Western North American Naturalist 80(1), © 2020, pp. 11–18

Habitat-dependent search behavior in the Colorado Checkered Whiptail (*Aspidoscelis neotesselata*)

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Abstract.—We compared the movement patterns of foraging Colorado Checkered Whiptails (*Aspidoscelis neotesselata*) in 2 different habitat types: shrub-grassland and pinyon pine–juniper woodland. We characterized movement by (1) segmenting movement paths into step lengths and turn angles and (2) determining first-passage times (FPTs). Lizards differed in their pattern of movement in the 2 habitats. FPTs were shorter in the pinyon pine–juniper woodland habitat and were positively correlated with ground cover. Lizards also moved more frequently, had longer step lengths, and traveled greater total distances in the pinyon pine–juniper woodland. There were no habitat differences in turn angles, net displacement, or movement path straightness. Habitat-based differences in movement might reflect differences in prey availability and predation risk.

Resumen.—Comparamos los patrones de movimiento de los lagartos cola de látigo cuadriculados de Colorado (*Aspidoscelis neotesselata*) en dos clases de hábitat: pradera de arbusto y bosque de piñón y junípero. Caracterizamos el movimiento por (1) segmentar las veredas de movimiento en longitudes de paso y ángulos de giro y (2) determinar el tiempo del primer avance (TPA). Se diferenciaban los lagartos en sus patrones de movimientos entre los hábitats. En el bosque de piñón y junípero, los TPA eran más cortos y se correlacionaban positivamente con la cobertura del terreno. Además, los lagartos acá se movieron más frecuentemente, tuvieron longitudes de paso más largos y viajaron distancias totales más largos. No había diferencias de ángulos de giro, desplazamiento neto o rectitud del camino entre los hábitats. Los tiempos del primer avance aumentaban con el nivel de cobertura vegetal en el hábitat del bosque. Las diferencias de movimiento basadas en el hábitat pueden reflejar diferencias de la disponibilidad de presa y el riesgo de depredación.

The movement of animals reflects how they perceive and respond to variation in their environment. Movement can be integral to activities such as foraging, breeding, dispersal, and migration. An appreciation of movement across spatial and temporal scales can also lead to an increased understanding of ecological processes that affect animals (Nathan et al. 2008, Smouse et al. 2010). Recent advances in technology and analysis methods have led to a greater ability to describe movement, examine the influence of environmental factors on movement, and predict the effect of environmental change on movement patterns (Nathan et al. 2008, Schick et al. 2008, Demšar et al. 2015, Kays et al. 2015). Search behavior involves movement with the objective of detecting resources whose location is not fully known. Animals are expected to engage in search strategies that reflect available information concerning resource distribution and detectability. Among foraging animals searching for food, diversity in habitat structure could warrant variability in search paths.

Many studies attempt to describe animal movement by re-creating movement paths. Viewing movement paths as a sequence of discrete displacements (step lengths) and bearings (turn angles) allows for describing the geometry of movement paths and provides insights into patterns of behavior (Turchin 1998, Edelhoff et al. 2016). Less data-intensive

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methods such as first-passage times (FPTs) also might be able to characterize movement in a fashion that still provides insights into behavior. First-passage time has been defined as the time required for an animal to leave a circle of a given radius (Johnson et al. 1992, Fauchald and Tveraa 2003). First-passage time has been used to identify changes in behavioral phase, area-restricted searching, or migration (Sommerfeld et al. 2013, Le Corre et al. 2014, Gurarie et al. 2016), and has been used to identify the scale at which animals interact with the environment (Johnson et al. 1992, Pinaud and Weimerskirch 2005, Bailleul et al. 2008, Le Corre et al. 2008) and to understand resource distribution (Pinaud and Weimerskirch 2005, Henry et al. 2016).

Interest in lizard movement and foraging has been keen for several decades; information has been collected for a large number of species and has provided insights into evolutionary ecology and physiology (Huey and Pianka 1981, Miles et al. 2007, Perry 2007). Most previous studies have relied on characterizing lizard movement through 2 common metrics: moves per minute and proportion of time moving (Cooper 2005, Perry 2007). Few have examined the actual spatial and temporal aspects of movement paths (Leu et al. 2016), and many studies have relied on single moves per minute or percent time moving values to characterize a species or population (Perry 2007). However, other studies have identified 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) in lizard search behavior. Variation in habitat structure can lead to changes in lizard moves per minute and percent time moving (Attum and Eason 2006, Wasiolka 2009a, 2009b, Donihue 2016). For lizards, flexibility in foraging (and more generally in movement) is severely understudied (Huey and Pianka 2007).

We examined variation in search behavior and its relationship to habitat structure for the Colorado Checkered Whiptail, *Aspidoscelis neotesselata*, a triploid parthenogenetic lizard occurring in southeastern Colorado (Walker et al. 1997). This species is found in a variety of habitats including grasslands, shrublands, pinyon pine–juniper woodlands, and human-disturbed areas, where they are diurnal foragers that eat a variety of arthropods (Knopf 1966, Paulissen et al. 1993, Hammerson 1999). They have overlapping home ranges and a relatively high tolerance for conspecifics (Knopf 1966, Leuck 1982, 1985). For a unisexual species with minimal conspecific agonistic behavior, foraging is the primary activity for surface-active individuals. We hypothesized that movement path measurements (step length and turn angle) and FPTs would be different for *A. neotesselata* foraging in shrub grasslands compared to those foraging in open woodlands. We expected shorter FPTs and longer step lengths at the woodland site because more open areas should require lizards to spend less time searching for prey than heavily vegetated areas, and because open areas expose lizards to a higher risk of predation.

Methods

We studied movement of adult *A. neotesselata* at the Fort Carson military installation (southeast of Colorado Springs, El Paso County, CO). From 5 June to 13 July 2018 between 08:00 and 11:30, we conducted observations of *A. neotesselata* movement in 2 populations at sites separated by >16 km; our first site ("grassland"; 38.467° N, 104.733° W) was dominated by grasses and shrubs, particularly Indian ricegrass (Poaceae: *Achnatherum hymenoides*), four-winged saltbush (Amaranthaceae: *Atriplex canescens*), needlegrasses (Poaceae: *Hesperostipa neomexicana* and *H. comata*), and blue grama (Poaceae: *Bouteloua gracilis*). Our second site ("woodland"; 38.465° N, 104.933° W) was characterized by trees, especially pinyon pine (Pinaceae: *Pinus* spp.) and juniper (Cupressaceae: *Juniperus monosperma*), with scattered shrubs and clumps of grass. In addition to differences in vegetation, our woodland site was more open and had more bare rock substrate than our grassland site (Figs. 1, 2).

We conducted focal observations for 15 min, characterizing movement using (1) first-passage times (FPT) and (2) path segmentation (i.e., distance and direction of travel for each 1-min interval during observations). We tracked movements by placing location markers for our focal *A. neotesselata* at the starting point and at each 1-min interval, resulting in 16 locations for a full observation. At the end of

Fig. 1. Grassland site, El Paso County, Colorado. We conducted observations in the foreground and did not work with lizards near the trees in the back.

Fig. 2. Woodland site, El Paso County, Colorado.

each observation, the lizard was captured by noosing, measured (mass [g] and snout–vent length [mm]), and marked with a unique color code that used nontoxic paint pens. No lizard was observed more than once.

Two or 3 researchers observed each focal animal. Researchers coordinated activity to maintain visual contact with the lizard, determine FPTs, and ensure accurate placement of markers. During observations, we maintained as great a distance as possible while maintaining visual contact (>5 m). Marker placement occurred only after the lizard was >10 m distant.

We used an imaginary circle with a 1-m radius centered on the lizard's initial position at the start of each 1-min interval for determining FPT. We opted for a single 1-m-radius

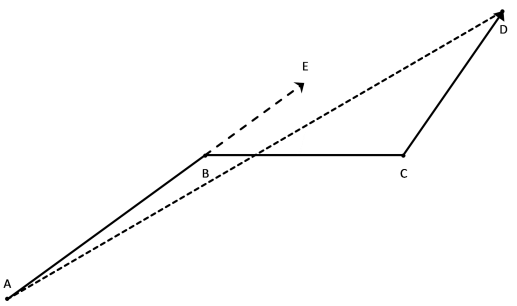

Fig. 3. Hypothetical movements of a lizard (solid lines) to demonstrate our 5 measurements for movement paths. Segments AB, BC, and CD depict step length. The angle EBC, representing the change in direction between consecutive steps AB and BC is a turn angle (0°–180°). The sum of the lengths for the segments representing sequential 1-min locations for the lizard (i.e., AB + BC + CD) is the path length. Net displacement, the straight-line distance the animal traveled (segment AD), is shown by the dashed line. The ratio of net displacement to path length (with values from 0 to 1) is the straightness index (i.e., AD/[AB + BC + CD]).

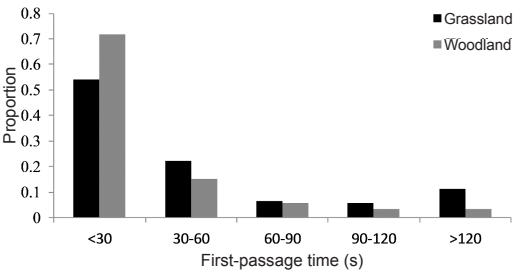

Fig. 4. First-passage time (FPT) distribution for grassland and woodland sites.

circle based on our initial observations as well as on previous work with similar species (Eifler et al. 2012). If a particular FPT lasted >1 min, the next FPT was initiated at the start of the subsequent 1-min interval. Prior to observations, observers practiced visually estimating 1-m distances and were proficient to within 5% (±5 cm). During observations, we also noted significant behaviors that might have affected FPTs (i.e., digging and eating). To minimize the bias of nonsearching behavior for FPTs, we excluded intervals wherein observations confirmed that the animal was engaged in digging behavior (Sommerfeld et al. 2013). For each FPT, we determined the proportions of trees and ground vegetation within the 1-m-radius circle by using line-intercept transects of 1 m in each of the 4 cardinal directions.

After observations, we measured the distance and direction between sequential 1-min location markers. From the sequence of locations, we calculated the path characteristics of *step length*, *path length*, *net displacement*, *straightness index*, and *turn angle* (Fig. 3). For intervals that involved movement, step-length is defined as the straight-line distance between consecutive 1-min locations, path length is the sum of all step lengths for an observation period, net displacement is the straight-line distance between initial and final locations, the straightness index is the ratio of net displacement to path length (values from 0 to 1), and turn angles are the change in direction between consecutive steps (values from 0° to 180°; Fig. 3). For analyses, step lengths, turn angles, and FPTs from all lizards in a habitat type were pooled, but each lizard's path length, net displacement, and straightness index were calculated and compared individually. Statistical analyses were conducted using R (version 3.4.3; The R Foundation for Statistical Computing, Vienna, Austria). We used chi-square analysis to compare frequency distributions for the 2 study areas. A general linear model was developed to examine the relationship between FPT (log-transformed) and habitat measurements: ground cover, tree cover, and their interaction with site. We used Mann–Whitney tests to compare linear path characteristics and FPT, and circular statistics (Watson–Williams, Watson's, and Raleigh tests) to make comparisons of mean turn angles, as well as to test for uniformity and conformity to von Mises distributions (Batschelet 1981).

Results

We observed 21 lizards at the grassland site and 22 lizards at the woodland site. Both FPT and path segmentation analysis indicate that foraging *A. neotesselata* moved differently in the 2 habitats. First-passage times were longer at the grassland site (Table 1), and the distribution of FPTs differed between sites (chi-square test: $\chi^2 = 12.4$, df = 4, $P = 0.014$; Fig. 4). FPT was related to habitat characteristics (ground cover, $F_{1,286} = 17.6$, $P < 0.001$; tree cover, $F_{1,286} = 7.3$, $P = 0.007$; tree cover * site interaction, $F_{1,286} = 5.0$, $P = 0.026$), with additional site differences not

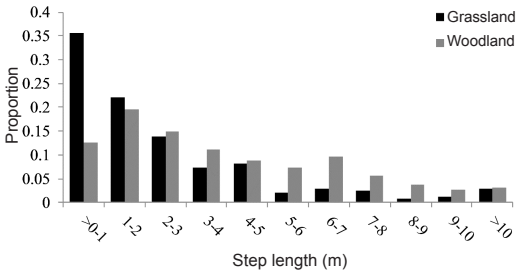

Fig. 5. Step length distribution for grassland and woodland sites. Intervals wherein there was no movement are not depicted.

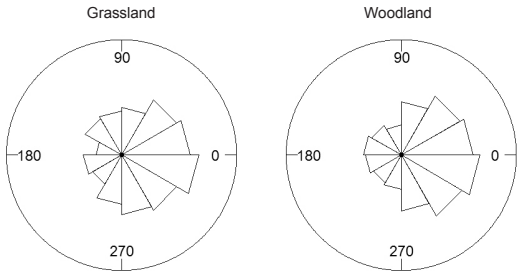

Fig. 6. Turn angle distribution for grassland and woodland sites. Turn angles are binned in 30° increments.

TABLE 1. Summary of movement parameters for each habitat. We pooled values from all observed lizards within each habitat to analyze FPT, step length, and turn angles (unit, pooled sample size for woodland, grassland sites); for other measures, we used values for each lizard with a complete observation for analyses. Values are presented as a median (range) or as a directional mean (circular variance) for turn angles. Most comparisons were made using Mann–Whitney tests (W); we used the Watson–Williams test for turn angles ($F_{1,471}$).

Measurement	Woodland	Grassland	Test statistic	P value
FPT (s; n = 169, 122)	19 (4–341)	28.5 (1–573)	19,727	0.007
Step length (m; n = 260, 231)	3.2 (1.6–15.4)	1.6 (1.0–13.8)	46,130	<0.0001
Path length (m; n = 18, 19)	42.5 (8.0–106.1)	23.9 (3.4–98.0)	428	0.009
Net displacement (m; n = 18, 19)	13.6 (3.5–89.8)	11.3 (12.9–87.5)	375	0.323
Straightness index (n = 18, 19)	0.39 (0.18–0.85)	0.56 (0.12–0.98)	282	0.071
Turn angle (°; n = 238, 210)	357 (32)	351 (36)	0.544	0.46

apparent ($F_{1,286}$ = 1.03, P = 0.312). In the grassland site, FPTs were not correlated with cover (ground vegetation, r = 0.05, P = 0.595; trees, r = 0.07, P = 0.455), but in the woodland site, FPTs were correlated positively with ground vegetation cover (r = 0.27, P = 0.001) and negatively with tree cover (r = −0.15, P = 0.048). In both sites, ground vegetation and tree cover were negatively correlated (grassland, r = −0.44, P < 0.001; woodland, r = −0.55, P < 0.001). Within FPT circles, ground vegetation cover was higher at the grassland site (Mann–Whitney test: W = 21210, P < 0.0001; median cover: 54.2% vs. 29.5%).

Movement path metrics revealed habitat-related movement differences. Step length was shorter at the grassland site (Table 1), and the distribution of step lengths differed between the sites (chi-square test: χ^2 = 52.7, df = 10, P < 0.0001; Fig. 5). Path length was shorter at the grassland site (Table 1). However, net displacement and straightness index were similar in both habitats (Table 1). In addition, lizards in the grassland site remained in the same location for a greater proportion of 1-min intervals (Z = 2.7, P < 0.007; 26% vs. 17% of intervals). Neither the distribution of turn angles nor the mean turn angle differed between sites (distribution of turn angles: χ^2 = 7.9, df = 5, P < 0.156; Fig. 6, Table 1). The turn angle distribution at both sites differed from uniformity (Raleigh test: grassland, R = 0.36, P < 0.001; woodland, R = 0.43, P < 0.001; Fig. 6) but did conform to a von Mises distribution (Watson's test: grassland, W = 0.02, P < 0.079; woodland, W = 0.03, P < 0.079).

DISCUSSION

Movement of *A. neotesselata* while it searches for food varies with habitat characteristics. Compared to the more heavily vegetated grassland site, FPTs of lizards on our more open woodland site were affected by ground vegetation cover, which is the characteristic that differed most obviously between our 2 sites (Figs. 1, 2). Habitat structure has been related to lizard movement; reductions in vegetation cover are associated with greater lizard moves per minute and greater percent time moving (Attum and Eason 2006, Wasiolka et al. 2009a) but are not associated with the aspects of movement patterns we observed (e.g., longer step length and greater net displacement),

pointing to the importance of detailed information on movement patterns to distinguish habitat-based differences in behavior.

Differences in vegetation can translate to a variety of environmental differences that can affect foraging. Vegetation cover could affect prey abundance, prey distribution, and a forager's ability to detect prey (Pitt and Ritchie 2002, Gebeyehu and Samways 2003, Debano 2006). In addition, factors such as thermal characteristics and predation risk vary with habitat structure (Snell et al. 1988, Kotler et al. 1991, Vasquez et al. 2002). Ultimately, both habitat structure and associated environmental characteristics can influence movement, with that movement providing insight into the relative importance of different aspects of habitat variation.

First-passage times lack some details regarding the nature of the animal's movement (Schick et al. 2008), but they can be used to identify differences in behavior contingent on habitat and as an indicator of search effort and resource distribution (Pinaud and Weimerskirch 2005, Henry et al. 2016). Habitat structure can affect an animal's FPT by influencing ease of movement, detection distance to predators and to prey, and predation risk. In a site that is more open structurally, a lizard might move more swiftly to reduce exposure to predation (Snell et al. 1988), resulting in a shorter FPT, which is a possible mechanism for the shorter FPTs that we found on our woodland site. Shorter FPTs are consistent with a need both to search denser vegetation more slowly and to proceed through exposed areas more quickly, factors that might be distinguished by examining step lengths and turn angles. Whiptails at our more open woodland site had longer step lengths, which might result from the need to move through open habitat more quickly, but they did not differ from lizards at the grassland site in their turn angles.

Animals are expected to switch between different step length distributions depending on how resources are distributed (Humphries et al. 2010), with step length influencing search effectiveness by affecting detection distance (O'Brien et al. 1990). When prey or habitat characteristics make locating prey difficult, smaller step lengths allow for less redundant searching and result in fewer unsearched areas. Lizards in our grassland habitat experienced higher overall vegetative cover, which could account for our observed shorter step lengths in that habitat. Periodic long moves, on the other hand, would be merited when a lizard needs to search for patchy prey distributed on a scale beyond the animal's sensory range (Bartumeus et al. 2002, 2005, Humphries et al. 2010). Our woodland site was associated with a greater proportion of long step lengths where lizards might have encountered a more heterogeneous pattern of either (1) high and low prey density areas or (2) easy- and hard-to-inspect areas. Animals can adjust their movement patterns to the density of food (de Knegt et al. 2007, Roshier et al. 2008), with increased tortuosity and slower speeds expected when food is available and the opposite when resources are scarce. Turn angles and path straightness did not differ between our sites, indicating that food density was not an important difference for lizards searching for food on the 2 sites. Common on our woodland site, however, was open bare rock, which appeared to have fewer insects than areas with vegetation. The more common long steps at the woodland site could stem from differences in prey distribution that are attributable to habitat structure.

First-passage time and path segmentation methods, combined with additional environmental information, can be used to understand animal movement at different spatial and temporal scales (Johnson et al. 1992, Bailleul et al. 2008, Le Corre et al. 2008, Pinaud 2008). The differences in movement patterns we observed between our 2 sites point to an influence of habitat on *A. neotesselata* behavior. Habitat-based variation in movement can reflect differences in predation risk and prey availability. The shorter FPTs and longer step lengths at the woodland site could indicate that whiptails are moving through open areas quickly because they can rapidly assess prey availability in the open but are also more vulnerable to predators there. While lizards at the grassland site have more vegetative cover from predators, the denser vegetation requires a higher search effort to acquire prey. *Aspidoscelis neotesselata* is known to occupy a wide range of habitats while also experiencing population declines due to anthropogenic development and resultant habitat loss (Hammerson 1999). Movement research might ultimately inform conservation efforts by helping elucidate how the species perceives and responds to human activity.

ACKNOWLEDGMENTS

We thank Anna Joy Lehmicke, James Kulbeth, and the Fort Carson Directorate of Public Works, Conservation Branch, for logistical assistance. Lise Aubry provided guidance and support. Kim Samsel is awesome. Ryan Armstrong, Liz McAlpine-Bellis, Rebecca John, Janine Klein, and Nicole Walbridge assisted with fieldwork. Elizabeth Liu provided the Spanish translation of our abstract. Financial support was provided through U.S. Fish and Wildlife Cooperative Agreement F17AC00326 and the Erell Institute. Field methods were approved through Colorado State University IACUC 18-7772A.

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Received 3 January 2019
Revised 9 August 2019
Accepted 17 September 2019
Published online 17 February 2020