and behavioural context associated with each movement. Previous studies have examined the effects of habitat or behaviour on locomotion individually, but have not addressed the potential interaction between these factors. In addition, studies often use induced behaviours or manipulated habitats to examine the effects of habitat and behaviour on locomotion. Although valuable, these approaches provide little information on the range of natural behaviours and habitats that animals occupy. To address these issues, we examined the effects of structural habitat, behavioural context, and their interaction on undisturbed locomotor speeds in the ornate tree lizard, *Urosaurus ornatus*. Detailed video analysis revealed that both habitat and behaviour affect locomotion individually; locomotor speed decreases with increasing perch height when animals move on woody substrates and while displaying and capturing prey. Surprisingly, we found no relationship between speed and perch diameter or substrate incline. Additionally, we show that the interaction between perch diameter and feeding behaviour results in a negative relationship between speed and perch diameter during feeding but not during other behaviours. In light of these findings, we suggest that the relationship between habitat, behaviour and speed is affected by the level of locomotor performance (maximal versus submaximal) that animals routinely use during undisturbed activity.

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Keywords: habitat; locomotion; ornate tree lizard; performance; substrate; *Urosaurus ornatus*

Organisms use locomotion to accomplish various fitness-related behavioural tasks such as home range defence, finding mates or food, escaping predators and dispersal (Swingland & Greenwood 1983; Dingle & Holyoak 2001). Furthermore, many organisms live in complex three-dimensional habitats and must negotiate substrates that vary in diameter, incline, height and texture, among other features (Turchin 1998). The specific behavioural task engaged in and the structural habitat are key factors that can alter the direction, speed and timing of locomotor movements (Garland & Losos 1994; Irschick & Garland

2001). Organisms may adjust their locomotion to simultaneously address the effects of habitat and behavioural task; therefore, the effects of these factors are likely to be complex and interactive. Studies that explicitly quantify how locomotion changes with habitat and behaviour individually, as well as collectively, are needed.

Prior studies have confirmed the pervasive effects of habitat on locomotion (e.g. perch diameter and speed in *Anolis* lizards, Losos & Sinervo 1989; wind speed and swarm structure in locusts, Dingle 1996; substrate type and speed in lacertid lizards, Vanhooydonck & Van Damme 2003; incline, diameter and limb kinematics in *Anolis* lizards, Spezzano & Jayne 2004; substrate structure and locomotor repertoire in orang-utans, Thorpe & Crompton 2005). Also, many studies have found that behavioural context affects locomotion (e.g. *Podarcis muralis*, Braña 2003; *Anolis*: Irschick & Losos 1998; Irschick 2000b; degu, Vásquez et al. 2002; bottlenose dolphin, Bailey &

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Thompson 2006). These studies shed light on how habitat or behaviour alone affect locomotion, but reveal less about interactions between habitat and behaviour. Furthermore, prior studies induced locomotion by simulating a behaviour (e.g. simulated prey capture and predator escape, Irschick 2000b) rather than recording locomotor movements associated with a range of undisturbed, natural behaviours.

Following prior studies, we used an approach that involves quantitative analysis of undisturbed locomotion, thus allowing us to measure the natural variation in movement speed across a range of behaviours and throughout the complexity of the structural habitat (Hertz et al. 1988; Garland 1993; Irschick & Garland 2001). We studied the ornate tree lizard, *Urosaurus ornatus*, because this species is active, conspicuous, abundant and behaviourally diverse. We had two goals. First, we examined the relative influence of behaviour and habitat on locomotor speed. We focused on three fitness-related behaviours, prey capture (feeding), predator escape and displaying, and four aspects of the structural habitat, perch height, perch diameter, incline and substrate type, that can influence locomotion. We acknowledge that these habitat variables are a subset of those that may affect locomotion. In terms of behaviour, we expected locomotor speeds to be fastest during display behaviour, intermediate during predator escape and slowest during prey capture (Braña 2003). In terms of habitat, we predicted smaller perch diameters and steeper inclines to negatively affect speed (Huey & Hertz 1982; Irschick & Jayne 1998, 1999; Jayne & Ellis 1998). We had no predictions for the effects of perch height or substrate type on speed. The second goal of this study was to test our expectation that the interaction between behaviour and habitat can alter how individual variables (habitat or behaviour alone) affect speed.

METHODS

Field Site

We studied a population of *U. ornatus* at Wet Beaver Creek, which is a mid-elevation site (1100 m) in central Arizona, U.S.A. This site (400 m long × 60 m wide) is a riparian zone consisting of a varied habitat ranging from complex three-dimensional clusters of woody debris to flat, open areas of loose sandy soil. *Urosaurus ornatus* was abundant at this site, and males were defending territories and mating during the sampling period (10–16 June 2005), which corresponded to the peak breeding period. This research was conducted under Ohio University approved research protocols and followed all regulations in Arizona Game and Fish Department permit number SP638616 to E.J.M.

Focal Observations

We gathered focal videos of 15 male *U. ornatus*. We filmed all videos on sunny days during hours of peak activity (0800–1900 hours) when ambient temperatures were 28–32°C. To gather a focal video, we systematically

searched the site to locate lizards. After locating a lizard, we used a 5-min assessment period to discern whether the lizard was disturbed by the observer (i.e. displayed or sprinted away from the observer). If either of these criteria were met within the 5-min assessment period we began searching for another individual. We filmed lizards with a handheld JVC–GR DVL 9800 Mini DV camcorder (30 frames/s). E.J.M. filmed all lizards and wore the same set of clothing throughout the filming period. Other studies using similar techniques have found that lizard behaviour is not affected by the observer (Irschick 2000a, b; Irschick et al. 2005; Mattingly & Jayne 2005). We gathered extended video sequences that ranged from 5.5 min to 46.9 min (average = 21.4 min). After filming, we captured each lizard via a handheld slip-noose and identified individuals by a unique toe-clipping pattern (all individuals were toe-clipped in the population as part of a larger study, ensuring that each individual was filmed once). After identification, lizards were released at the point of capture.

Video Analysis

We followed similar methodologies as in previous studies that documented the behaviour and structural habitat associated with locomotion in lizards (Irschick 2000a, b; Braña 2003). In the field, we reviewed videos frame by frame to quantify aspects of the habitat associated with each movement. First, we identified whether the movement was a jump or a run. However, we only included running locomotion in our analysis because of the biomechanical differences between running and jumping and because jumping was usually associated with travelling behaviour (only one prey capture and two displays were associated with jumping locomotion). Next, we quantified movement distance by placing flagging at the point of each pause (each movement is preceded and followed by a pause) and measuring the straight-line distance (to the nearest 4 cm) between consecutive substrate landmarks. To quantify habitat structure, we recorded perch height at the end of each movement and the perch diameter, incline and substrate (wood, rock, ground) on which each movement occurred. Perch height and diameter were recorded with a tape measure to the nearest 1 cm and incline was recorded with an analogue inclinometer to the nearest 5°. Lizards always paused when major changes in substrate occurred (e.g. wood to ground or flat incline to uphill incline); therefore, we did not make any measurement adjustments to control for habitat heterogeneity within a single movement.

In the laboratory, we reviewed videos frame by frame to quantify movement duration and the behavioural task associated with each locomotor movement (following Braña 2003). We quantified movement duration as the amount of time associated with each movement to the nearest 0.1 s. We calculated movement velocity as movement distance (recorded in the field) divided by movement duration. Next, we assigned a behavioural task to each locomotor movement, which included displaying, prey capture, predator escape and travelling. During

displays, male *U. ornatus* use a combination of head bobbing, push-ups, dorsoventral flattening and dewlap extension (Purdue & Carpenter 1972); therefore, we defined a display behaviour as any pause after a locomotor movement during which the lizard performed at least one of these behaviours. Prey capture behaviours were defined as any locomotor movement that attempted (successful or unsuccessful) to approach, capture and consume prey. Predator escape behaviours were defined as any movement that served to escape or deter a potential predator. We observed only one predator escape behaviour and thus it was not used in subsequent analyses. Many of the movements we observed were not associated with displays, prey capture, or predator escape per se; rather, they were used to travel between two locations. We refer to these movements as 'travelling' behaviour.

Statistics

We used JMP 5.0 and SAS 9 (SAS Institute, Cary, North Carolina, U.S.A.) for all analyses. We simultaneously tested for differences in locomotor velocity due to behaviour, habitat and their interaction using multiple regression. Speed was the response variable and behaviour, habitat and their interaction were predictor variables. Behavioural variables and substrate types were coded using dummy variables (for each variable, the behaviour/substrate was coded as '1' and all other behaviours/substrates were coded as '0'). One potential problem with interpretation of dummy variables is intercorrelation among variables. To address this issue, we present mean values of speeds for lizards on different substrates and during different behaviours so that the reader can evaluate the biological significance of these factors for locomotion. Preliminary analyses indicated that interaction terms were strongly correlated with their components, which is problematic for multiple regression (Quinn & Keough 2003). We addressed this issue by centering all predictor variables (by subtracting the mean from each observation), which eliminates correlations without affecting regression slopes (Aiken & West 1991). After centering, we found no problems with collinearity (variance inflation factors were less than two, Quinn & Keough 2003). To find the 'best' model we estimated all possible regression models given our data and then used the Bayesian Information Criteria (BIC), Akaike Information Criteria (AIC), and Mallow's C_p to choose the best-fitting model (Mac Nally 2000; Quinn & Keough 2003). These criteria select the model that includes the smallest number of predictor variables while still explaining a large amount of variation. We detected no problems with residual plots, outliers (Mahalanobis distances), or leverage (Cook's D).

We had multiple observations from the same individuals (mean number of movements per individual = 33 movements, range 1–58 movements), which could lead to some individuals driving slope estimates in the regression. To address this issue, we reran our regression analyses with individual as a predictor variable (coded using dummy variables). This reanalysis showed that four

individuals ran at slower speeds than the other 11. To eliminate the possibility that individual differences were driving our findings, we used a jackknife approach to address each individual's influence on slope estimates. We removed each individual, reran the multiple regression, and compared each slope in each jackknifed model with the 95% confidence intervals of the slope in the full (all individuals) model. We found no instances of any of the jackknifed slopes falling outside the 95% confidence intervals of the full-model slopes. Thus, we are confident that no single individual was driving the slope estimates in the full model. As advocated by other studies that have used multiple regression for examining locomotion in lizards (and thus, that took repeated measurements of the same individual; e.g. Mattingly & Jayne 2005), we emphasize results with conservative P values ($P < 0.005$).

RESULTS

The best regression model had the lowest values of three selection criteria: Mallow's C_p (3.28), AIC (-433.27) and BIC (-428.56). This model explained a significant amount of the variation in locomotor speed (Table 1). Individually, both habitat and behaviour had significant effects on locomotor movements (Table 2). On the tallest perches (>120 cm), speeds were approximately 90% slower than speeds on the shortest perches (<120 cm, Fig. 1a). On woody substrates, speeds averaged 0.1 m/s, which was 50% slower than speeds on rocky substrates (0.2 m/s) and 80% slower than speeds on the ground (0.5 m/s). The fastest speeds used during displaying and prey capture were approximately 45% and 60% slower, respectively, than maximum racetrack speeds (Table 3). During displays, speeds averaged 0.09 m/s, which was 40% slower than speeds during prey capture (0.15 m/s), 67% slower than speeds during travelling (0.27), and 81% slower than speeds during predator escape (0.48 m/s) (Table 3). The standardized regression coefficients of behavioural and habitat effects were approximately equal in magnitude (Table 2), suggesting that these factors have similar magnitude effects on speed. However, the two habitat variables that we expected to have significant effects on speed (incline and perch diameter) had no relationship with speed. In addition, prey capture behaviour and perch diameter interacted to affect locomotor speed (Table 2). This interaction is important because the negative relationship between perch diameter and locomotor speed occurs only during prey capture behaviour (Fig. 1c).

Table 1. Sum-of-squares table for the best-fit multiple regression model

Source	df	Sum of squares	Mean square	F	P
Model	12	22.19	1.85	11.95	<0.0001
Residual	226	34.98	0.15		
Total	238	57.18			

Table 2. Partial regression coefficients from the 'best' multiple regression modelling the effects of habitat, behaviour, the interaction between habitat and behaviour, and individual on locomotor speed

Variable	Coefficient	SE	Standardized coefficient
Intercept	-0.481***	0.119	0
Perch height	-0.115***	0.038	-0.205
Display	-0.289***	0.081	-0.268
Feed	-0.333***	0.104	-0.175
Rock substrate	-0.241**	0.121	-0.219
Wood substrate	-0.431***	0.150	-0.366
Perch diameter × display	-0.004*	0.002	-0.120
Perch diameter × feed	-0.012**	0.006	-0.110
Perch height × display	0.172*	0.104	-0.135
Individual 2	-0.257**	0.103	-0.176
Individual 10	-0.393**	0.166	-0.126
Individual 14	-0.183***	0.068	-0.161
Individual 18	-0.514**	0.160	-0.177

Significance of each coefficient determined by *t* tests and associated *P* values.

P* < 0.10; *P* < 0.05; ****P* < 0.005.

DISCUSSION

The study of animal movement is a central paradigm in behavioural ecology (Swingland & Greenwood 1983; Stamps 1995; Dingle 1996; Turchin 1998). Research has focused on quantifying the relationship between habitat and locomotion for a single, easily induced behaviour (e.g. predator escape) rather than the full range of behaviours realized in nature. While useful, these studies do not provide a full understanding of how habitat, behaviour and locomotion are related (Kenagy & Hoyt 1989; Stamps 1995; Firlie et al. 1998). In this respect our study represents a novel approach to understanding how animals move. Our findings show that habitat and behaviour, individually, are important for undisturbed locomotion. We confirmed that habitat (perch height, substrate type) and behaviour (displaying, feeding) significantly affect undisturbed locomotor speed (Tables 1, 2, Fig. 1a, b). In addition, we show that behaviour and habitat can interact to affect how animals move (Table 2, Fig. 1c).

Individual Effects of Habitat and Behaviour on Locomotion

Research examining the individual effects of habitat or behaviour on locomotor performance can be dichotomized into studies that measure maximal performance under idealized laboratory conditions and field studies that measure ecological performance of animals moving through their natural environment (Garland & Losos 1994; Irschick & Garland 2001). Previous studies of locomotor performance in lizards have found significant relationships between habitat (perch diameter and incline) and both maximal locomotor performance (e.g. Losos & Sinervo 1989; Losos & Irschick 1996) and ecological locomotor performance (Jayne & Irschick 2000; Mattingly & Jayne 2004). Surprisingly, our study found no relationship between incline, perch diameter and undisturbed speed.

In a field study of undisturbed ecological locomotor performance in the fringe-toed lizard, *Uma scoparia*, Jayne & Irschick (2000) found that undisturbed speed significantly decreased when lizards ran on steeper inclines. *Uma scoparia* lives in an open sand dune desert that has a fundamentally different structural habitat than the riparian Wet Beaver Creek habitat of *U. ornatus*, complicating direct comparisons of these species. A more comparable study found that habitat effects were minor in several species of arboreal *Anolis* lizards (Mattingly & Jayne 2004) whose structural habitat is more akin to that of *U. ornatus*. One explanation for the disparity between the findings for *Anolis* and *Urosaurus ornatus* versus *Uma scoparia* may be that both *Anolis* and *U. ornatus* generally move at submaximal locomotor speeds (Table 3), whereas *U. scoparia* routinely moves near its maximum speed during undisturbed locomotion (Jayne & Irschick 2000). *Uma scoparia* may typically move fast because it is especially vulnerable to predators while moving across relatively open sand dunes, whereas *U. ornatus* and *Anolis* may typically move slowly because they are more sheltered from predators within a complex three-dimensional arboreal habitat. This is supported by the relatively slow speed (0.48 m/s) that *U. ornatus* used during the single predator escape behaviour that we observed (a lizard moving away from a large insect). Thus, the influence of habitat variables apparent for maximal or near-maximal field speeds may not be relevant for animals that routinely use submaximal field speeds during undisturbed locomotion (see also Mattingly & Jayne 2005). However, we detected a significant effect of substrate type and perch height on speed, showing that previously overlooked habitat variables may be important for affecting undisturbed locomotion. Our results suggest that both behaviour (e.g. displaying and prey capture) and habitat (substrate, perch height) can influence undisturbed ecological performance, but many of the traditionally measured habitat variables (e.g. incline, perch diameter) have little influence on undisturbed speeds for animals moving at submaximal speeds.

We note that this hypothesis is testable and could prove general for arboreal or semiarboreal animals that move on complex surfaces. Future research could test this hypothesis among species in different habitat (e.g. desert dunes, arboreal, saxicolous) as well as within a single species that occurs in different habitat types (*U. ornatus* would be ideal for this type of study). We note that variability in maximal speed among individuals can be problematic when comparing undisturbed field speeds to average maximal speed. This could be addressed by gathering maximal speeds and field speeds from the same individuals and examining the effect of individual variation on the relationship between speed, habitat and behaviour. In addition, research focusing on locomotion during predator escape, the effects of other habitat components (e.g. substrate texture) and the relevance of additional performance traits (e.g. acceleration) would be beneficial. Finally, we suggest that findings based on maximum laboratory performance and experimentally manipulated habitat be examined in light of data on undisturbed field locomotion to determine whether and when habitat or behaviour affect ecological performance.

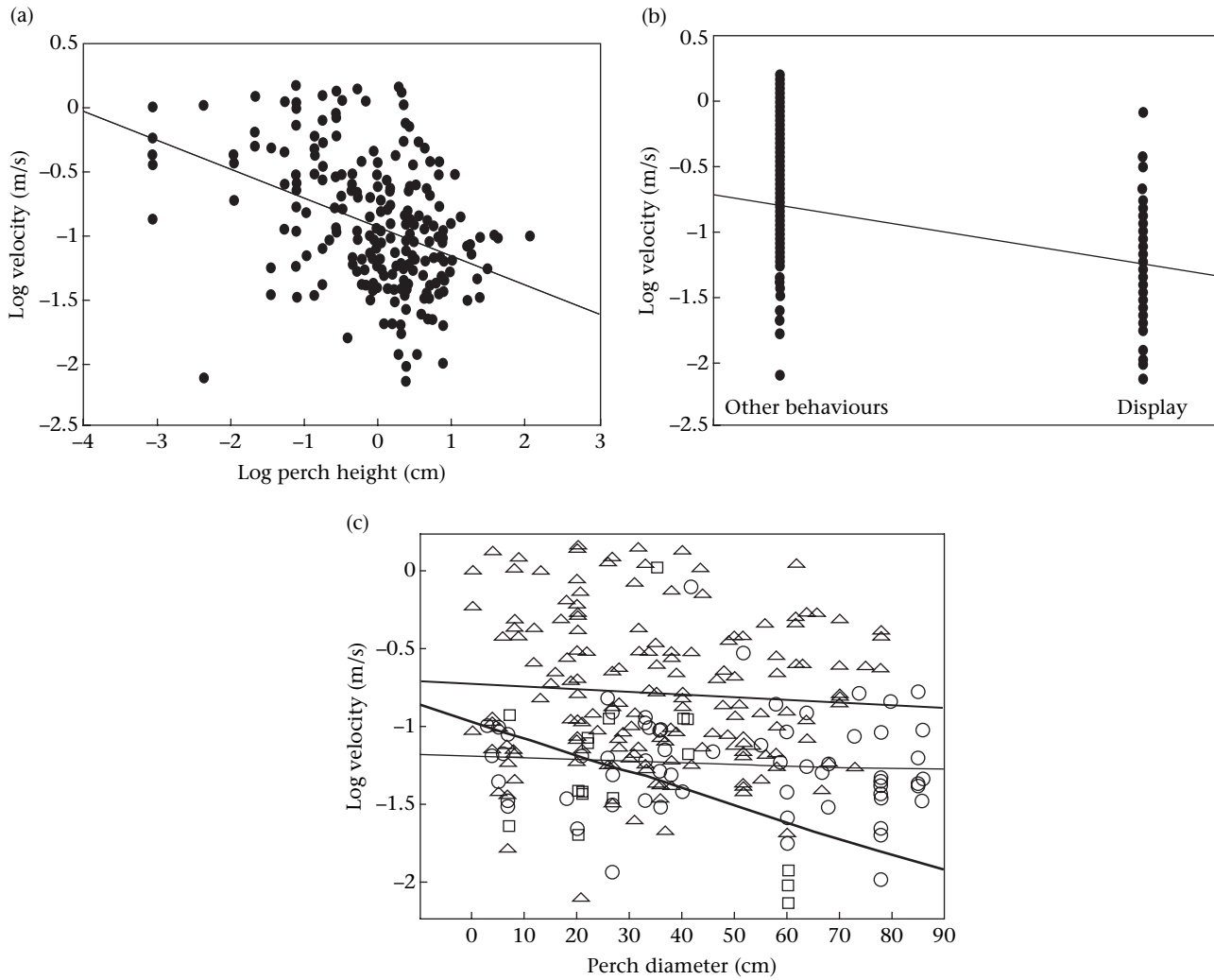


Figure 1. Relationship between habitat/behavioural variables and locomotor velocity for *Urosaurus ornatus* during undisturbed field locomotion. (a) Significant individual relationships in the multiple regression model between (a) perch height and velocity and (b) behaviour and velocity. (c) Relationships between perch diameter and velocity, grouped by behaviour (Δ : travelling; \square : feeding; \circ : displaying). Regression coefficients and significance tests are reported in Table 2.

A potential problem with comparing laboratory and field performance is that the distance and duration of movements in the field may limit an animal's ability to reach maximum speeds observed in the laboratory. Most laboratory racetracks measure maximum sprint speed over

0.25-m intervals along a 2-m racetrack (e.g. *U. ornatus*: Miles 1994; Meyers et al. 2006). In addition, laboratory studies show that lizards approach maximum speeds within $\sim 0.2\text{--}0.4$ s when running from a stand-still (Huey & Hertz 1982; Irschick & Jayne 1998). In our study,

Table 3. Patterns of habitat use and locomotor velocity during different behaviours in *Urosaurus ornatus*

	Perch height (cm)	Perch diameter (cm)	Incline (degrees)	Velocity (m/s)	Maximum speed (%)*	Distance
Feed	33.78 \pm 5.61 (4–87)	31.00 \pm 3.70 (7–60)	6.94 \pm 6.14 (–35 to 60)	0.15 \pm 0.07 (0.01–1.1)	5 \pm 1 (1–40)	18.37 \pm 5.82 (5–77)
Display	50.24 \pm 4.57 (0–200)	45.21 \pm 3.15 (3–86)	8.85 \pm 3.33 (–70 to 80)	0.09 \pm 0.01 (0.01–0.8)	6 \pm 3 (1–55)	27.28 \pm 4.38 (5–148)
Travel	29.11 \pm 2.20 (0–140)	34.15 \pm 1.54 (0–78)	–0.88 \pm 2.01 (–90 to 90)	0.27 \pm 0.02 (0.02–1.5)	16 \pm 2 (1–75)	16.12 \pm 1.11 (4–78)
Escape				0.48	24	

Means \pm SE and ranges (in parentheses) are presented for 15 adult males.

*Calculated from maximum sprint speed (ca. 2 m/s; Miles 1994; D. J. Irschick & J. J. Meyers, unpublished data).

mean movement distance was 0.17 m and mean movement duration was 2.1 s. These results show that *U. ornatus* probably had enough distance and time to generate maximum sprint speed during most movements, but chose not to do so.

Interactive Effects of Habitat and Behaviour on Locomotion

One of our key findings was the interactive effect of prey capture behaviour and perch diameter on locomotor speed. Our results show that *U. ornatus* experienced no change in speed when moving across a variety of perch diameters. However, the interaction between behaviour and habitat revealed a different conclusion: *U. ornatus* actually experiences a negative effect of perch diameter on speed during feeding behaviour but not during other behaviours (Fig. 1c). This finding highlights the need to take into account both the behavioural context and the habitat when attempting to understand variation in speed, direction and frequency of animal movement. Future research could attempt to unravel how habitat, behaviour and locomotor movements are causally related by experimentally manipulating the structural habitat within seminatural enclosures (e.g. Pounds 1988).

Acknowledgments

We thank Arizona Game & Fish for timely processing of our application. Molly Morris, Nancy Stevens and two anonymous referees gave comments that greatly improved the manuscript. This work was supported by National Science Foundation grants to D.J.I. (IOB 0421917) and S.M.R. (IOB 0520100).

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