Sex and age differences in habitat selection of the mountain dragon lizard (Diploderma splendidum) from Western China

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Abstract

Habitat selection in animals results from a careful balance of individual requirements, environmental conditions, and ecological disturbances. Preferences can vary across sexes and ages due to differences in survival and reproductive priorities. Despite this variability, most studies have traditionally focused on isolated aspects of either sex or age-related differences in habitat selection, rather than considering a comprehensive range of influencing factors. The mountain dragon lizard (Diploderma splendidum) exemplifies a species adapted to shrub habitats in the dry-hot river valleys of the lower Jinsha River, western China, playing a crucial role in regional ecosystem stability. In this study, we examined the influence of 11 ecological factors on habitat selection by male and female D. splendidum across two distinct age classes (juvenile and adult) to explore sex and age-related disparities. The lizards showed considerable similarity in habitat preferences, but notable differences in their selection of specific ecological factors. Compared to adult females, adult males displayed a preference for higher tree positions, lower light intensity, and moderate vegetation density. Compared to juvenile females, juvenile males favored higher tree positions, low rock formations, and shrubby grassland and forest. Compared to juvenile females, adult females preferred higher tree positions and habitats further from water. Compared to juvenile males, adult males preferred higher tree habitats. Overall, habitat selection complexity in D. splendidum was significantly influenced by sex and age factors. This study contributes to our understanding of how these lizards respond to different physiological structures and resource requirements. These findings enhance current knowledge on reptile habitat selection and provide theoretical insights crucial for ecological restoration and species protection in the hot and dry valley areas of Hengduan Mountain.

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1. INTRODUCTION

Selection of suitable habitats is a critical process for animal survival and reproduction (Danchin et al., 1998). Habitat quality significantly influences resource utilization among species, as resources are often unevenly distributed, compelling all species to compete for the most suitable habitats to maximize resource acquisition (Paterson et al., 2018). Consequently, the factors shaping wildlife habitat selection are complex, encompassing both biotic and abiotic elements (Reunanen et al., 2002). These factors may arise from distinct physiological structures or phenotypic adaptations, including the intricate interplay between structure and function (Kaliontzopoulou et al., 2010; Popova et al., 2021). They also encompass dynamics of inter- and intraspecific competition, anti-predator behavior, and external forces such as seasonal changes or initiation of breeding seasons (Seki et al., 2022; Li et al., 2022; Bergstrom et al., 2019). Thus, habitat characteristics affecting fitness may vary spatially or temporally depending upon the phenotype of individuals or prevailing environmental conditions (Delaney et al., 2016).

Sexual dimorphism often leads to distinct habitat preferences among individuals due to physiological disparities and variations in life history strategies (Boinski, 1988; Calsbeek, 2009). Males typically exhibit greater habitat flexibility, investing more in selecting habitats suitable for social displays or territorial defense (Gabbert et al., 1999; Delaney et al., 2016). Conversely, females typically prioritize habitats with reduced security threats and enhanced predation avoidance strategies, with a preference for habitats conducive to oviposition, parturition escape, and concealment (Hahn et al., 2006; Kidawa et al., 2011). Optimal habitat for pregnant and lactating females is characterized by lower predator presence and abundant food resources, crucial for promoting reproductive success and offspring fitness (Bongi et al., 2008; Rachlow et al., 1998). McLoughlin et al. (2002) found that female barren-ground grizzly bears (*Ursus arctos*) favor riparian habitats with tall shrubs and eskers, known for their abundant food resources, while females with cubs prefer less threatening tussock or hummock successional tundra, despite lower food availability, due to reduced predation risks.

Differential habitat selection can also result from varying resource needs across different developmental stages, leading to distinct patterns of selection (Barten et al., 2001). Adults typically prioritize habitats that facilitate sexual communication and territorial defense, essential for breeding (Boinski, 1988). In contrast, juveniles often seek out locations with reduced competition and increased food availability to optimize their growth (Zhu et al., 2015). Kearney et al. (2007) observed that adult swamp rats (*Rattus lutreolus*) prefer densely vegetated areas for effective concealment during foraging, while juveniles tend to select sparsely vegetated habitats to minimize interspecific competition. Furthermore, juveniles tend to favor sheltered locations to reduce predation risks, given their limited defensive capabilities and smaller size (Faegre, 2017). Li et al (2022) found that juvenile black-necked cranes (*Grus nigricollis*) primarily inhabit lakes situated near mountain ranges, benefiting from abundant water and vegetation resources that offer ample food and refuge.

Extensive research has been conducted on habitat selection in animals, including lizards. However, most previous studies have focused on single aspects, such as sex or age-related differences in habitat selection, rather than considering a comprehensive range of factors (AlRashidi et al., 2021; Lortie et al., 2020; Zhu et al., 2015). The mountain dragon (*Diploderma splendidum*) serves as a notable case study in habitat selection due to its dense distribution, pronounced sexual and age-related variation, and consistent activity patterns. *In the study, we quantified the specific habitat preferences of D. splendidum across different sex and age groups from multiple perspectives to elucidate their unique ecological requirements and analyze the key factors influencing the distribution in diverse habitats. This research not only enhances our* understanding of the factors shaping organismal distribution across landscapes, *but also provides robust theoretical support and scientific guidance for wildlife conservation efforts and habitat restoration in the Jinsha River Basin.*

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2. MATERIALS AND METHODS

2.1. Survey region

This study was conducted in the lower Jinsha River valley, situated in Leibo County (28. 16°N, 103. 34°E), Sichuan Province, Western China. The region features a typical subtropical mountainous climate, characterized by distinct seasonal variations and notable diurnal temperature fluctuations. Annual average precipitation measures 900 mm, with approximately 1 250 hours of sunshine each year. The lizards predominantly inhabit exposed rocks and sparse brush, with a high population density of approximately 10 lizards/ha. Vegetation primarily consists of shrubs (e.g., *Rumex acetosa* L. and *Trema cannabina dielsiana*) and small trees (e.g., *Leucaena leucocephala* , *Jacaranda mimosifolia* , *Ficus virens* , and*Dodonaea viscosa*), interspersed with many planted forests (e.g.,*Citrus reticulata* and *Zanthoxylum piasezkii*).

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2.2. Individual capture and measurement

In 2021, a total of 125 *D. splendidum* lizards were captured using manual and noose techniques during their peak activity periods from July to August between 10: 00 and 16: 00 hours. Sex determination relied primarily on assessment of dorsal color patterns and the presence or absence of a hemipenis bulge. Snout-vent length (SVL) was measured using a digital caliper (Ningbo Deli Tools Co., Ltd.) to nearest 0.01 mm. Based on preliminary anatomical data from *D. splendidum* specimens, individuals with an SVL greater than 67 mm were classified as adult females, those with an SVL greater than 71 mm were classified as adult males, and the remaining individuals were categorized as juveniles. Each lizard was assigned a unique identification number for tracking purposes. Capture location was marked with uniquely coded plastic cards to facilitate subsequent habitat data collection and release at the original capture sites. After collecting morphological and habitat data, all lizards were released back into their respective capture sites.

2.3. Habitat data collection

Upon locating a lizard, a 5 m × 5 m experimental plot was established, centered on the stationary point of lizard activity. Additionally, a control plot of the same size, representing potential available habitat, was randomly selected within surrounding area using the random riprap method. After excluding data with significant errors and strictly adhering to matching rules, a total of 219 plots were selected, consisting of 94 used plots and 125 selected plots. Eleven ecological factors were assessed in each plot using corresponding survey instruments, including seven numerical ecological factors and four classified ecological factors (Table 1). The definition and classification of each ecological factor followed criteria outlined in previous studies (Yang et al., 2019; Farha et al., 2020; Table 1).

Table 1 Categorization of ecological factors investigated in this study

Ecological factor type	**Ecological factor**	**Definition**
Numerical factors	Tree height (cm)	Average height of trees within 5 m × 5 m plots.
	Perch height (cm)	Vertical elevation of arboreal habitat utilized by lizard, meas
	Rock height (cm)	Average height of all rocks within 5 m × 5 m plots.
	Rock size (cm)	Average size of all rocks within 5 m × 5 m plots.
	Distance from nearest water (m)	Minimum horizontal distance from plot to water source (incl
	Distance from nearest road (m)	Horizontal distance from plot to nearest road (including tran
	Light intensity (Lux)	Light intensity at capture point or centroid of plots.
Classified factors	Vegetation type	Main vegetation types were determined according to the vege
	Vegetation density	Quantity of trees in plot with three categories: lower (< 1 m
	Vegetation coverage	Proportion of upper canopy coverage relative to ground surfa
	Substrate status	Looseness of substrate in plot with three categories: loose (so

2.4. Statistical analyses

Before conducting statistical analyses, the Kolmogorov-Smirnov and Levene's tests were employed to assess data normality and homogeneity of variance, respectively.

To analyze the habitat selection preference of *D. splendidum* across different sex and age groups, Pearson correlation analysis was conducted to assess autocorrelation among numerical ecological factors, Kendall correlation analysis was conducted to assess autocorrelation among classified ecological factors, and Spearman correlation analysis was conducted to assess autocorrelation between numerical and classified ecological factors. Factors exhibiting high autocorrelation ($|r| > 0.8$; Gardiner et al., 2015; Chiaverini et al., 2023) were subsequently excluded. Perch height, reflecting species-specific preferences, was omitted from habitat selection preference analysis. Subsequently, a random forest model was constructed using these numerical and classified factors, and trend charts were generated for the Mean Decrease Gini index (Zhang et al., 2020;

R Development Core Team, 2018). Based on the differential importance of predictor variables indicated by the mean decrease Gini index, partial dependence plots were generated for various habitat factors.

To compare differences in habitat preference factors among different sex and age groups, a general linear model (GLM) was initially employed to quantify the effects of sex, age, and their interactions on habitat selection (Delaney et al., 2016). Subsequently, simple effect analysis was conducted to evaluate the influence of ecological factor interactions, excluding non-significant interactions. For numerical factors conforming to a normal distribution, differences in habitat selection between different sex and age groups were assessed using independent sample t -tests. In cases where numerical factors did not follow a normal distribution, differences in habitat selection among populations were assessed using the Mann-Whitney U test (Li et al., 2022). Chi-square tests were performed to analyze disparities in classified factors, such as slope direction and vegetation type, regarding sex and age preferences (Shilereyo et al., 2021). When significant differences were observed ($P < 0.05$), Vanderploeg & Scavia's selection index was employed to elucidate population-specific habitat preferences.

All statistical analyses were conducted using R Studio (v23.3.1, Racine et al., 2012) and SPSS software (v22.0).

3. Results

3.1. Habitat preferences across different sex and age groups

Autocorrelation analysis revealed a significant negative correlation between rock size and rock height ($r = 0.970$, Figure 1). Therefore, rock size was excluded from subsequent analyses to minimize experimental error. The importance values of variables in the random forest model for predicting suitable *D. splendidum* habitat, as determined by the mean decrease Gini index, are shown in Figure 2. Results identified substrate status (SS), tree height (TH), light intensity (LI), rock height (RH), and, to a lesser extent, vegetation coverage (VC), vegetation density (VD), and vegetation type (VT) as the primary factors influencing habitat selection among individuals of different sexes and ages.

The partial dependence graph derived from the random forest model indicated a significantly increased probability of adult male occurrence when the roosting height exceeded 90 cm and rock height surpassed 90 cm (Figure 3). Juvenile males were most likely to occur in habitats with tree heights greater than 90 cm and light intensity ranging from 10 000 to 22 000 Lux (Figure 3). The occurrence probability of adult females was higher in habitats with tree heights over 270 cm, distances from the nearest water sources less than 240 m, and rock heights greater than 45 cm (Figure 3). Juvenile females were more likely to be found in habitats with tree heights over 80 cm, light intensity ranging from 32 000 to 49 000 Lux, distance from nearest road source less than 10 m, distances from nearest water source between 250 m and 350 m, and rock heights greater than 8 cm (Figure 3).

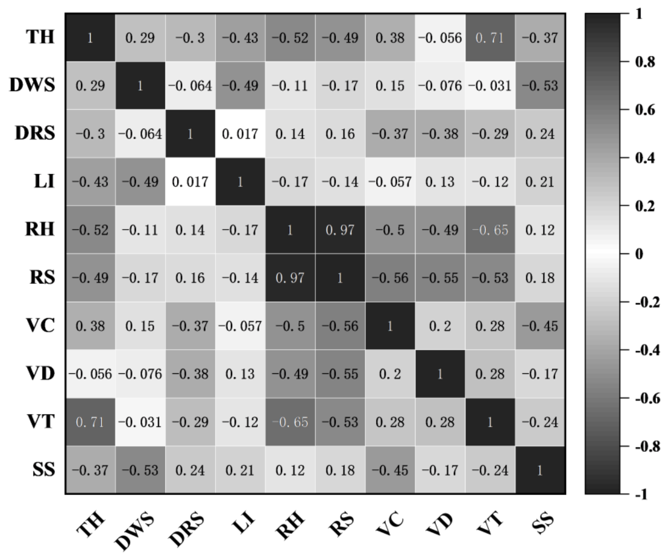

Figure 1 Autocorrelation analysis of habitat factors in *Diploderma splendidum* . TH: tree height; DWS: distance from nearest water; DRS: distance from nearest road; LI: light intensity; RH: rock height; VT: vegetation type; VD: vegetation density; VC: vegetation coverage; SS: substrate status.

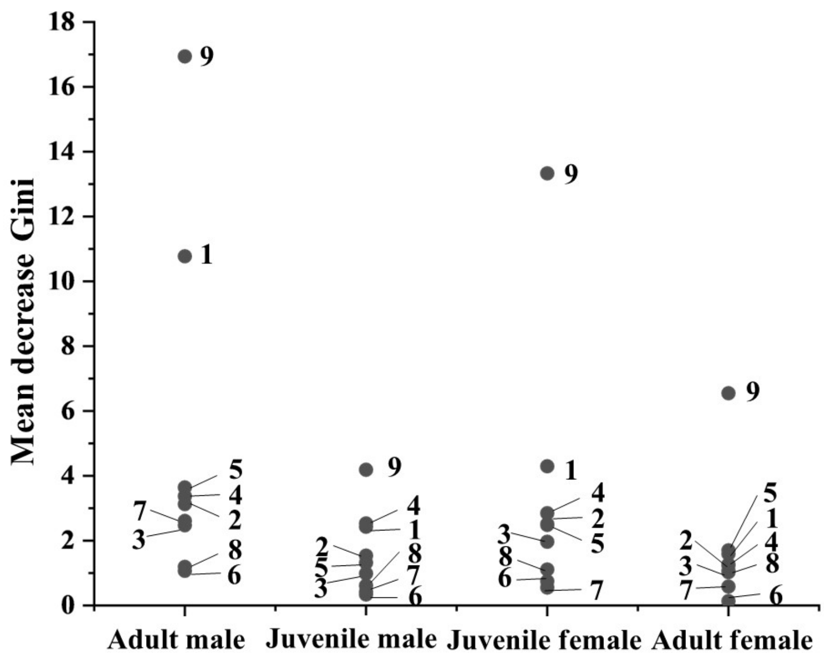

Figure 2 Relative importance of ecological factors in *Diploderma splendidum* varied across different sex and age groups. 1: Tree height (TH); 2: Distance from nearest water (DWS); 3: Distance from nearest road

(DRS); 4: Light intensity (LI); 5: Rock height (RH); 6: Vegetation coverage (VC); 7: Vegetation density (VD); 8: Vegetation type (VT); 9: Substrate status (SS).

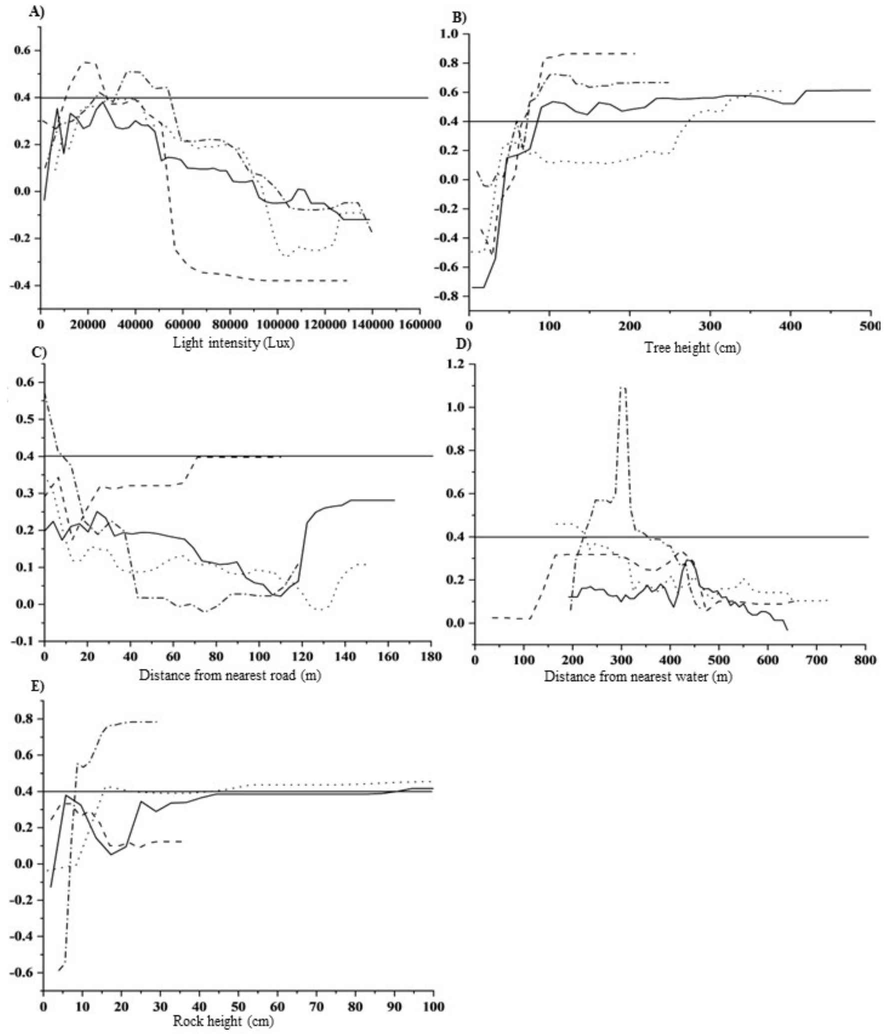

Figure 3 Importance values and partial dependence plots for each predictor variable in *Diploderma splendidum* across different sex and age groups. Y-axes are partial dependence (dependence of probability of occurrence on one predictor variable after averaging out effects of other predictor variables in the model). Full line: adult males; Short transverse line: juvenile males; Dotted line: adult females; Dotted and transverse line: juvenile females.

3.2. Sex and age-related variations in habitat selection

Given the absence of interactions between different sexes and ages, subsequent analysis focused on univariate effects (Table S1). Compared to juveniles, adults showed a preference for higher trees (F = 0.183, P = 0.004) and sites more distant from water (Z = -2.276, P = 0.023). Compared to females, males showed a preference for higher tree positions (Z = -3.611, P = 0.000). Compared to adult females, adult males exhibited a preference for higher tree positions (Z = -2.216, P = 0.027, Figure 4A) and areas with lower light intensity (Z = -2.034, P = 0.042, Figure 4D) and moderate vegetation density ($\chi 2$ = 14.230, P =0.001, Table 2). In comparison to juvenile females, juvenile males showed a preference for higher tree positions (Z = -2.75,P = 0.006, Figure 4B), low rock formations (F = -2.17,P = 0.03, Figure 4E, Table S2), and shrub and forest habitats over herbaceous habitats ($\chi 2$ = 8.842, P = 0.031, Table 2, Table S2).

Compared to juvenile females, adult females exhibited a preference for higher tree positions (Z = -2.031, P = 0.042, Figure 4C) and sites more distant from water (F = -2.051, P = 0.040, Figure 4F). In comparison to juvenile males, adult males displayed a preference for elevated tree habitats (F = -2.002, P = 0.045, Figure 4I). Additionally, adults favored habitats with general or firm substrate status ($\chi 2$ = 15.082, P = 0.001, Table 2, Table S2).

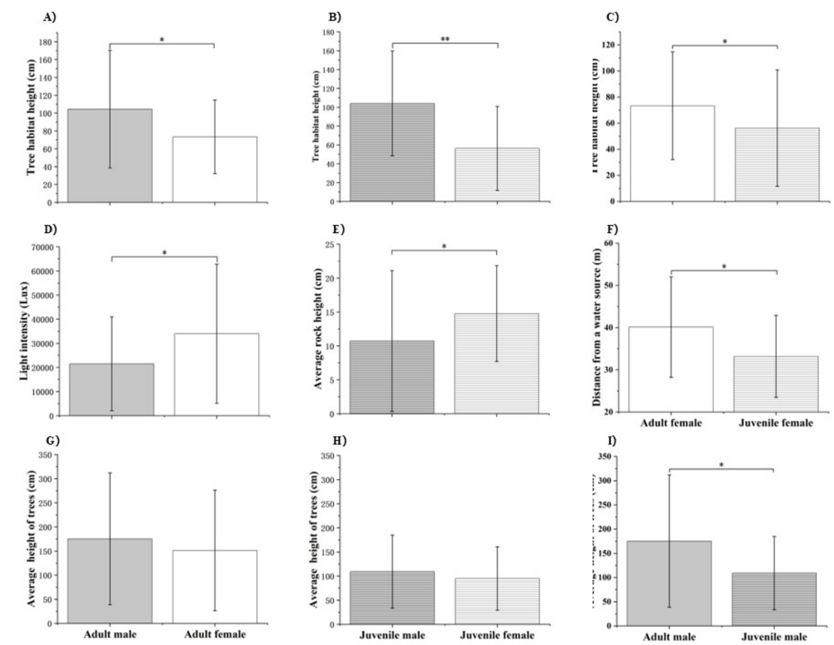

Figure 4 Selection and utilization of numerical variables in*Diploderma splendidum* across different sex and age groups. Light gray: adult male; Empty white: adult female; Light gray and line: juvenile male; Empty white and line: juvenile female.

Table 2 Selection and utilization of classified ecological factors by individual preference in *Diploderma splendidum*

Habitat type	Adult male (n = 52)		Adult female (n = 35)		Juvenile male (n = 18)		Ju
	Wi	Ei		Wi	Ei		Wi
Vegetation type	Herb	0.571	0.391		0.583	0.400	
	Shrub and herb	0.538	0.366		0.556	0.379	
	Forest and herb	0.559	0.382		0.56	0.383	
	Forest shrub and herb	0.579	0.397		0.571	0.391	
Vegetation coverage	Lower	0.500	0.200		1.000	0.500	
	Middle	0.559	0.254		0.475	0.176	
	Upper	0.567	0.26		0.684	0.345	
Vegetation density	Lower	0.029	0.029		0.568	0.260	

Habitat type	Adult male ($n = 52$)		Adult female ($n = 35$)	Juvenile male ($n = 18$)		Ju
Substrate status	Middle	0.385	0.385	0.545	0.242	
	Upper	0.259	0.259	0.571	0.264	
	Loose	0.429	0.125	0.500	0.200	
	General	0.565	0.258	0.576	0.268	
	Firm	1.000	0.500	0.000	-1.000	

Notes: Wi, selectivity coefficient; Ei, selection index.

4. DISCUSSION

Despite extensive research on habitat selection, limited knowledge exists regarding habitat selection status for individual species under multivariate conditions. In this study, we investigated the habitat selection patterns of *D. splendidum* across different sex and age groups. Results indicated that adult males preferred higher tree positions and areas with lower light intensity and moderate vegetation density. Adults favored higher tree positions and more distant from water sources. Juvenile males showed a preference for higher tree positions, lower rock formations, and shrub and forest habitats while avoiding herbaceous areas. Juvenile females preferred higher rock habitats and or scrubby herbaceous areas.

The observed differences in habitat selection among individuals of different sexes can may be attributed to variations in physiological structure, living habits, and behavior (Conde et al., 2010; Eifler et al., 2007). Adult males generally exhibited a preference for elevated habitats within moderately vegetated environments, similar to the preference for higher tree perches observed in territorial lizards such as *Anolis sagrei* (Delaney et al., 2016). Male lizards tend to occupy higher tree positions to enhance visibility for guarding territory, engaging in interspecific communication, displaying behavior, and foraging (Song et al., 2017). However, given the greater threats inherent in occupying higher positions, males also prefer habitats with denser vegetation to reduce their risk exposure (Browne et al., 2014; Robert et al., 2006). Females, especially pregnant females, tend to prefer areas with higher safety indices due to their significant investment in reproduction (Eifler et al., 2012; Jerosch et al., 2018). Our results indicated that females preferred lower tree positions or higher rocks, which provide better opportunities to escape from predators. and reduce risks associated with slower mobility, similar to the preference for lower perches and higher foraging observed in female arboreal lizards such as *Anolis polylepis* (Andrews, 1971). Lizards are ectotherms and their physiology is influenced by external conditions, especially light and temperature (Tan et al., 2019). Notably, we found that adult females preferred higher light intensity, likely to elevate their body temperature, enhance physiological and biochemical responses, and promote gonadal development, thereby influencing habitat selection decisions (Harvey et al., 2010; Melville et al., 2001). Adult females also preferred higher vegetation densities, further facilitating body temperature regulation (Melville et al., 2001).

The differences in habitat selection among individuals of varying ages may also be related to their developmental and physiological diversity (Ficetola et al., 2013). Our findings indicated that adult lizards typically preferred habitats with taller vegetation, which offer more abundant food sources, better concealment, and an extensive canopy that assists in thermoregulation. Vegetation characteristics in microhabitats have been shown to facilitate thermoregulation in animals (Bradley et al., 2022). Similarly, previous studies have revealed that preference differences between adults and juveniles may help reduce ecological niche competition and cannibalism, especially under high population densities (Keren-Rotem et al., 2006). Our results indicated that juvenile males, facing higher predation risks, tended to select larger rocky shelters, shrubs, and ground-level sites in forested areas. This behavior helps reduce daytime visual predator tracking, increase the availability of retreat sites, and lower predation risk (Niewiarowski et al., 1997). Similarly, Keren-Rotem et al. (2006) found that the juvenile common chameleons (*Chamaeleo chamaeleon*) prefer low grasslands for concealment, while adults favor shrubs and trees. Our results also demonstrated that adults preferred general or compacted substrate conditions, similar to the habitat selection observed in rock lizards (*Iberolacerta bonnali*) (Arribas et al., 2009). This preference aligns with the idea that both species select habitats that minimize negative impacts, thereby facilitating escape or enhancing predation rates (Song et al., 2017; Nemes et al., 2006; Mackey et al., 2010).

Our results revealed significant differences in habitat selection among lizards based on sex and age classes, contributing to existing knowledge on reptile habitat selection and enhancing our understanding of the distribution and specific characteristics of these lizards. Additionally, our findings offer theoretical support and scientific guidance for the conservation of lizards and other species in the dry and hot river valleys of the Hengduan Mountain region. However, the low occurrence rate of lizards during winter and early spring in the study area limited data collection. Consequently, only habitat selection data from the breeding period were analyzed, as year-round data collection was not feasible. It is important to note that habitat selection may vary across seasons, and factors such as temporal migration and interspecific interactions could influence specific habitat preferences of individuals. Therefore, future research will continue to monitor habitat changes influenced by various factors at different scales to address and resolve these uncertainties.

5. CONCLUSIONS

In conclusion, this study identified tree height, perch height, light intensity, vegetation density, vegetation type, and substrate status as the primary determinants of habitat selection for the mountain dragon lizard in the hot-dry river valley ecosystem of the lower Jinsha River Basin. Other environmental factors and interspecific interference were not found to be limiting resources. These findings suggest that the mountain dragon lizard may serve as a valuable environmental indicator for ecological changes and conservation efforts. However, further research is needed to determine the sensitivity of this species to the temporal migration.

Based on the results of this study and the challenges encountered during field experiments, several recommendations for artificial vegetation cultivation in the lower reaches of the Jinsha River are proposed. 1) Given the harsh natural environment downstream of the Jinsha River in Leibo County, most areas consist of forested land or sandy terrain. While these conditions support basic survival and reproduction, they constrain hiding and feeding opportunities. Implementing artificial planting on degraded land can provide broad-leaved forest habitats, thus increasing food abundance and concealment opportunities. 2) During artificial tree planting, it is important to retain the grass and shrub conditions around the trees to enhance vegetation coverage and increase canopy density, particularly for the survive of female lizards. 3) Land reclamation should be restricted to prevent habitat fragmentation. Reclaimed land should be planted with diverse vegetation types to not only increase food abundance but also help lizards avoid predators. These recommendations aim to improve habitat conditions for the mountain dragon lizard and support conservation efforts in the lower Jinsha River Basin.

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AUTHOR CONTRIBUTIONS

Dongqing Zhen conceived, designed, and conducted the experiments, analyzed the data, prepared figures and/or tables, authored and reviewed drafts of the paper, and approved the final draft. Ling Li conceived, designed, and conducted the experiments, analyzed the data, prepared the figures and/or tables, and approved the final draft. Wei Gao conducted the experiments, beautified figures and/or tables, reviewed drafts of the paper. Meiqi Chen conducted the experiments, beautified figures and/or tables, reviewed drafts of the paper. Peng Guo conceived and designed the experiments, authored and reviewed drafts of the paper, and approved the final draft. Yayong Wu conceived and designed the experiments, performed the experiments, authored and reviewed drafts of the paper, and approved the final draft.

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CONFLICT OF INTEREST STATEMENT

The author declares no competing interests.

DATA AVAILABILITY STATEMENT

All raw data and analysis code are stored in DRYAD (DOI:10.5061/dryad. mcvdnck87). All analyses were performed with publicly available programs. All analysis codes can be publicly accessed and utilized.

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