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Age-dependent search behavior in the Colorado checkered whiptail (*Aspidoscelis neotesselatus*)

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Abstract.—We compared movement and space use patterns of foraging adult and juvenile Colorado checkered whiptails (*Aspidoscelis neotesselatus*) in pinyon pine–juniper woodland. Through focal observations, we characterized (1) movement paths as a series of step lengths and turn angles at 30-s intervals, and (2) habitat use reflected by the proportion of time spent in different vegetation types and in the open. Adults and juveniles differed in both movement and habitat use. Adults spent more time in the open and in association with mountain mahogany (*Cercocarpus montanus*), while juveniles were more frequently found in association with dead wood, grass, and juniper (*Juniperus monosperma*). Adults also moved greater distances than juveniles and made use of larger areas. Movement patterns differed between age classes, with adults having longer step lengths. Adults and juveniles also engaged in different step length–turn angle sequences. For both classes, movement characteristics differed with habitat type.

Resumen.—Comparamos los patrones de movimiento y de uso del espacio entre adultos y juveniles lagartos cola de látigo cuadriculados de Colorado (*Aspidoscelis neotesselatus*) en el bosque de piñón y junípero. Con observaciones focales, caracterizamos (1) los caminos de movimiento como una serie de longitudes de paso y ángulos de giro a intervalos de 30 s, y (2) el uso del hábitat reflejado por la proporción de tiempo pasado en diferentes tipos de vegetación y en lugar despejado. Adultos y juveniles se diferenciaban en ambos movimiento y uso del hábitat. Adultos pasaron más tiempo en lugar despejado y en asociación con caoba de montaña (*Cercocarpus montanus*), mientras juveniles se asociaron más frecuentemente con madera muerta, pasto y junípero (*Juniperus monosperma*). Además, adultos se movieron distancias más largas que juveniles y usaron áreas más grandes. Patrones de movimiento diferían entre clases de desarrollo, en que los adultos tenían longitudes de paso más largos. Adultos y juveniles también se metieron en diferentes secuencias de longitud de paso y ángulo de giro. Para ambas clases, las características del movimiento diferían con tipo de hábitat.

Age is an important factor contributing to intraspecific variation in behavior and ecology. Juveniles and adults have different physiological abilities and constraints due to age or size disparities (Herrel and Gibb 2006). In addition to gaining experience with age, ontogeny involves a series of changes in diet, habitat requirements, social circumstances, and predation threats (Werner and Gilliam 1984, Siqueira and Rocha 2008). Combined with the smaller absolute size of juveniles relative to adults, developmental shifts throughout ontogeny can result in behavioral variation with age class. Thermoregulation is vital to lizards and greatly affects their reproductive ability, physiology, pattern of activity, and mobility, all of which can be reflected in their behavior (Shine and Harlow 1993, Angilletta 2001). Temperature constraints are evident in juvenile whiptails, which use warmer open spaces than adults use (Paulissen 1988a). Intraspecific variation in behavior and ecology that can be attributed to size or sex can be explored through examining movement.

Lizard movement has been the subject of investigation for several decades, with information being collected for many species (Huey and Pianka 1981, Miles et al. 2007, Perry

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2007). Most previous studies have relied on characterizing lizard movement through 2 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 (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 lizards have identified intraspecific variation in search behavior (Huey and Pianka 1981, Eifler et al. 2007, Childers and Eifler 2015, Garrison et al. 2017). For lizards, differences 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.

Our study describes animal movement by assessing movement paths, wherein movement is viewed as a sequence of discrete displacements (step lengths) and bearings (turn angles) representing the geometry of the movement path, while providing insights into patterns of behavior (Turchin 1998, Edelhoff et al. 2016). Whiptail lizards (genus *Aspidoscelis*) are diurnal foragers and primarily consume arthropods that they locate, even below the surface, through chemical sampling (Knopf 1966, Anderson and Karasov 1988, Anderson 1993, Paulissen et al. 1993, Cooper 1995). Whiptails can spend the majority of their activity period in motion because they search for food, and they typically exhibit high PTM coupled with MPM <1.0 (Perry 1999, 2007). As opposed to many lizard species that locate their food by remaining stationary until prey moves within their detection range, the path chosen by foraging whiptails influences success and should reflect intraspecific variation in diet and detection ability. We examined variation in search behavior relative to age and size for the Colorado checkered whiptail, *Aspidoscelis neotesselatus*, a triploid parthenogenetic lizard occurring in southeastern Colorado (Walker et al. 1997). The species occupies a variety of habitats, including grasslands, shrublands, pinyon pine–juniper woodlands, and human-disturbed areas (Knopf 1966, Hammerson 1999). Colorado checkered whiptails are wide ranging, and their movement can vary with habitat structure (Utsumi et al. 2020). Their home ranges overlap, and they have a relatively high tolerance for conspecifics (Knopf 1966, Leuck 1982, 1985). As a unisexual species with minimal conspecific agonistic behavior, foraging is the primary activity for surface-active individuals. Size-based differences in diet have been identified in multiple species of whiptail (Paulissen 1987a, 1987b, Paulissen et al. 1993, Sales et al. 2012). Adult *A. neotesselatus* at some sites rely heavily on Orthoptera (grasshoppers) or Isoptera (termites), while juveniles rely more on Araneae (spiders), Homoptera (leafhoppers), and adult Lepidoptera (moths) (Paulissen et al. 1993). Although *A. neotesselatus* diet can vary with site and time of year (Paulissen et al. 1993), size-based differences in diet are reasonable to expect. We hypothesized that movement path measurements and the resulting patterns of space use would be different for adult and juvenile *A. neotesselatus* foraging in open pinyon pine–juniper woodlands. Through our characterization of their movement patterns, we anticipated finding intraspecific variation in foraging behavior between adult and juvenile *A. neotesselatus*.

Methods

We studied adult and juvenile *A. neotesselatus* movement at the Fort Carson military installation on a woodland site characterized by trees, especially pinyon pine (Pinaceae: *Pinus* spp.) and juniper (Cupressaceae: *Juniperus monosperma*), with scattered shrubs, forbs, and clumps of grass (southeast of Colorado Springs, El Paso County, Colorado; 38°27.57′ N, 104°55.7′ W, datum WGS84) (Fig. 1). We conducted focal observations of 1-h duration on active *A. neotesselatus* individuals from 19 June to 11 July 2019, between 08:30 and 13:00. Each observation was conducted on a single animal by 3 observers from about 5 to 10 m away, which allowed for unbroken visual contact without disturbing lizard movements. For each observation, one person was tasked with recording data, one with timing and placing location markers, and one with maintaining visual contact with the focal lizard. Lizards seemed undisturbed by the presence of observers; they often moved in the direction of observers, even to the extent of walking over an observer's shoes, and were commonly observed feeding, pursuing prey, digging, and

Fig. 1. Study site, El Paso County, Colorado, USA.

Table 1. Summary of movement characteristics for each age class of *Aspidoscelis neotesselatus*. Sample size is reported as number of adults followed by number of juveniles. Values reported are the means (±SE) for each age class. Step length values only include intervals during which animals moved. Step length, turn angle, and utilization distribution (UD) were log transformed prior to between-group analyses; the untransformed values are presented here.

Movement characteristic	Sample size	Adults	Juveniles	Test statistic	*P* value
Step length (m)	1343, 1417	1.77 ± 0.05	1.08 ± 0.03	$F_{1, 28} = 16.3$	<0.001
Path length (m)	15, 15	158.2 ± 15.0	102.0 ± 7.9	$t_{21} = 3.39$	0.003
Net displacement (m)	15, 15	36.8 ± 7.1	23.0 ± 4.1	$t_{22} = 1.67$	0.108
Straightness	15, 15	0.23 ± 0.04	0.22 ± 0.03	$t_{26} = 0.29$	0.774
Turn angle (°)	1286, 1357	61.0 ± 1.3	64.6 ± 1.3	$F_{1, 28} = 1.07$	0.310
95% Kernel UD (m^2)	15, 15	1870 ± 561	739 ± 202	$t_{27} = 2.87$	0.008

interacting with conspecifics. During each 1-h focal period, we placed a location marker at the lizard's starting location and then placed an additional marker every 30 s thereafter, yielding 121 locations per observation. We placed numbered location markers after the animal left the vicinity (>10 m distant) to minimize disturbance to the focal animals. If placement of multiple markers was delayed while an animal was using an area, we relied on notes and sketches to accurately place the markers. We did not measure PTM and MPM, being unable to record additional variables. If we lost eye contact with our focal lizard during the observation, we deducted the amount of time the animal was out of sight from our cumulative observation time but continued the observation until we completed 1 h with the lizard in sight. In addition to recording the lizard's location every 30 s, we also recorded whether the foraging-related behaviors digging, eating, and predation attempts occurred during each 30-s interval (Table 1). Digging often resulted in food items being uncovered and eaten. Predation attempt refers to rushing toward and attempting to capture an aboveground, potentially elusive food item, such as a grasshopper or moth. After each observation,

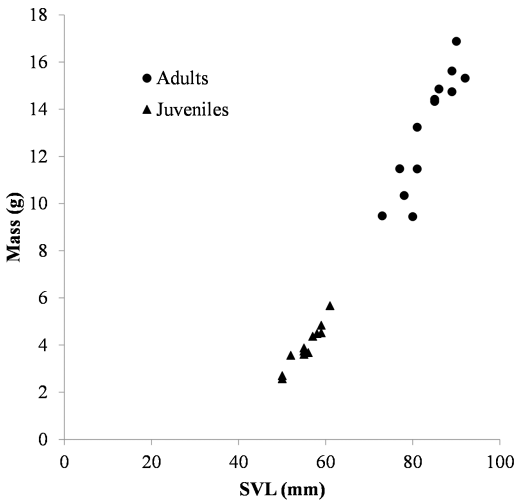

Fig. 2. The relationship of SVL to mass for adult and juvenile *Aspidoscelis neotesselatus* from southeastern Colorado, USA.

the focal lizard was captured by noosing, measured (mass [g] and snout–vent length [SVL, mm]), given a unique color code with nontoxic paint pens, and toe clipped. We classified lizards as adult or juvenile (<65 mm) based on their body size (Fig. 2). Each lizard was observed only once. Each day, we attempted to observe a balanced number of adults and juveniles, equally spread throughout the session, to prevent an inadvertent temperature or time bias.

After each observation, we retrieved location markers and then, for each marker, recorded which of 7 habitats corresponded to the lizard's location: mountain mahogany (*Cercocarpus montanus*), juniper (*Juniperus monosperma*), pinyon pine (*Pinus edulis*), grass, dead wood, open, or other. Most locations (99%) were in stand-alone plants. On the few occasions where one plant was under another (1%), we noted the habitat as the plant species with the lower canopy. In addition, we measured the distance and direction between sequential 30-s location markers. We recorded directions to the nearest degree, using a compass held over a tape measure stretched between location markers, which allowed a level of precision at which repeat measurements taken for standardization purposes were typically within 3° of each other. From the sequence of locations, we calculated the following path characteristics: step length, path length, net displacement, straightness index, and turn angle (for a visualization of measurements, see Utsumi et al. 2020). For intervals that involved movement, we defined step length as the straight-line distance between consecutive 30-s locations, path length as the sum of all step lengths for an observation period, net displacement as the straight-line distance between initial and final locations, straightness index as the ratio of net displacement to path length (values from 0 to 1), and turn angle as the change in direction between consecutive steps (values from 0° to 180°). For analyses, step lengths and turn angles for all lizards of the same age class were pooled, but each individual lizard's path length, net displacement and straightness index were calculated individually.

Statistical analyses were conducted using R (ver. 3.4.3; R Core Team 2018). We used chi-square analyses to compare distributions, examining standardized residuals to identify observations that differed strongly from expectations. We assessed space use of foraging lizards by calculating the 95% kernel utilization distribution (R package '*adehabitatHR*'; Worton 1995). For estimating the 95% kernel utilization distribution, we used the href smoothing parameter with the grid having maximum and minimum x- and y-coordinates equal to x or $y_{max/min} \pm 30\%$ range x or y. For step length and turn angle, we compared age classes by pooling measurements from all individuals and developing a generalized linear mixed-effects model (GLMM), with age class as a fixed effect and individual lizard as a random effect. We applied t tests to comparisons of the remaining movement variables and feeding behaviors, and Z tests to comparisons of proportions. When the initial data were not normally distributed, we first applied a log-transformation to normalize the data. Step length, turn angle, and utilization distributions were log transformed prior to between-group analyses. We examined movement relative to habitat by associating (1) each turn angle with the habitat recorded for the vertex of the angle and (2) each step with the habitat in which the lizard was located at the step's beginning. We explored differences in movement metrics associated with habitat using GLMM, with age class, habitat, and the age-by-habitat interaction as fixed effects and individual lizard as a random effect, followed by

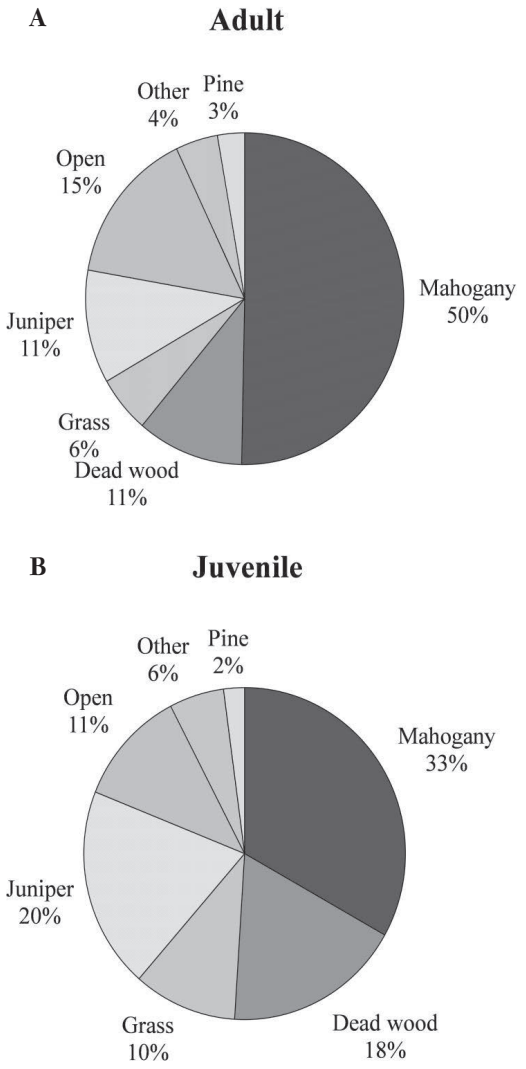

Fig. 3. Habitat use by (A) adult *Aspidoscelis neotesselatus* and (B) juvenile *A. neotesselatus*. Charts depict the proportion of 30-s intervals during which lizards were observed in specific habitats (adults: $n = 1817$; juveniles: $n = 1710$).

post hoc comparisons using Tukey tests. To examine the pairing of step length and turn angle, we compared the 3 turn categories (forward [0°–45°], lateral [45°–135°], and back [135°–180°]) with step lengths pooled into 2 length categories (short [≤1 m] and long [>1 m]) using a log-linear model to determine whether the observed pairings of step length and turn angle differed from random expectations or differed among the demographic classes. We tested for possible observer effects by determining the mean step length and mean turn angle for each lizard during the first and last 10 min of its observation, and we then compared means from the first and last 10 min for each measure using paired *t* tests.

RESULTS

We observed 15 adult *A. neotesselatus* (mass [$\bar{x}$ ± SE]: 13.2 ± 0.7 g; SVL: 83.5 ± 1.6 mm) and 15 juveniles (mass [$\bar{x}$ ± SE]: 3.9 ± 0.3 g; SVL: 55.5 ± 1.0 mm; Fig. 2). The movement of lizards, as indicated by step lengths and turn angles, did not change for either age class during the course of an observation period, indicating that observer presence did not dramatically affect lizard behavior (adult step length $t = 1.36$, $P = 0.19$; adult turn angle $t = 0.92$, $P = 0.37$; juvenile step length $t = 1.59$, $P = 0.13$; juvenile turn angle $t = 1.05$, $P = 0.31$). Foraging-related behaviors did not differ between age groups. Digging was a common activity for both age classes, with every individual digging during multiple intervals and some individuals digging in as many as half of all 30-s intervals. Digging frequency did not differ between age classes (20.8 ± 4.1 intervals per observation for adults versus 14.3 ± 3.6 intervals per observation for juveniles; $t = 1.36$, df = 27, $P = 0.184$). Eating also was commonly observed, with all the juveniles and 80% of adults feeding during observations. Eating frequency did not differ between age classes (2.6 ± 0.7 intervals per observation for adults versus 3.3 ± 0.7 intervals per observation for juveniles; $t = 1.29$, df = 24, $P = 0.209$). Predation attempts were observed for 67% of juveniles and 80% of adults. The frequency of predation attempts did not differ between age classes (1.6 ± 0.6 intervals per observation for adults versus 1.9 ± 0.6 intervals per observation for juveniles; $t = 0.32$, df = 27, $P = 0.754$). Although foraging behaviors did not differ between age classes, habitat use, movement, and space use characteristics did differ.

Habitat Use

Although adults and juveniles occurred in the same areas and were commonly seen within the same field of view, they differed in their use of habitat ($\chi^2 = 174.716$, df = 6, $P < 0.001$; Fig. 3). For both age classes, mountain mahogany was the most commonly used

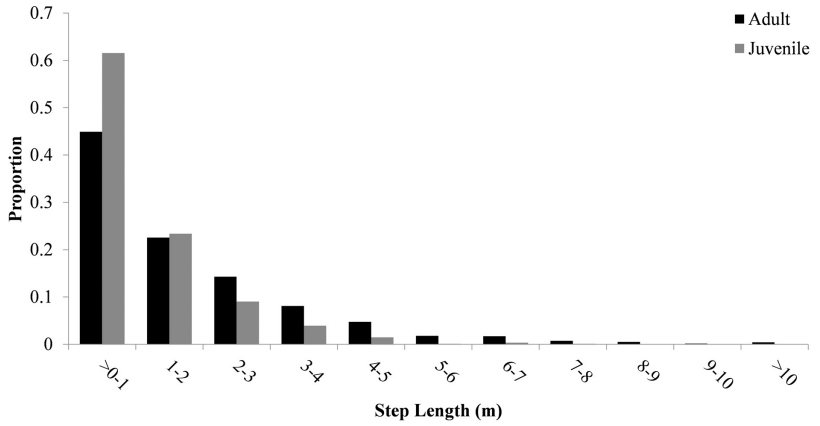

Fig. 4. Frequency distribution of step lengths for adult and juvenile *Aspidoscelis neotesselatus* (adults: $n = 1343$; juveniles: $n = 1417$).

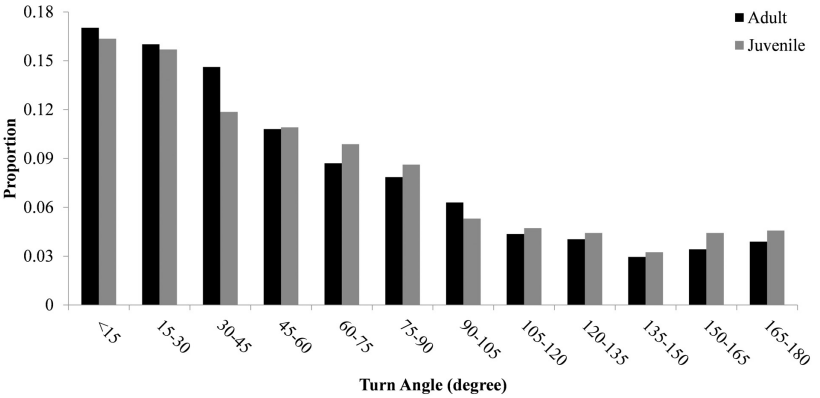

Fig. 5. Frequency distribution of turn angles for adult and juvenile *Aspidoscelis neotesselatus* (adults: $n = 1286$; juveniles: $n = 1357$). Turn angles are binned in 15° increments.

habitat type (Fig. 3), but standardized residuals ($\geq |2|$) indicated that age class differences largely reflected the heavy use of mountain mahogany and open areas by adults in combination with the marked use of dead wood, grass, and juniper by juveniles (Fig. 3).

Movement and Space Use

Adults had more 30-s intervals without travel than juveniles (26% versus 19% of intervals; $Z = 5.17$, $P < 0.001$), but during intervals with movement, adults had longer step lengths (Table 1). The distribution of step lengths differed with age class ($\chi^2 = 146.9$, df $= 5$, $P < 0.001$; Fig. 4). Path length was longer for adults, but net displacement, straightness, and mean turn angle did not differ between adults and juveniles (Table 1). The distribution of turn angles did not differ with age class ($\chi^2 = 9.57$, df $= 11$, $P = 0.569$). Turn angles were not uniformly distributed for either age class but were biased toward smaller turns for both demographic groups (adults: $\chi^2 = 450$, df $= 11$, $P < 0.002$; juveniles: $\chi^2 = 379$, df $= 11$, $P < 0.001$; Fig. 5). Utilization distributions (95%) were smaller for juveniles than for adults (Table 1). Step-length and turn-angle pairings differed from random expectations (log-linear model: $G = 85.7$, df $= 4$, $P < 0.0001$) and between age classes ($G = 153.9$, df $= 7$, $P < 0.0001$), with short, lateral moves being most common for juveniles and long, forward moves most common for adults (Fig. 6).

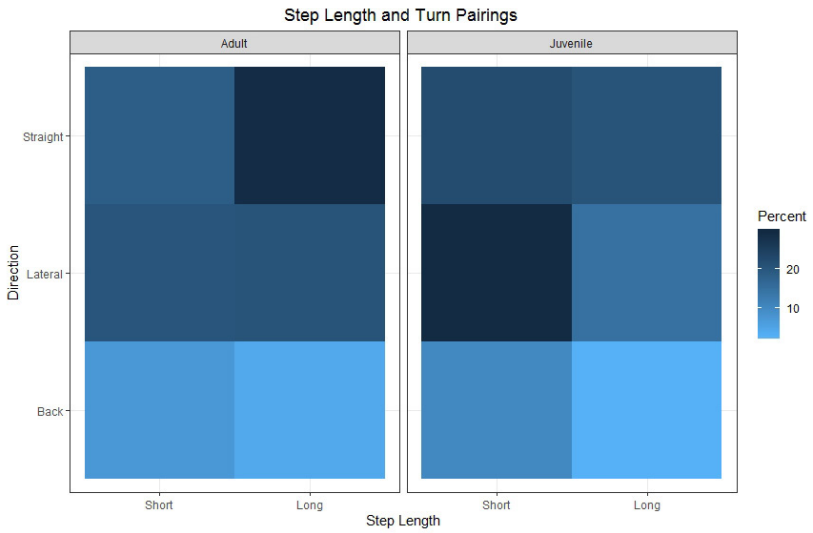

Fig. 6. Heat map indicating the frequency of moves by adult and juvenile *Aspidoscelis neotesselatus* that we observed for each possible categorical pairing of step length (short and long) and turn angle (straight, lateral, and back).

TABLE 2. Movement measurement means (±SE) by habitat for *Aspidoscelis neotesselatus*. Step length varied by age class and habitat. Turn angle varied by habitat. Habitats with no shared letters are significantly different (Tukey test, $P < 0.05$).

	Step length (m)		Turn angle (°)
Habitat	Adults	Juveniles	All
Mountain mahogany	1.46 ± 0.06	0.91 ± 0.05 C	70.5 ± 1.6 A
Deadwood	1.79 ± 0.16	0.98 ± 0.06 C	63.2 ± 2.5 A, B
Grass	1.63 ± 0.19	1.07 ± 0.08 B, C	59.9 ± 3.2 A, B
Juniper	2.21 ± 0.16	1.16 ± 0.06 A, B	59.3 ± 2.2 B
Open	2.21 ± 0.13	1.39 ± 0.09 A	51.6 ± 2.1 B

Habitat-Based Movement

Our examination of movement by habitat type indicated that movement was habitat dependent (Table 2). Adults tended to have longer steps than juveniles ($F_{1,30} = 31.1$, $P < 0.001$; Table 2). Step length also varied by habitat ($F_{4,2482} = 11.7$, $P < 0.001$). Open habitat and juniper were associated with longer steps, while dead wood and mahogany were associated with the shortest mean step lengths. The interaction between age class and habitat was not strong for step length ($F_{4,2482} = 2.0$, $P = 0.087$). Turn angles did not differ between age classes ($F_{1,36} = 1.7$, $P = 0.198$), nor was there an interaction between age and habitat type ($F_{4,2059} = 0.6$, $P = 0.687$; Table 2). Turn angle was habitat related ($F_{4,2059} = 9.8$, $P < 0.001$; Table 2), with open habitat and juniper associated with smaller turn angles than mountain mahogany.

DISCUSSION

Habitat selection and use is shaped by many factors, because each habitat contains variable combinations of resources, risks, and environmental conditions. Movement patterns can reflect how animals perceive and respond to their environment. The behavior of *A. neotesselatus* shows age-based differences in both habitat and movement.

Habitat

Although we found that foraging-related behaviors—eating, digging, and predation attempts—did not differ between age groups, there were differences in habitat use. We found members of both age classes in all habitat types, with adults most commonly in mountain mahogany and open areas and juveniles in dead wood, grass, and juniper. Several factors could contribute to the differing extents

to which each class used particular habitats. First, interactions (e.g., social or predator-prey) can drive habitat use. Individuals sometimes use habitat based on their social status, with dominant individuals influencing the habitat use of others (Baird et al. 1996, Eifler et al. 2007). However, social interactions seem unlikely to affect *A. neotesselatus* habitat use since their social system involves mutual tolerance (Knopf 1966, Leuck 1985), wherein individuals of different age classes are often in visual contact without any overt response (personal observation). We did not observe any intraspecific aggression. In addition, different size classes might select habitats based on predation risk (Stamps 1983, Keren-Rotem et al. 2006). Smaller juvenile lizards often face greater risks from a larger array of potential predators than adults (Schmidt-Nielsen 1984, Husak 2006). More frequent use of dead wood, grass, and juniper by *A. neotesselatus* juveniles might occur if predators were less likely to find them there. We encountered potential snake and bird predators infrequently and without any apparent habitat specificity (e.g., coachwhips [*Masticophis flagellum*], bullsnakes [*Pituophis catenifer sayi*], prairie rattlesnakes [*Crotalus viridis*], and greater roadrunners [*Geococcyx californianus*]). A potential role for predation risk in habitat use requires further investigation.

Second, habitat selection could occur in response to the mosaic of thermal characteristics attributable to different plant species. Temperature preference plays an important role in the habitat selection and foraging activity of ectotherms (Huey 1982, Webb and Shine 1998, Castilla et al. 1999, Angilletta et al. 2002, Zhu et al. 2015). Smaller ectotherms are characterized by having a lower heat storage capacity but higher thermal conductivity relative to larger individuals (Castilla and Bauwens 1991, Xu and Ji 2006, Zhu et al. 2015). Within a species, adult and juvenile lizards often exhibit different temperature preferences, and different habitats can provide a range of thermal conditions (Tang et al. 2013, Zhu et al. 2015). Soil temperatures in open patches compared to patches under the canopy of pinyon pine–juniper habitats can vary by 10 °C (Breshears et al. 1998). On our study site, with the possible exception of seedlings, juniper trees are more extensively canopied than mountain mahogany and probably offer cooler conditions, which could account for differences in use of the 2 habitats by adults and juveniles (Fig. 3). In *A. sexlineatus*, one of the parental species for *A. neotesselatus*, adults and juveniles use different microhabitats, which has been attributed to differing thermal constraints (Paulissen 1988a). However, adult and juvenile *A. sexlineatus* do not differ in their temperature preferences in the field or laboratory (Paulissen 1988b).

As a third alternative, differences in habitat preferences could be reflective of foraging differences. *Aspidoscelis neotesselatus* generally consumes arthropods, and size-based differences in diet have been identified in multiple species of whiptail (Paulissen 1987a, 1987b, Paulissen et al. 1993, Sales et al. 2012). Intraspecific differences in lizard body size often are associated with variation in the size and type of invertebrate prey consumed, as well as the extent of reliance on plant material (Schoener 1968, Pough 1973, Simon 1976, Capel-Williams and Pratten 1978, Paulissen 1987a, Whiting and Greeff 1997). Although we observed foraging-related behavior (eating, digging, and predation attempts), there were no differences between groups in the frequency of these behaviors, and prey items were generally not identifiable (e.g., Kusaka et al. 2021). The age-class differences in habitat use that we observed could be reflective of specific prey-microhabitat associations, an idea that merits further investigation.

Movement

Lizard foraging can vary by age or size and result in differences in diet and ability to detect food, thus influencing movement patterns (Paulissen 1987a, Perry 1996, Greeff and Whiting 2000, Eifler et al. 2007). For lizards, differences in diet often are associated with differences in search strategy (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. Foragers can structure their search pattern based on their sensory abilities as well as characteristics of their food (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). If juveniles rely on more difficult-to-detect food items, the shorter step lengths (= slower movement) and more frequent moves we recorded could improve their foraging efficiency. Even if adults and juveniles consume the same prey, juveniles have a reduced field of view associated with their smaller body size. Juveniles are closer to the ground, and the area that they can effectively scan is smaller than that of adults, simply due to differences in height above the substrate. Further investigations into the detection abilities, viewing abilities, and prey selection by adults and juveniles could clarify the importance of these factors in habitat choice and movement patterns by *A. neotesselatus*.

Ontogenetic shifts in habitat and movement can improve our understanding of the underlying age-related selection pressures of a species (Stamps 1983). We found differences in the habitat use and movement patterns between age classes. Predation risk, thermal characteristics, habitat preferences, and prey detection abilities associated with size and age class are important factors that might have influenced our results, and they merit future investigation.

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