Slip slidin' away: Demographic variation in movement behavior of the dune-dwelling lizard *Meroles anchietae*

Douglas A. Eifler [a], Maria A. Eifler [a,b,*], Elizabeth F. Liu [b], Brendan Luyanda [c], Kaera L. Utsumi [a,b], Tanaka E. Muradzikwa [c], Michael K. Kanyanga [d,1], Colleen A. Buchanan [b]

[a] *Erell Institute, 2808 Meadow Drive, Lawrence, KS, 66047, USA*
[b] *University of Kansas Biodiversity Institute, 1345 Jayhawk Boulevard, Lawrence, KS, 66045, USA*
[c] *Department of Wildlife Management and Ecotourism, University of Namibia, Private Bag, 1096, Katima Mulio, Namibia*
[d] *Namibia University of Science and Technology, 13 Jackson Kaujeua Street, Private Bag, Windhoek, 13388, Namibia*

A B S T R A C T

The shovel-snouted sand lizard, *Meroles anchietae,* is a small lacertid that inhabits the aeolian sand dunes of the Namib Desert. We conducted focal observations to characterize the movement patterns of adult male, adult female, and juvenile *M. anchietae* in their preferred habitat: dune slip faces. Movement varied considerably among demographic classes. Both adult males and females made longer moves than juveniles, but males moved less frequently than females or juveniles. Males exhibited shorter path lengths and shorter net displacements than females or juveniles. Turn angle distributions varied among classes, with females differing from the other two classes. For all three classes, the distribution of movement directions differed from uniform, with lateral moves across the slip face being most common. Movement across the slip face reflects both the ease with which lizards can navigate the substrate and behavioral factors such as foraging strategy and social interactions. Distance and direction pairings differed both from random expectations and among the demographic classes. Movement characteristics indicate that demographic classes respond to the environment differently, even while using the same habitat.

1. Introduction

Movement patterns reflect how animals perceive and respond to variation in their environment. Whether foraging, maintaining social relationships, thermoregulations or avoiding predation, movement is integral (Nathan et al., 2008; Smouse et al., 2010). Movement analysis can be used to understand responses to different environmental factors, as well as differences in how animals react to the same conditions (Nathan et al., 2008; Schick et al., 2008; Demšar et al., 2015; Kays et al., 2015). Sex and age are important factors contributing to intraspecific variation in behavior and ecology. Males and females can experience different social and reproductive challenges (Shine and Wall, 2005) which in turn affect their behavior. Ontogeny involves a series of physiological challenges and changes in diet, habitat requirements,

social circumstances, thermal constraints, and predation threats (Werner and Gilliam, 1984). Demographic variation in behavior and ecology can be explored through an examination of movement.

Lizard movement has been the subject of investigation for several decades, with information being collected for many species (e.g., Huey and Pianka, 1981; Miles et al., 2007; Perry, 2007). Most previous studies have relied on characterizing lizard movement through two common metrics: moves per minute (MPM) and proportion of time moving (PTM; Cooper, 2005; Perry, 2007). Few have examined the actual spatial and temporal aspects of movement paths (e.g., Leu et al., 2016; Utsumi et al., 2020), and many studies have relied on single MPM or PTM values to characterize a species or population (Perry, 2007). However, other studies on lizard search behavior have identified incidents of intraspecific variation (Huey and Pianka, 1981; Eifler et al., 2007; Childers and

Eifler, 2015; Garrison et al., 2017) or behavioral flexibility (Pietruszka, 1986; Durtsche, 1992; Eifler and Eifler, 1999; Greeff and Whiting, 2000; Eifler et al., 2008), which could be missed with single measurements of movement. In addition, variation in habitat structure can lead to changes in a lizard species' MPM and PTM (Attum and Eason, 2006; Wasiolka et al., 2009a, 2009b; Donihue, 2016). For lizards, flexibility in foraging (and more generally movement while foraging) is severely understudied (Huey and Pianka, 2007) and is best detected through measurements that include spatial or temporal aspects of movement paths.

The shovel-snouted sand lizard, *Meroles anchietae* (formerly *Aporosaura anchietae*), is a small lacertid that inhabits the aeolian sand dunes in the hyper-arid Namib Desert (Louw and Holm, 1972). The species is omnivorous and consumes a variety of plants and arthropods (Robinson and Cunningham, 1978; Murray and Schramm, 1987; Robinson, 1987; Nagy and Shemanski, 2009). Reproduction appears to be aseasonal with breeding possible throughout much of the year (Louw and Holm, 1972; Goldberg and Robinson, 1979). *Meroles anchietae* has many morphological adaptations for inhabiting sand, including fringed toes that allow running across dunes at high speeds and a shoveled snout for both penetrating into and moving within sand when buried (Louw and Holm, 1972; Arnold, 1995). The ability of *M. anchietae* to dive into and move within the sand to evade predators, as well as extreme microclimatic variation, is a behavior that has allowed them to exploit dune tops and slip faces, which are often devoid of vegetation (Louw and Holm, 1972). Their locomotion has become so specialized that they have difficulty moving effectively on other substrates (Louw and Holm, 1972; Robinson and Barrows, 2013). Even in a relatively simple environment (i.e., open sand), variation in movement is likely because lizards of different sizes could experience varying levels of difficulty when moving across the sand (Carothers, 1986; Jayne and Ellis, 1998; Jayne and Irschick, 2000).

Our study describes animal movement by re-creating movement paths, wherein movement is viewed as a sequence of discrete displacements (step lengths) and bearings (turn angles) that represents the geometry of the movement path and provides insights into patterns of behavior (Turchin, 1998; Edelhoff et al., 2016). Through our characterization of their movement patterns, we anticipated finding demographic variation among adult male, adult female, and juvenile *M. anchietae*.

2. Materials and methods

We collected data on the slip faces of Station Dune at the Gobabeb Research and Training Centre (GRTC), located in the Namib-Naukluft National Park, Namibia (23.561836°S, 15.041708°E), from December 29, 2018 to January 14, 2019. We collected data each day during morning (08:30–11:00 h) and afternoon (16:30–18:30 h) activity periods (Seely and Pallett, 2012; Evans et al., 2017). Focal observations were carried out by teams of 3 people, lasting for 15 min or until the observed lizard left the slip face or disappeared from the observers' view. One person monitored movement, relaying data to a second person who recorded the information. The third person used binoculars to observe non-movement behaviors. Prior to the start of the study, we practiced observation components until interobserver variation was <2% for observers performing the same task. Observers performing the same tasks participated in training sessions where they observed the same animals and compared recordings. In addition, observers responsible for estimating distances practiced their estimations against known distances, from the distances at which focal observations were conducted. When we sighted an unobserved *M. anchietae* in our study area, we slowly approached the lizard to within ca. 10–15 m of the slip face base, which we deemed far enough to minimize disturbance while providing a clear view of the animal. Observers did not come onto or closer to slip faces during observations. Most observation periods were conducted without the observers needing to move from their initial location. We allowed lizards a 5 min habituation period before we began

recording data for the focal observation. Lizards appeared unaffected by observer presence, as they continued to forage and make moves that often brought them closer to the observers.

To characterize movement, we tallied the number of moves a lizard made during the observation periods, as well as the direction and the length of each move. We defined a move as any body displacement of at least 1 body length that was separated from other moves by any perceptible pause in motion. We measured angular direction on the slip face so that movement perpendicular to the base and towards the crest = 0° and movement perpendicular to the crest and towards the base = 180°. To facilitate data collection, we envisioned the slip face as the face of a clock, with 12:00 at the crest and 6:00 at the base. Lizard movement on the clock face was estimated to the closest 1-h (i.e., 30°) increment. If the lizard appeared to be directly between two increments, we rounded to the next increment in a clockwise direction. Move lengths were estimated to the nearest 0.5 m.

Each lizard was observed only once; we captured unmarked lizards at the end of each observation, measured their snout-vent length (SVL) and mass, and confirmed their sex by probing. Lizards ≤32 mm SVL were too small to sex and were classified as juveniles. Finally, each lizard was uniquely marked using colored beads attached to the base of the tail (e.g., Evans et al., 2017). We released lizards where they were first sighted within 24 h of capture. Several juveniles we observed eluded capture, in which case we recorded their age class and refrained from additional observations on that slip face section to avoid a second observation on the unmarked lizard.

For non-movement behaviors, we recorded the number of head turns, body repositions, and head taps. We defined head turns as movement of the head on any plane while the body remained stationary, body repositions as shifts of the torso involving at least 2 limbs with a displacement of <1 body length, and head taps as lowering and then raising of the head to and from the ground. The presumed function of these behaviors was investigation or monitoring, with head tapping possibly serving a function related to olfaction (Louw and Holm, 1972).

We calculated path length as the sum of all move lengths for an observation period and net displacement as the straight-line distance between the location of the lizard at the start and end of an observation period; path length and net displacement were only determined for animals observed for an observation period of full duration (i.e., 15 min). To determine the end point of an observation, we designated the start location as (0,0) and used each move length and associated angular direction to calculate the lizard's location (i.e., x,y coordinates) at the end of each move and ultimately the end of the observation. In addition, we calculated moves per minute (MPM; = number of moves observed/min observed). We determined turn angles by calculating the difference in direction of adjacent moves.

Move directions and turn angles were binned into 30° increments for analyses. We further combined directions for some comparisons. To compare frequency of moves relative to the base-crest line, mirror directions were combined (i.e., 90° and 270°). Further, we combined directions to create broad directional categories: up (= 330°, 0° and 30°), down (= 150°, 180° and 210°), and lateral (= 60°, 90°, 120°, 240°, 270°, and 300°). We examined the pairing of move length and move direction by comparing the three direction categories, up, lateral, and down, with move lengths pooled into three length categories, short (0.5 m), medium (1 and 1.5 m), and long (≥2 m). We used a log-linear model to determine whether the observed pairings of move length and move direction differed from random expectations or among the demographic classes.

We performed generalized linear model analyses, using a stepwise selection process (entry and exit = 0.1), to distinguish the relative role of demographic class and SVL on movement variables. For move length, path length, move rate, and net displacement, demographic class was the lone variable in the resulting statistically significant models, indicating that class was more pertinent than body size for our metrics. We proceeded with analyses comparing demographic classes. We initially compared all three demographic classes using the Kruskal-Wallis test,

followed by a Dunn's test for pairwise comparisons. For movement direction, turn angles, and movement lengths, we used a chi-square test to compare the distributions of values among all three classes, with additional chi-square analyses for pairwise comparisons. We examined standardized residuals to aid interpretation of chi-square results. We used Minitab version 18 (State College, PA USA), and R version 3.5.1 (R Core Team, 2018) for data analyses with a P = 0.05 significance level.

3. Results

We observed 63 lizards, which made 2332 moves: 16 adult males (232 moves), 13 adult females (543 moves), and 34 juveniles (1557 moves). Size differences were apparent among the three demographic classes (males > females > juveniles; Table 1, Fig. 1).

The behavior of *M. anchietae* on the slip faces varied considerably among demographic classes. Both males and females exhibited longer move lengths than juveniles (Dunn's: z = 3.64, P = 0.0003; z = 2.06, P = 0.039, Table 2), but males moved less frequently than females or juveniles (MPM; Dunn's: z = 2.43, P = 0.015; z = 3.43, P = 0.0006, Table 2). Males exhibited shorter path lengths than females and juveniles (Dunn's: z = 2.17, z = 0.0301; z = 2.95, P = 0.0031, Table 2). Males also traversed less area during an observation, as evidenced by their smaller net displacement compared to females and juveniles (Dunn's: z = 2.48, P = 0.131; z = 2.61, P = 0.0089, Table 2). Head turns and body repositions did not vary among classes, but males tapped their heads to the substrate less frequently than juveniles (Dunn's: z = 3.32, P = 0.0009, Table 2).

For all three classes, the distribution of move directions on the slip face varied from uniform (males: χ^2 = 25.69, df = 11, P = 0.007; females: χ^2 = 162.36, df = 11, P < 0.001; juveniles: χ^2 = 455.84, df = 11, P < 0.001, Fig. 2). Further, there were differences in the distribution of move directions among the three classes, with each class differing from the others (Table 3, Fig. 2). Although lateral movement was the most common move direction for all three classes, standardized residuals ($\geq|2|$) indicated a strong tendency for males to move upslope (0°) and not directly right or left (90° and 270°, respectively), and for females to show a disinclination to move towards the crest. Most turn angles were relatively small; the most common turn category was 0° for all three classes (Fig. 3). Turn angles varied among classes, with pairwise comparisons indicating that females differed from the other two classes (Table 3, Fig. 3). Move length distributions also varied among classes, with all classes being different in pairwise comparisons (Table 3, Fig. 4). Standardized residuals ($\geq|2|$) indicate that longer moves were more common for males and females than for juveniles.

Move length and direction pairings differed from random expectations (Log-linear model: G = 38.2, df = 12, P = 0.0001, Fig. 5) and among the classes (G = 96.1, df = 16, P < 0.0001). Lateral moves of short and medium length were most common for all classes (Fig. 5). An examination of each class revealed that distance and direction were not independent for males and juveniles (males: χ^2 = 14.0, df = 4, P = 0.007; juveniles: χ^2 = 14.0, df = 4, P = 0.007), but they were for females (χ^2 = 5.6, df = 4, P = 0.229). For juveniles, medium moves downslope were observed more than expected, and long moves upslope occurred less than expected. For males, long lateral moves were more frequent than expected, and long moves upslope were less common than expected.

Table 1

Body size for each demographic class. Values are presented as mean (SE), followed by ANOVA results indicating significant variation among classes. All pairwise comparisons were different (Tukey test, P < 0.001).

|	Juveniles	Females	Males	
	N = 31	N = 13	N = 16	
SVL (mm)	28.7 (0.3)	43.3 (0.5)	49.1 (0.6)	$F_{2,57}$ = 693, P < 0.001
Mass (g)	0.76 (0.02)	2.73 (0.08)	4.15 (0.14)	$F_{2,57}$ = 558, P < 0.001
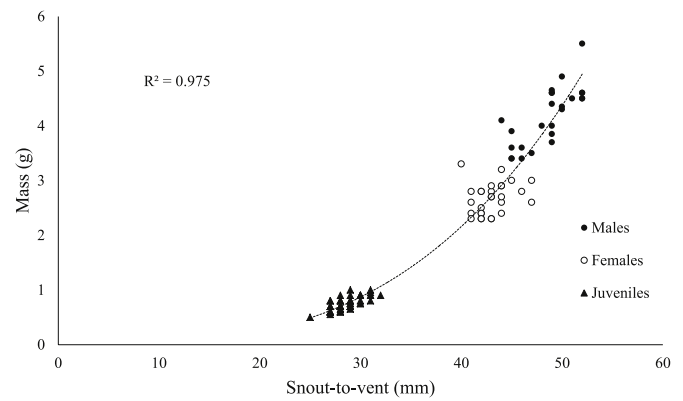
Fig. 1. Body size for *Meroles anchietae* by demographic class.

Table 2

Summary statistics for behavioral variables. Values are presented as medians (range). Overall comparisons were made with Kruskal-Wallis tests. Classes within a row with unlike subscripts were statistically different (Dunn's test, see Results text for test statistics).

	Juveniles	Females	Males	Kruskal-Wallis Test Statistics
Move length (m)	0.7 (0.5–1.4)$_a$	0.8 (0.6–4.2)$_b$	1.0 (0.6–1.7)$_b$	H = 13.6, P = 0.001
Path length (m)	32 (12–90)$_a$	30 (8–103)$_a$	7 (2–31)$_b$	H = 9.2, P = 0.010
Move rate (MPM)	2.6 (0.1–9.7)$_a$	2.5 (0.2–10.5)$_a$	0.6 (0.1–5.5)$_b$	H = 12.8, P = 0.002
Net displacement (m)	12 (0–29)$_a$	13 (2–41)$_a$	4 (1–11)$_b$	H = 8.55, P = 0.014
Head turn (/min)	2.7 (0.8–7.3)	3.3 (1.1–5.7)	2.3 (0.0–6.3)	H = 1.38, P = 0.501
Body reposition (/min)	0.4 (0.0–1.5)	0.4 (0.0–1.2)	0.1 (0.0–1.5)	H = 5.23, P = 0.073
Head tap (/min)	0.9 (0.0–5.2)$_a$	0.3 (0.0–5.5)$_{a,b}$	0.1 (0.0–2.3)$_b$	H = 12.8, P = 0.002
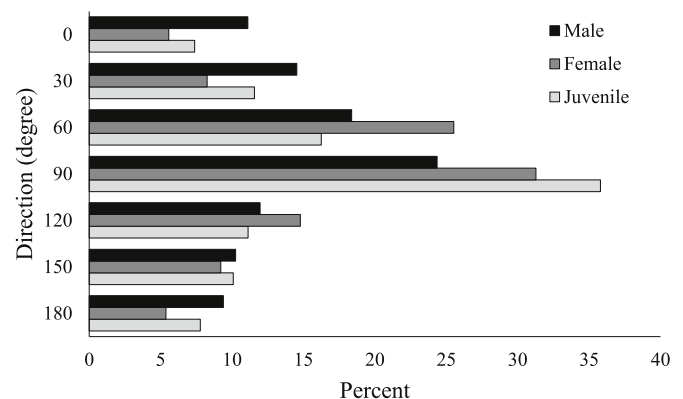
Fig. 2. Move direction for three demographic classes of *Meroles anchietae*. Directions are binned in 30° increments, with mirror directions pooled. Movement directly up the slip face = 0° and directly down = 180°. The frequency distributions were assembled using 1557 juvenile, 543 adult female, and 232 adult male movements.

4. Discussion

Movement patterns differed among *Meroles anchietae* demographic classes. However, body size is tightly tied to demographic class and certainly plays a role in movement. Physical features, such as compactness of the sand and angle of incline, likely interact with biotic

Table 3

Statistical results from comparing the distributions of movement variables. Results are presented as χ^2_{df} (P).

	Overall	Male-Female	Male-Juvenile	Female-Juvenile
Direction (0–180°)	49.5_{12} (<0.001)	24.3_6 (<0.001)	14.2_6 (0.028)	33.9_6 (<0.001)
Turn angle (°)	24.1_{12} (0.020)	13.8_6 (0.032)	10.6_6 (0.100)	12.9_6 (0.044)
Step length (m)	87.9_{10} (<0.001)	31.1_5 (<0.001)	80.7_5 (<0.001)	21.5_5 (0.001)
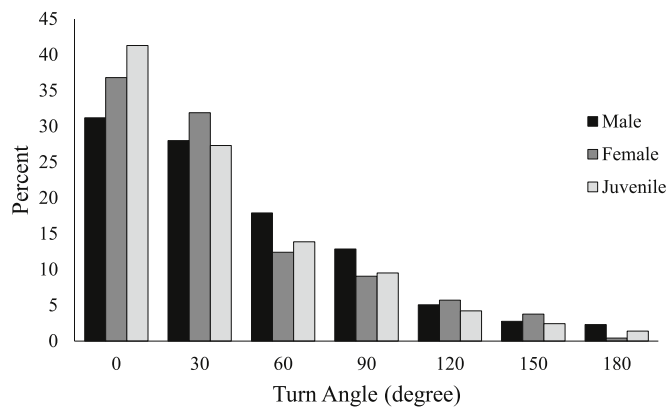
Fig. 3. Turn angles for three demographic classes of *Meroles anchietae*. Directions are binned in 30° increments. The frequency distributions were assembled using 1523 juvenile, 508 adult female, and 215 adult male turns.
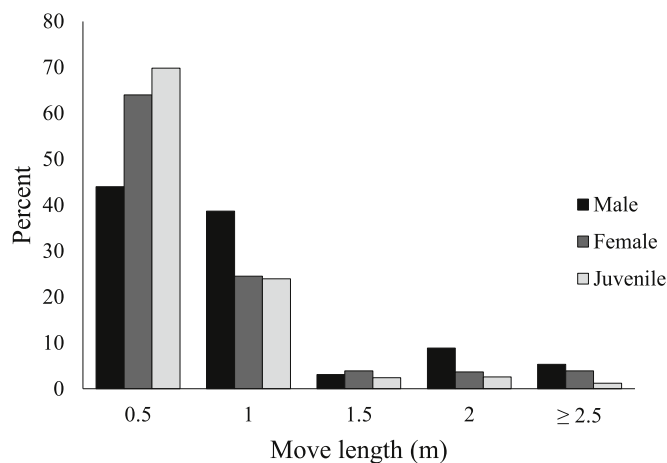
Fig. 4. Movement lengths for three demographic classes of *Meroles anchietae*. Lengths were estimated to the nearest 0.5 m. The frequency distributions were assembled using 1557 juvenile, 514 adult female, and 225 adult male movements.

constraints arising from differences in body size, which are reflected in foraging or energetic costs, to influence differences in movement patterns we observed. All three classes occur in the same structurally simple habitat (steep sand slopes virtually devoid of vegetation), but differences in movement patterns could arise from differential challenges as they search for food, avoid predation, or more generally try to move efficiently through the environment.

Movement on slip faces, which are very steep and unstable surfaces, is challenging; the slightest disturbance can cause sand to slide down slope. Regardless of compactness of the surface, moving upslope can be energetically costly (Farley and Emshwiller, 1996) and performance on inclines, as measured by speed and form of locomotion, also can be

negatively affected (Irschick and Jayne, 1999). Lizards moving across loose sand choose paths that reduce energetic costs and increase effectiveness (Carothers, 1986; Jayne and Ellis, 1998; Jayne and Irschick, 2000). The lizard *Callisaurus draconoides* avoids running up or down dune slopes, preferentially choosing lateral escape paths (Irschick and Jayne, 1999). *Meroles anchietae* exhibited a similar tendency to rely heavily on lateral moves, while minimizing the frequency and distance of movements directly up slope. The dune dwelling lizard *Uma scoparia* avoids moving directly downhill on very steep surfaces, instead tending to run uphill (Jayne and Irschick, 2000). Species differences in the tendency to run up slope might reflect differences in slope characteristics, experienced energetic costs, or other ecological factors. Although we did not measure slope incline, we estimate that the slip faces where we conducted observations exceeded 45° from horizontal, with some considerably steeper. Slope incline can affect the paths lizards choose (Jayne and Irschick, 2000), but the possible effect of body size differences between adults and juveniles on movement cannot be ignored.

Energetic costs and movement efficiency vary with body size and substrate, with smaller lizards being less influenced by incline and substrate (Huey and Hertz, 1982, 1984), which could account for the tendency of *M. anchietae* juveniles to engage in prolonged runs across a slip face in response to a threat, whereas adults tend to bury themselves (Evans et al., 2017). Mass of the average juvenile *M. anchietae* we measured was about $\frac{1}{5}$ the mass of an adult male (Table 1); juveniles will likely incur relatively lower costs and experience different levels of effectiveness than adults when traveling in the same direction over the same distance on a slip face. If juveniles can undertake higher rates of movement with lower costs than adults, differences in ecology could promote further differences in movement. Male *M. anchietae* tend to move up slope more commonly than the other classes, a potentially energetically costly strategy for the largest demographic class. Investigations on the relative energetic costs of movement on sandy slopes by demographic class or body size are merited. Perhaps, for example, seeking positions higher on slopes provides males an advantage for monitoring for food or engaging in social interactions.

Foraging can play a role in shaping movement patterns when the demographic classes vary in their diet and ability to detect food. Lizard foraging can vary with sex (Durtsche, 1992; Lister and Aguayo, 1992; Eifler and Eifler, 1999), as well as age or size (Paulissen, 1987; Perry, 1996; Greeff and Whiting, 2000; Eifler et al., 2007). Intraspecific differences in lizard body size often are associated with variation in the size and type of invertebrate prey consumed (Schoener, 1968; Simon, 1976; Capel-Williams and Pratten, 1978; Paulissen, 1987), as well as the extent of reliance on plant material (Pough, 1973; Whiting and Greeff, 1997). *Meroles anchietae* is omnivorous, but the demographic classes appear to differ in their consumption of plants and arthropods, with females consuming seeds more than males and juveniles eating smaller food items than adults (Robinson and Cunningham, 1978; Murray and Schramm, 1987; Robinson, 1987; Nagy and Shemanski, 2009). For lizards, differences in diet are often associated with differences in search strategy ($\approx$ foraging mode; Huey and Pianka, 1981). Patterns of food availability and variation in the detection range of animals based on their body size will influence the movements that most effectively allow them to encounter prey. Lizards often search for prey using a series of movements and pauses (= saltatory search; O'Brien et al., 1990), with food more likely to be detected during pauses (O'Brien et al., 1986; Avery, 1993). Foragers can structure their saltatory search pattern to food characteristics and their abilities (Pietruszka, 1986; Evans and O'Brien, 1988; Ehlinger, 1989). Short, frequent moves allow for effective detection of hard to find food types (Andersson, 1981; Getty and Pulliam, 1991; Anderson et al., 1997), and are an effective search strategy for animals with limited detection ranges (O'Brien et al., 1990). Our method of describing *M. anchietae* movement readily detects demographic differences in the move-pause patterns of their foraging. If *M. anchietae* juveniles rely on more difficult to detect food items, the
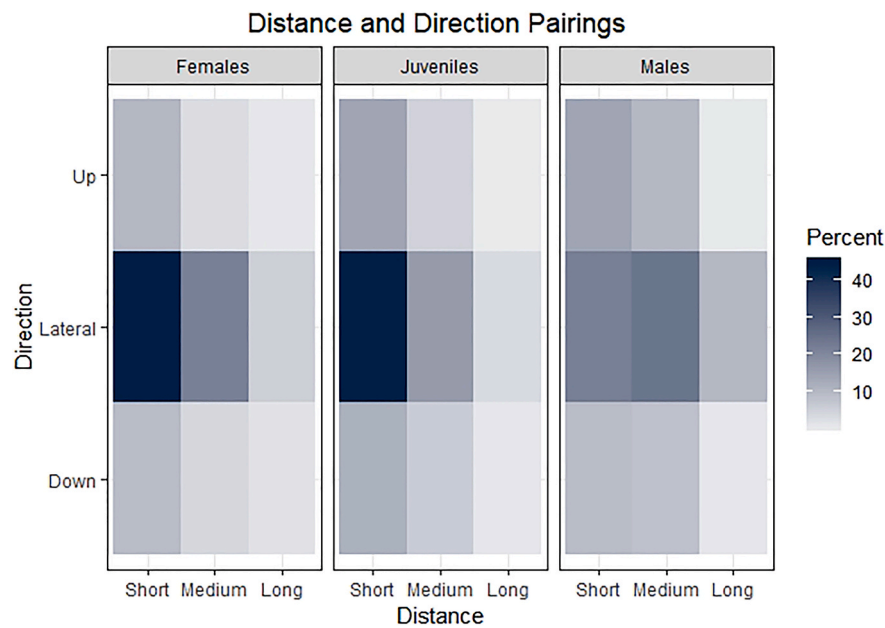
Distance and Direction Pairings

Fig. 5. Heat map indicating the frequency of observed moves, with pairings of distance (short, medium, and long) and direction (up, lateral, and down). N = 527 female moves, 1556 juvenile moves, and 226 male moves.

shorter, more frequent moves we recorded could improve their foraging efficiency. Similarly, if head tapping functions in olfactory monitoring related to food, the higher rates exhibited by juveniles could be related to demographic differences in foraging strategy and diet. Even if adults and juveniles have the same diet, shorter, more frequent moves would be expected of juveniles because of the reduced field of view associated with smaller body size. Juveniles are closer to the ground, and the area that they can effectively scan is less than that of adults merely due to differences in height above the substrate.

Foraging considerations and the energetics of moving on slip faces align with our observations of *M. anchietae* movement. But other factors can influence movement strategies as well. Slip face surfaces can reach potentially lethal temperatures for *M. anchietae*, which employs a range of thermoregulatory behaviors, including its renowned "hot-foot dance" and sand-diving (Louw and Holm, 1972). Body size can influence thermoregulation (Martín and López, 2003; Angilletta, 2009), and could account for differences in the movement patterns we recorded. Lizard social behavior can be a consequence of both age and sex differences (Baird et al., 1996; Eifler et al., 2007). The social system of *M. anchietae* needs more detailed characterization to understand how movement might relate to social functions. Even though *M. anchietae* is not considered territorial, we have observed aggressive conspecific interactions. Aggression, coupled with a breeding system that appears to occur year round (Louw and Holm, 1972; Goldberg and Robinson, 1979) suggests that the different demographic classes could have markedly different social requirements, which could influence movement patterns. Finally, predation risk can vary demographically for lizards and lead to differences in behavior (Stamps, 1983). Indeed, *M. anchietae* adult males sometimes predate on juveniles (Liu et al., 2019), presenting a risk that adults do not encounter. Predation risk can be associated with both increases and decreases in movement, depending on the circumstances (Downes and Bauwens, 2002). The role of head tapping is unclear, but if involved in olfactory monitoring (Louw and Holm, 1972), head tapping could be used to assess predation risk and could account for the higher rates exhibited by juveniles. Lizards can assess predation risk using olfactory cues (Downes and Adams, 2001). The extent to which additional factors influence movement requires further investigation.

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