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Demographic Differences in Behavior, Movement, and Habitat Use in the Toad-Headed Agama (*Phrynocephalus versicolor)* of the Gobi Desert (Dornogovi, Mongolia)

Kaera Utsumi [1], Alicia Pham [1,2], Batdelger Erdenetsetseg [3], Maria Eifler [1] and Douglas Eifler [1,*]

[1] Erell Institute, Lawrence, KS 66047, USA; kaera.utsumi@gmail.com (K.U.); aliciapham37@gmail.com (A.P.); maria.eifler@gmail.com (M.E.)
[2] Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, KS 66045, USA
[3] Department of Biology, National University of Mongolia, Ulaanbaatar 14200, Mongolia; erkaecology@gmail.com
* Correspondence: deifler@erell.ngo

Abstract

Demographic constraints can have a profound effect on behavioral ecology. Yet examinations of intraspecific variation considering both sex and age are rare. We assess age and sex-specific habitat use, movement, and behavior in variegated toad-headed agamas (*Phrynocephalus versicolor*) in the Gobi Desert, Mongolia. We predicted that juveniles would move and forage more than either adult sex and would engage in more random movement paths (i.e., higher entropy) than adults. We conducted 15 min focal observations, marking locations every 30 s to delineate the movement path of individuals. We recorded foraging and tail displays throughout the observation and habitat data at each marker. We found no sex-specific variation in behavior, number of moves, or entropy, but did record sex-specific variation in habitat use and movement paths. Age-specific variation in behavior, movement, entropy, and habitat use was prevalent and nuanced. Juveniles ate, dug, moved, and tail displayed more than adults, and they had movement paths with higher entropy than either adult sex. Sex and age-based variation in behavior, movement, and habitat use could arise from differential body size, experience, or reproductive status. Future work is needed to understand the function of tail displays and the relationship of entropy in movement paths to behavioral ecology.

Keywords: behavioral ecology; demography; entropy; movement ecology; tail display

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1. Introduction

Because of the varying challenges, abilities, and opportunities experienced by different demographic groups, intraspecific variation in behavior and habitat use commonly exists [1–3]. Hatchling, juvenile, and adult individuals vary in size, experience, and ability, which can affect ecological constraints manifested in behaviors such as foraging or anti-predator defense [4,5]. Understanding the nature of intraspecific differences is requisite for appreciating the ecology of a species [4,6], but adult behavior and habitat use has been disproportionately the focus of studies that consider demographics [7].

Often, body size can have important implications for resource partitioning and threat deterrence [8]. Juvenile lizards, for example, might occupy different habitats to avoid cannibalism, investing in habitats less favorable to adults [9,10]. Body size also can determine the variety of possible predators, which can then influence social organization [11]. Due to their

smaller size, juveniles also are more thermally sensitive than their adult counterparts, which could influence habitat use and activity [12–14]. At the same time, juveniles are usually the least studied components of a population, despite experiencing the highest mortality [15] and representing a life stage critical to conservation and management decisions [7].

Movement data are commonly used to reveal ecological patterns that otherwise might not be apparent. Conceptually, detailing movement patterns by recording turn angles and step lengths can provide behavioral insights into space use, mating systems, and movement syndromes (i.e., migration vs. dispersal; [16,17]). Empirically, movement path analyses have provided a basis to examine niche partitioning of ecologically similar species [18,19]. More generally, path analysis, using sequences of locations obtained over short time scales, has been used to identify ecological strategies and behavioral phases [16,20–23] that then lead to the development of testable, mechanistic hypotheses [24,25]. Examining the combination of step lengths and turn angles as an animal moves can be used to address large ecological issues, such as the impact of habitat modification on wildlife, as well as ecological concepts, such as foraging efficiency [26–29]. Direct movement trajectories occur commonly during dispersal or migration, whereas animals engaged in foraging or searching often make use of large turn angles and small step lengths along their movement paths [16,30,31].

We use short-term movement data to investigate age and sex class differences in the behavioral ecology of an oviparous lizard iconic to the Gobi Desert, the variegated toad-headed agama (*Phrynocephalus versicolor*), which occurs in China, Mongolia, Kazakhstan, and Kyrgyzstan [32,33]. Variegated toad-headed agamas are active from April to October and can be found in a variety of habitats, including desert, semi-desert, steppe terrains with sand mounds fixed by vegetation in open areas, dry riverbeds, and rocky landscapes [32,34–37]. Previous research has focused primarily on their morphology and thermoregulation [14,38–40], but little is known about their behavioral ecology.

We hypothesize that adult male and female variegated toad-headed agamas will differ from each other and from juveniles in their movement patterns, behavior, and habitat use. We use path analysis to identify strategies that can, in turn, be used to generate hypotheses regarding the ecological factors underlying demographic-based movement patterns. While obtaining movement data, we also obtained data on foraging behavior (eating and digging), habitat, and tail display behavior. Tail displays are widely used among *Phrynocephalus* species [41], most often functioning in a social context and conveying information about the displayer [42–47]. During our preliminary observations of variegated toad-headed agamas, adult males and juveniles conspicuously raised their tails when approached by conspecific individuals, possibly serving as a communication signal. Variegated toad-headed agamas can occur at high densities of >100 individuals/ha [33,48,49]. At such high densities, intraspecific variation in behavior and communication might play an important role in mediating competition. Tail displaying by a congener has been postulated to represent a territorial defense signal [50], whereas tail displaying in other species of lizard has been postulated to serve as a pursuit-deterrence signal [51,52]. We predict that the frequency of tail raising by demographic group will provide a framework from which future researchers can examine the function of tail displays. In addition, we predict that juveniles will move more and forage more than adults due to their higher energetic needs, and that juveniles will exhibit the least predictable movement paths. We expect juveniles to be moving the most and along the most unpredictable paths because they are likely to be exploring the habitat and establishing foraging and refuge locations. Alternatively, juveniles could move less because they are at greater risk of predation—many predators detect prey by their movements, and moving more could increase vulnerability to predation. We expect adult males to move often and along direct paths, as they are likely to be patrolling, whereas adult females are likely to move more locally to balance foraging and predation concerns [53,54].

2. Materials and Methods

Our study was carried out in the Gobi Desert of southeastern Mongolia, ca. 15 km east of Sainshand, Dornogovi (44.872072 °N 110.210272 °E, datum = WGS84). The site occupied ca. 5.3 ha in desert and desert steppe habitat consisting of an aeolian sand or gravel substrate dominated by wild onions (*Allium* spp.), shrubs, bushes, and grasses (Figure 1; Table S1). During daylight hours (08:00–18:00 h) from 28 July–8 August 2024, four observers searched synchronously for toad-headed agamas in a section of the site, with different sections of the site being searched each day. When an unmarked (i.e., unobserved) lizard was sighted, we gathered ca. 5–10 m from the focal lizard and waited 5 min (=habituation period) for the lizard to acclimate to our presence prior to beginning 15 min focal observations, during which we recorded their movement, habitat use, and behavior. During the habituation period, we recorded the substrate temperature (Fluke 62 Max+ infrared thermometer; Everett, WA, USA) and measured the average wind speed at ground level (Kestrel 1000; Nielsen-Kellerman, Boothwyn, PA, USA). Based on previous studies, we determined 5 min to be the length of time we needed to obtain temperature and windspeed recordings, to prepare for recording movement data, and for the lizard to resume normal activity.

Figure 1. The sample habitat on the study site is a patchy sand and gravel substrate with interspersed low shrubs and herbaceous plants. Pictured are wild onions (*Allium* spp.) and devil's thorn, with some small shrubs to the upper right.

For focal observations, one person (MAE) kept track of time and quietly announced the passing of every 30 s, at which point two of us (KU and AP) marked the focal lizard's location, including the start (n = 31 locations per observation). We placed location markers either after the lizard moved >5 m from a location, or once the observation was complete, based on detailed maps of the lizard's movements we made during the observation. The fourth observer (DAE) counted behaviors that we recorded (Table 1). Upon completion of an observation, we captured the focal lizard with a lasso attached to the end of an extendable pole (i.e., uurga) or by hand. We brought captured lizards inside to measure (snout-vent length (SVL), tail length, and mass), sex (using probes), and mark with bands of unique color combinations on the base of the tail using non-toxic paint pens. Juveniles were not sexed as they were too small to probe. All animals were released at their capture location, most within 4 h, but some were retained overnight to obtain fecal samples for a separate study on diet.

Table 1. Definitions for variables recorded during focal animal observations.

	Behavior	Definition
Behavior	Dig	The anterior feet and legs displace substrate material, creating a depression.
	Eat	Consumption of food involves opening and closing the mouth before swallowing.
	Move	A change in location of the body involving a displacement of ≥1 body length.
	Tail display	Tail raised by curling upwards, then straightening, exposing the ventral surface. Often repeated in a rapid series.
Movement Path	Step length	Straight-line distance between consecutive 30 s markers.
	Path length	Sum of all step lengths for an observation period.
	Turn angle	Change in direction between consecutive step lengths. Possible values = 0–180°, with 0° = an unchanged orientation by the focal animal from the previous step.
	Search area	Size of the area (minimum convex polygon) occupied during the observation.

Using the markers placed during observations, we determined the distance and compass direction between consecutive markers. We then generated Cartesian coordinates of the 31 location points to determine the path analysis metrics ([17]; Table 1) of step length, path length, turn angle, search area, and habitat at the location of each marker (open or in a plant, the species of the plant, and if the lizard was perching off the ground). When a focal animal was within 1 body length of a plant, we considered the lizard to be using the plant. Using the R package varrank (version 0.5), we calculated an estimate of Shannon entropy for the step lengths of each lizard as a measure of the predictability of the movement path.

We used Shapiro–Wilk tests to assess data for normality and then applied nonparametric statistics when appropriate. ANOVA was used to compare body size, with pairwise Tukey comparisons of demographic groups. We compared the distributions of turn angle and step length (excluding step lengths = 0, occurring when an animal did not move) for pairwise comparisons of demographic classes using Kolmogorov–Smirnov tests. We examined the relationship between step length and turn angle using a mixed effects model, with lizard ID as a random factor, and turn angle and demographic group as model variables. To assess whether the frequency of digging bouts, tail displays, moves, eating events, and 30 s intervals with no movement, as well as step length entropy, differed by sex or age class, we used Kruskal–Wallis tests. For post hoc comparisons, we used Dunn's tests with $p < 0.05$. We assessed whether environmental conditions (i.e., temperature and wind speed) affected behavior with Pearson correlation tests and determined whether the demographic groups differed in the environmental conditions under which they were observed using ANOVA. To compare habitat use, we pooled the counts of habitat variables by demographic class and applied chi-square analyses, interpreting differences in habitat use by examining the resulting standardized residuals. We used Minitab (version 21.4.2, 2023; Minitab, Inc., State College, PA, USA) and R (R version 4.2.1; R Core Team, 2022), applying a significance level of $p \leq 0.05$ to all tests. To characterize search areas, we used the 31 locations obtained during an observation period to calculate a minimum convex polygon with the program Ranges (Ranges7eXtra, Anatrack Ltd., Wareham, UK).

3. Results

3.1. Between Demographic Class Comparisons

We conducted observations of 100 lizards (29 females, 18 males, and 53 juveniles). The demographic groups differed in size, with males being larger than females and females larger than juveniles (ANOVA: SVL: $F_{2,97} = 671$, $p < 0.001$; Mass: $F_{2,97} = 625$, $p < 0.001$; Table 2). In addition, the proportion of tail length to body size (SVL) varied by demographic group, with females having proportionately shorter tails than males and juveniles (Kruskal–Wallis test: $H = 27.23$, $p < 0.0001$; Table 2). Because an initial examination of our data

revealed no significant correlations between environmental conditions (temperature and wind speed) and any behavioral or movement variables (Pearson correlation: $p > 0.2$) and the environmental conditions during which each demographic group was observed did not differ (ANOVA: substrate temperature $F_{2,94} = 1.02$, $p = 0.36$; windspeed $F_{2,96} = 1.37$, $p = 0.26$), we did not include temperature or windspeed in any of our observation analyses.

Table 2. Summary statistics, with sample sizes (body size; behavior, movement, entropy) for adult male, adult female, and juvenile (Juv) variegated toad-headed agamas. Body size (SVL and mass) values (mean ± SE) include ANOVA results ($F_{2,97}$ (p)). Medians (range) are presented for the ratio of tail length/SVL, behavior (dig, eat, tail display), movement (moves, no move intervals, path length, search area), and entropy for each demographic group. We compared median values across demographic groups with Kruskal–Wallis tests (H (p)). Significant p-values are in **bold**. Values that do not share the same superscript are significantly different (Table 2).

Value (units)	Males (n = 21; 18)	Females (n = 31; 29)	Juv (n = 61; 53)	Statistic
SVL (mm)	52.3 ± 0.6 [a]	50.2 ± 0.5 [b]	30.6 ± 0.4 [c]	**671 (<0.001)**
Mass (g)	5.9 ± 0.2 [a]	5.2 ± 0.1 [b]	1.2 ± 0.1 [c]	**625 (<0.001)**
Tail length/SVL	1.28 (1.04–1.37) [a]	1.19 (1.07–1.38) [b]	1.29 (1.15–1.43) [a]	**27.23 (<0.0001)**
Dig (n)	0 (0–4) [a]	0 (0–3) [a]	1 (0–27) [b]	24.41 (**<0.001**)
Eat (n)	0 (0–9) [a]	0 (0–10) [a]	3 (0–20) [b]	25.6 (**<0.001**)
Tail display (n)	0 (0–14) [a]	0 (0–8) [a]	9 (0–42) [b]	30.65 (**<0.001**)
Move (n)	19.5 (0–49) [a]	7 (0–36) [a]	35 (10–110) [b]	42.58 (**<0.001**)
No moves (n intervals)	17.5 (0–30) [a]	25 (12–30) [a]	17 (2–28) [b]	21.82 (**<0.001**)
Path length (cm)	382 (0–4658) [a,b]	174 (0–1813) [a]	646 (34–4569) [b]	13.73 (**0.001**)
Search area (m^2)	0.9 (0–171.8) [a,b]	0.33 (0–36.89) [a]	3.32 (0–130.34) [b]	13.45 (**0.001**)
Entropy	0.77 (0–1.99) [a]	0.42 (0–1.74) [a]	1.41 (0.35–2.36) [b]	25.96 (**<0.001**)

During 15 min focal observations, adults and juveniles differed in their frequency of: digging bouts, tail displays, moves, eating events, and intervals with no movement, as well as in their entropy (Table 2). Pairwise comparisons between demographic groups revealed that adult males and females did not differ significantly from each other for any of our variables, while juveniles differed from adult females for all behavioral, movement, and entropy measures (Table 3). Adult males also differed significantly from juveniles in all the behaviors we measured and in entropy, but among the movement variables, only in the number of intervals with no movement. Specifically, during observations, juveniles dug, ate, tail displayed, and moved more, had higher entropy, and fewer intervals with no movement than adults of either sex. Juveniles also had longer path lengths and larger search areas than adult females. Step length was related to turn angle (Mixed effects model: $F_{1,654} = 4.1$, $p = 0.043$), demographic group ($F_{2,147} = 11.46$, $p < 0.001$), and their interaction ($F_{2,635} = 7.2$, $p = 0.001$).

Movement path characteristics differed among demographic groups. Turn angle distributions for adult males differed significantly from females and juveniles (Kolmogorov–Smirnov test (D (p)), males vs. females: 0.168 (0.041); males vs. juveniles: 0.159 (0.008); females vs. juveniles: 0.051 (0.912)). Visual inspection of the data indicated that males exhibited a higher proportion of small turn angles (Figure 2). Step length distributions for males also differed significantly from females and juveniles (males vs. females: 0.238 (<0.001); males vs. juveniles: 0.178 (0.001)), females vs. juveniles: (0.090 (0.212)). The cumulative proportions of step lengths by demographic group indicate that males had a larger proportion of long step lengths than females and juveniles (Figure 3). Step length and turn angle were independent of each other for females (Mixed effects model: $F_{1,83} = 0.22$, $p = 0.637$) and juveniles ($F_{1,479} = 0.09$, $p = 0.760$), but negatively correlated for males ($F_{1,90} = 4.97$, $p = 0.028$).

Table 3. Pairwise comparisons of demographic group (F = female, M = male, Juv = Juvenile) behavior, movement, and entropy (Dunn's tests: Z (p)), as well as in proportionate size (tail length/SVL). Sample sizes are given in Table 1. Significant values are in **bold**.

	Value (units)	F-M	F-Juv	M-Juv
	Tail/SVL	3.52 (**0.0004**)	5.09 (**<0.0001**)	0.44 (0.66)
Behavior	Dig (n)	0.80 (0.42)	4.62 (**<0.001**)	3.07 (**0.002**)
	Eat (n)	0.56 (0.57)	4.64 (**<0.001**)	3.31 (**<0.001**)
	Tail display (n)	0.74 (0.46)	5.14 (**<0.001**)	3.48 (**<0.001**)
Movement	Move (n)	1.26 (0.21)	6.18 (**<0.001**)	3.85 (**<0.001**)
	No moves (n intervals)	1.58 (0.11)	4.60 (**<0.001**)	2.16 (**0.03**)
	Path length (cm)	1.26 (0.21)	3.65 (**<0.001**)	1.70 (0.09)
	Search area (m^2)	1.26 (0.21)	3.62 (**<0.001**)	1.67 (0.09)
	Entropy	0.27 (0.79)	4.55 (**<0.001**)	3.56 (**<0.001**)

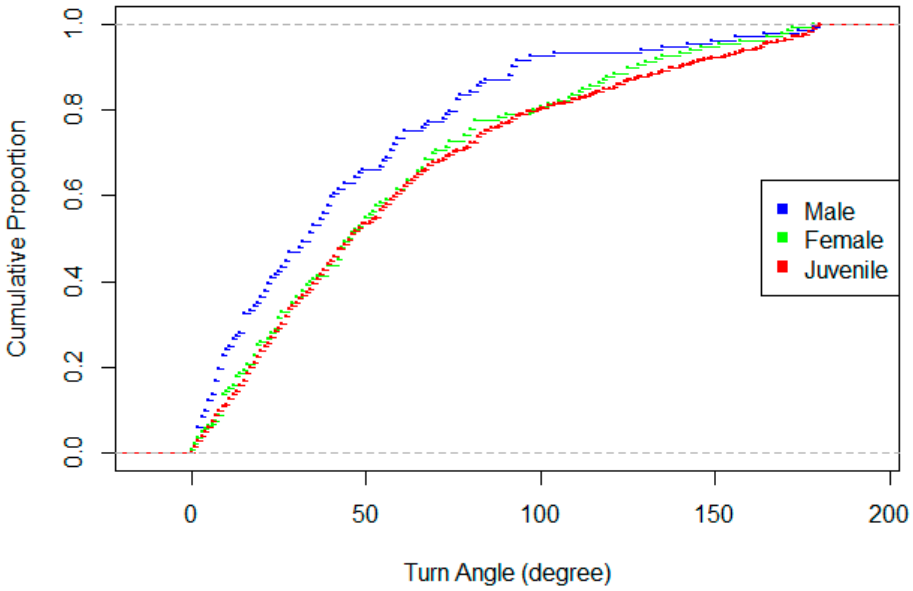

Figure 2. Cumulative proportion of turn angles for each demographic group.

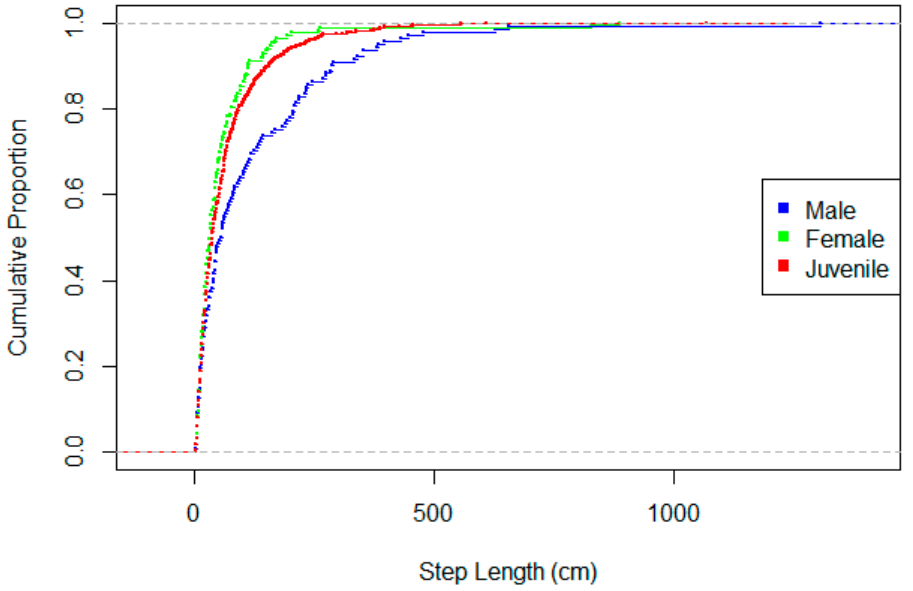

Figure 3. Cumulative proportion of step lengths for each demographic group. We excluded intervals that did not involve movement (i.e., step length = 0).

3.2. Within Demographic Class Comparisons

Within each demographic group, body length (SVL) and mass were highly correlated (Pearson's correlation; $p < 0.001$ for all: males $r = 0.86$, females = 0.83, juveniles = 0.93). For further analyses, we only used SVL for body size. The spatial measures of path length and search area were also positively correlated within all 3 groups ($r > 0.8$, $p < 0.001$), and entropy was correlated with higher levels of activity (i.e., moves; Tables 4–6). Although both entropy and moves were positively correlated with eating for adults, among juveniles, eating was positively correlated with moves but not with entropy (Tables 4–6).

Table 4. Correlation matrix for adult male body size (SVL), behavior (eat, dig, tail display), movement (moves, no move intervals (= 0 MovInt), path length, search area), and entropy (Pearson's r (p)). Significant *p*-values are in **bold**.

	Body Size	Behavior			Movement			
	SVL	Eat	Dig	Tail Display	Moves	0 MovInt	Path Length	Search Area
Eat	−0.50 **(0.04)**							
Dig	−0.46 **(0.05)**	0.31 (0.21)						
Tail display	−0.27 (0.34)	−0.08 (0.79)	0.52 **(0.05)**					
Moves	−0.36 (0.14)	0.54 **(0.02)**	0.66 **(0.003)**	0.40 (0.14)				
0 MovInt	0.42 (0.08)	−0.45 (0.06)	−0.37 (0.13)	−0.25 (0.36)	−0.59 **(0.01)**			
Path length	−0.23 (0.36)	0.50 **(0.03)**	0.56 **(0.02)**	0.52 **(0.05)**	0.85 **(<0.001)**	−0.56 **(0.02)**		
Search area	−0.19 (0.45)	0.47 **(0.05)**	0.45 (0.06)	0.31 (0.26)	0.67 **(0.003)**	−0.47 **(0.05)**	0.95 **(<0.001)**	
Entropy	−0.42 (0.08)	0.7 **(0.001)**	0.47 **(0.05)**	0.36 (0.19)	0.91 **(<0.001)**	−0.58 **(0.01)**	0.69 **(0.002)**	0.48 **(0.04)**

Table 5. Correlation matrix for adult female body size (SVL), behavior (eat, dig, tail display), movement (moves, no move intervals (= 0 MovInt), path length, search area), and entropy (Pearson's r (p)). Significant *p*-values are in **bold**.

	Body Size	Behavior			Movement			
	SVL	Eat	Dig	Tail Display	Moves	0 MovInt	Path Length	Search Area
Eat	−0.14 (0.47)							
Dig	−0.26 (0.19)	0.19 (0.34)						
Tail display	−0.51 **(0.009)**	0.21 (0.31)	−0.07 (0.74)					
Moves	−0.31 (0.10)	0.58 **(0.001)**	0.12 (0.53)	0.47 **(0.02)**				
0 MovInt	0.29 (0.12)	−0.59 **(0.001)**	−0.06 (0.78)	−0.38 (0.06)	−0.95 **(<0.001)**			
Path length	−0.31 (0.10)	0.30 (0.12)	0.14 (0.48)	0.14 (0.51)	0.63 **(<0.001)**	−0.55 **(0.002)**		
Search area	−0.14 (0.49)	0.017 (0.93)	0.01 (0.96)	−0.01 (0.96)	0.23 (0.23)	−0.13 (0.51)	0.87 **(<0.001)**	
Entropy	−0.13 (0.51)	0.53 **(0.003)**	0.10 (0.62)	0.22 (0.29)	0.86 **(<0.001)**	−0.91 **(<0.001)**	0.56 **(0.002)**	0.15 (0.44)

Table 6. Correlation matrix for juvenile body size (SVL), behavior (eat, dig, tail display), movement (moves, no move intervals (= 0 MovInt), path length, search area), and entropy (Pearson's r (p)). Significant *p*-values are in **bold**.

	Body Size	Behavior			Movement			
	SVL	Eats	Digs	Tail Display	Moves	0 MovInt	Path Length	Search Area
Eat	0.04 (0.78)							
Dig	0.02 (0.87)	−0.19 (0.18)						
Tail display	−0.20 (0.19)	0.17 (0.25)	0.25 (0.09)					
Moves	−0.12 (0.39)	0.40 **(0.003)**	0.02 (0.90)	0.50 **(<0.001)**				
0 MovInt	0.07 (0.61)	−0.31 **(0.02)**	−0.04 (0.78)	−0.44 **(0.002)**	−0.85 **(<0.001)**			
Path length	0.01 (0.92)	0.06 (0.67)	−0.08 (0.60)	0.26 (0.08)	0.73 **(<0.001)**	−0.67 **(<0.001)**		
Search area	0.06 (0.69)	−0.03 (0.86)	−0.12 (0.41)	0.11 (0.48)	0.59 **(<0.001)**	−0.46 **(0.001)**	0.93 **(<0.001)**	
Entropy	−0.04 (0.76)	0.14 (0.31)	0.13 (0.35)	0.47 **(0.001)**	0.64 **(<0.001)**	−0.79 **(<0.001)**	0.42 **(0.002)**	0.26 (0.06)

3.2.1. Adult Males

The more males moved during observations, the more they tended to eat and dig (Table 4). Males with higher levels of digging also had a higher incidence of tail displays. In addition, larger males ate and dug less often. Movement metrics were not correlated with male body size, but path length was positively correlated with all the behaviors we measured (i.e., eating, digging, and tail displays; Table 4). In addition, larger search areas

among males were positively correlated with eating and entropy. Finally, males with higher step length entropy tended to eat and dig more and have longer paths consisting of more moves contained within a larger search area (Table 4).

3.2.2. Adult Females

The more a female moved, the more she tended to eat and tail display (Table 5), although tail display frequency was negatively correlated with body size. Movement also was positively correlated with path length and entropy, but not with search area (Table 5).

3.2.3. Juveniles

Body size among juveniles showed no significant correlations with our behavioral or spatial metrics (Table 6). Juveniles who moved more tended to eat and tail display more (Table 6). In addition, more movement was correlated with longer path lengths and a larger search area. Higher step length entropy was associated with more moves, longer path length, and larger search area (Table 6).

3.3. Habitat Use

Regardless of demographic class, we found individuals in the open ca. 44% of the time (J 44.3%, F 44.5%, M 44.6%), but they differed in their use of plant species (chi-square test, x^2 = 539.263, df = 18, $p < 0.0001$; Figure 4). The plant species used most often by toad-headed agamas were Gray's sparrow saltbush (*Salsola passerina* = saltbush), leeks (*Allium polyrhizum*), devil's thorn (*Tribulus terrestris*), Dzungarian reaumuria (*Reaumuria soongorica* = reaumuria), grasses (Poaceae), and Mongolian leek (*Allium mongolicum*) (Table S1). Salsola and reaumuria were used more by adults and less by juveniles than predicted when equal use and availability are assumed (chi-square test). The opposite trend was evident for devil's thorn and leeks—juveniles used them more and adults less than predicted for random usage. In addition, adult females used grass more while adult males and juveniles used grass less than randomly expected. Finally, adult males used Mongolian leeks more and adult females less than random (Figure 4).

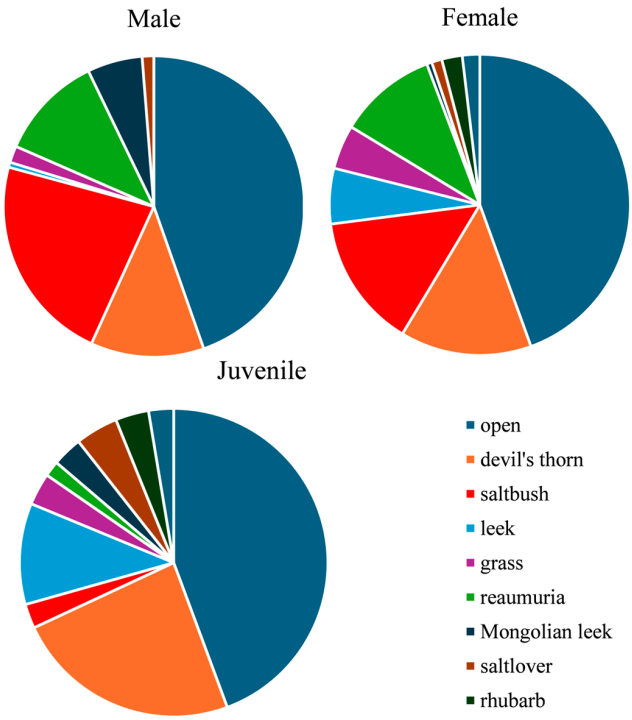

Figure 4. Percent of habitat types in which we found individuals from each demographic group.

In addition to plant species use, the classes differed in their use of open habitat (chi-square test, $x^2 = 82.1$, df = 4, $p < 0.0001$; Figure 5). Juveniles were located on ant mounds more frequently than expected, while females never visited ant mounds during observations. Adult males perched in the open on deadwood more than expected, and adult females less than random. Females used open bare ground more than expected, and males less than randomly expected.

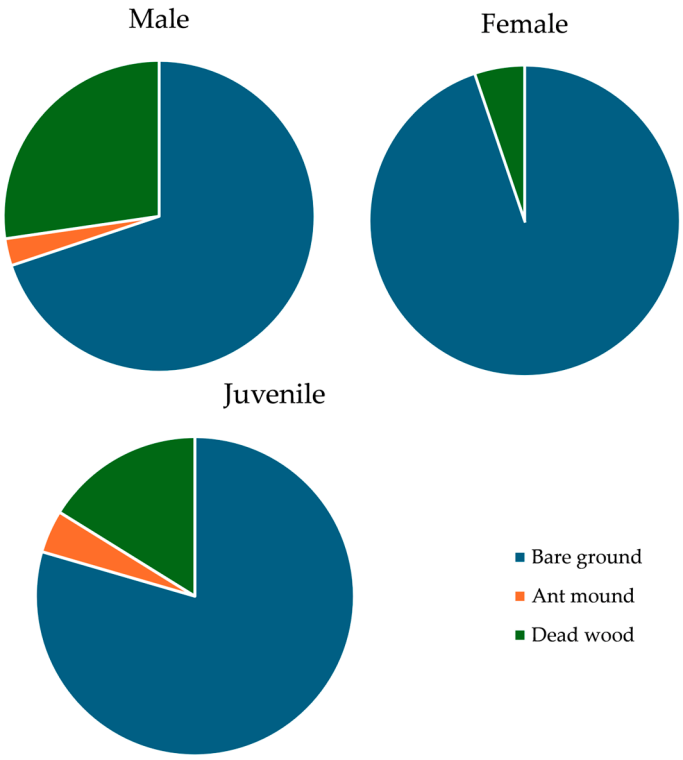

Figure 5. Percent of substrate types within open habitat in which we found individuals from each demographic group.

4. Discussion

Our hypothesis that adult male and female variegated toad-headed agamas will differ from each other was partially supported. The adult sexes did not differ from each other in their behavior or entropy, and most aspects of their movement patterns were not significantly different. However, adult males did differ from adult females and from juveniles in two aspects of movement: turn angle distribution and step length distribution. In addition to some differences in movement paths, we found demographic differences in habitat use. Regardless of class, we recorded individuals as occupying open habitat most of the time, but vegetation and perch use differed with sex and age. Adult males, females, and juveniles differed in their use of plant species (Figure 4) with males using Mongolian leeks more than females, while adult females used grass more than males. In addition, adult males perched in the open on dead vegetation and used ant mounds more than females.

Although we could not collect ecological data that distinguished reasons underlying age or sex-based variation in behavior, movement, or habitat use, movement path analyses are useful for generating hypotheses on ecological mechanism for observed patterns that can prompt detailed investigations to better understand observed differences. For example, smaller turn angles reduce the likelihood of revisiting areas and result in more directional movement [55,56]. Adult male variegated toad-headed agamas exhibited a higher proportion of smaller turns (Figure 2) and longer step lengths (Figure 3) than females and juveniles, indicating, as we predicted, that males moved in more direct paths. The pattern

leads us to hypothesize that male variegated toad-headed agamas engage in territorial defense as part of their mating system. In some mating systems, males commonly patrol territories containing food or reproductive resources while concomitantly decreasing or foregoing eating and foraging in exchange for defending those resources [57,58]. The mating system for variegated toad-headed agamas is unknown, although other members of their genus (*Phrynocephalus*) exhibit male territorial defense [50,59,60]. The movement pattern we observed, coupled with the fact that larger males ate less and that we found adult males perching in the open on raised surfaces (i.e., dead vegetation) more than the other demographic groups, is consistent with territorial behavior. By contrast, the short path lengths we recorded for adult females made them the least active demographic group. Coupled with their tendency to occupy vegetation, we hypothesize that female variegated toad-headed agama behavior and movement reflects their balance of reproductive constraints with thermoregulatory, foraging, and energetic needs. The behavioral patterns of female lizards often differ from those of males due to different reproductive costs (e.g., females invest in oviposition while males invest in territorial defense; [54,61–63]). Further behavioral studies are needed to confirm and assess the extent of territoriality and sex-based reproductive costs in variegated toad-headed agamas.

Our hypothesis that juveniles would differ from adults in behavior, movement, and habitat use was also partially supported. Consistent with having higher energetic needs, juveniles ate, dug, moved, and tail displayed more than adults (Table 1). Juvenile behavior could vary relative to adults due to developmental differences in body size, predation risk, thermal inertia, and energetic constraints [4,53]. The high energetic requirements needed for juveniles to grow are coupled with being the most vulnerable demographic group because of their small size and wider range of predators [15,64]. Although we did not assess predation pressure, aggression can occur within *Phrynocephalus* species [50], and cannibalism of juveniles is not uncommon in lizards [1,15,65,66]. More detailed studies of juvenile behavior and predation risks (including possible cannibalism threat) are merited to understand the differences we observed in juveniles relative to adults.

The movement patterns of juveniles differed from those of adult females by having longer path lengths and larger search areas (Table 1). Their high levels of movement and large search areas could arise as a strategy to minimize competition for food and space or to find predator-free (or adult-free) areas. High levels of movement also could be part of a movement syndrome such as dispersal [67,68], which commonly occurs among juvenile lizards [69]. Monitoring movements of juveniles over longer time spans is necessary to distinguish factors affecting their high levels of movement and to determine whether competition, predation, or a movement syndrome such as dispersal underlies the movement patterns we recorded. In support of our prediction, juvenile movement patterns also had higher entropy (i.e., less predictability) than either adult sex. Entropy in movement paths can reflect behavioral plasticity, with levels of entropy changing during development [70]. When adjustments to a movement path are accompanied by a change in the predictability of the movement pattern, entropy can be used to understand the properties of search [71,72] and escape behavior [73,74]. For example, lower entropy can indicate higher levels of routine movements [75] while higher entropy (i.e., less predictable movement) can increase the ability of an individual to evade predators [73]. The application of entropy analyses to movement ecology is in a nascent stage and, to our knowledge, has not been used to compare conspecific juvenile and adult movement paths. The high entropy in juvenile movement paths we recorded, coupled with their longer movement paths and larger search areas lead us to hypothesize that juvenile movement represents a balance among energetic constraints, predation concerns, and competition, an area of study meriting future investigations.

Juveniles also used the habitat differently from adults in some ways. Like adult males, juveniles made use of ant mounds (Figure 5). However, although adult males used ant mounds primarily as elevated perches, juveniles used them as foraging locations (pers. obs.). Habitat use differences were also apparent in age-specific plant use. Juveniles used two plants less often than adults (salsola and reaumuria) while plants frequently used by juveniles (devil's thorn and leeks) were rarely used by adults (Figure 4). One hypothesis resulting from our findings is that the differences in habitat use arise from body size differences. Salsola and reaumuria have large canopies and dense foliage that can provide good thermoregulatory opportunities and shelter from predators for larger individuals (i.e., adults) whereas devil's thorn grows low to the ground and leeks provide only small amounts of shade, potentially making them better suited to smaller individuals (i.e., juveniles; Figure 1). Alternatively, another hypothesis is that differences in adult and juvenile habitat use arise from age-specific social concerns. Adults might make some plants unavailable to juveniles—young lizards can be relegated to less favorable or different microhabitats as adults secure preferred locations [53,76,77] or as they avoid adults and adult-preferred habitats to minimize the threat of cannibalism [1,15]. In addition to tests of these hypotheses, an assessment of plant availability relative to plant use by different demographic groups is needed to provide insights into preferences rather than simply usage.

Perhaps as part of the process of establishing social relationships and search areas, juveniles raised their tail more than adults, and the more juveniles moved, the more frequently they displayed their tail (Tables 1 and 6). Lizards display and communicate using their limbs [52], dewlaps [78], heads [79], and tails [41,50,80,81]. Tail movements as signals occur in several lizard species [51,81,82], but their meaning can be difficult to determine [83,84]. Tail displays among *Phrynocephalus* can have multiple characteristics, as the direction, speed, and portion of the tail moved can vary [45,46,83,85]. Although there has been extensive work on tail displays by adult *Phrynocephalus* [10,42,44–47,85], to our knowledge, the structure and function of tail displays by juvenile *Phrynocephalus* remain unstudied. The differential use of tail displays among demographic groups in our study could arise from signals varying in function based on the sex and age of the signaler. In the Qinghai toad-headed agama (*P. vlangelii*) juveniles move their elevated, straight tail side to side, possibly as a pacifying signal aimed at appeasing larger adults, but adults use different tail displays to defend burrows from conspecifics [50]. Tail length in proportion to body length adds an interesting dimension to considerations of tail signaling. In our population, adult males and juveniles had relatively longer tails than females, which is consistent with some other congeners where adult males have relatively longer tails than adult females, with differences not appearing until adulthood (*P. vlangalii*, [86]; *P. guinanensis*, [87]; *P. przewalskii*, [88]). Based on tail length relative to body length, the frequency tail displays, and the movement patterns we recorded, we hypothesize that tail displays among adult males in our study population communicate presence and fitness, perhaps playing a role in territorial defense while juveniles use tail displays as pursuit-deterrent signals [52,81] to fend off aggression by conspecifics or predators while moving through their search area. Further research quantifying the types of tail signals, their structure, and their context would provide valuable insight into lizard communication.

5. Conclusions

Overall, adult males and females were similar in behavior, movement, and entropy, but differed in habitat use, possibly due to varying sex-based constraints. Juveniles differed from adults of both sexes in many of our measured variables, likely arising from a combination of size and experience constraints. Our entropy analysis of movement paths supports

the idea that juveniles are actively identifying a search area with suitable food resources and refuges, as does our data concerning tail displays. More detailed studies are needed to verify the function of tail displays and the exact context of the signal's use, as well as to determine the meaning of the higher randomness (i.e., entropy) in juvenile movement paths. For all individuals, the randomness of their movement paths (i.e., entropy) was positively correlated with activity levels (i.e., number of moves and path length). The entropy values we recorded were higher than those recorded previously [31,89]. Movement behavior can be amenable to assessment couched in information content, as the data encoded in movement reflect the predictability of movement or differences in movement patterns [90,91].

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d17090659/s1, Table S1: Plants visited by toad-headed agamas at 30 s interval markers during 15 min focal observations.

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