

# Picking a tree: habitat use by the tree agama, *Acanthocercus atricollis atricollis*, in South Africa

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We studied tree agama (*Acanthocercus a. atricollis*) habitat use in the Magaliesberg mountain range in northern South Africa using sightings of marked individuals, and in a few cases, radio-telemetry. *Acanthocercus a. atricollis* preferentially selected thorn trees (46%; *Acacia karroo*), followed by common sugarbush (10%; *Protea caffra*) and dead trees (9%). The type of tree selected was unrelated to lizard age class or sex. Multivariate analysis failed to show any age class or sex effects for specific tree physical characteristics, but did reveal a preference for trees with greater diameter, canopy cover and incidence of parasitic plants. We suggest that more 'complex' trees may enhance crypsis, facilitate escape from predation, or provide a foraging advantage. *Acanthocercus a. atricollis* selected night-time perches higher than those used during the day, possibly further offsetting predation risk.

**Key words:** tree selection, age-sex differences, nocturnal retreat sites, lizard, reptile.

## INTRODUCTION

Habitat selection by animals has been defined as the active choice of an area from a range of alternatives in the absence of constraints (Partridge 1978). In reality, no area is free of constraints and habitat selection depends on the physical structure of the environment, the physiology of the animal, food availability and protection from predators (Ward & Lubin, 1993). There are numerous studies on habitat selection of arboreal and semi-arboreal lizards, mostly dealing with the polychrotid genus *Anolis* (e.g. Rand 1964; Andrews 1971; Vitt *et al.* 1981). For arboreal lizards, tree structure is of obvious importance because trees provide foraging sites, nest sites, and refuges from predators and trees that have greater surface area and complexity are often more favourable (Cooper 1993). Retreat sites with suitable thermal conditions are also crucial for ectotherms as behavioural and physiological processes are strongly dependent on temperature (Huey 1982).

Habitat selection may also involve differences in sexual or ontogenetic responses to the physical environment (Heatwole 1977). Differences in body size have been shown to influence inter-specific habitat use (Vitt *et al.* 1981) and should similarly influence different size classes within the same species (Jenssen *et al.* 1998). Often, differences in foraging behaviour (Bartosiewicz 1987) and predation risk (Shine 1989) cause males,

females and juveniles to use different habitats. Competition avoidance may be another cause of intraspecific habitat segregation when individuals are competing for similar sized prey and taxa (Jenssen *et al.* 1998). Little data exists on habitat use in southern African lizards (but see Pianka 1986). Such data are important for comparative purposes and for understanding life history patterns. Furthermore, tree harvesting is increasingly placing pressure on the environment and baseline data on arboreal species dependent on trees may be important for future conservation plans.

The objective of this study was to determine habitat selection in the tree agama (*Acanthocercus a. atricollis*). Tree agamas occur throughout Africa, from Ethiopia in the north to coastal KwaZulu-Natal, South Africa in the south. *Acanthocercus a. atricollis* are large (120–150 mm snout–vent length), diurnal, arboreal lizards that are sexually dimorphic in size and colouration. Mature males are larger than females and have a bright blue head and throat and a broad yellow-green vertebral stripe, while females remain olive-coloured with black marbling (Branch 1998). They are ambush foragers, spend most of their time foraging in trees, and show no sexual differences in diet or foraging behaviour (Reaney & Whiting 2002). We set out to determine 1) if *A. a. atricollis* select trees nonrandomly; 2) the physical attributes of trees they use; 3) if there are sexual and age/size-related differences in habitat use; and 4) what nocturnal retreat sites they use.

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## MATERIALS & METHODS

### Study area

Field observations were conducted at Mountain Sanctuary Park, Magaliesburg, North West Province (25°50'S, 27°28'E), South Africa during the 2000 breeding season (September–November; wet season). The mean ambient temperature in the area for the last 30 years (1960–1990) was 18.7°C (15.5 range; 10.9–26.5°C), while annual rainfall averaged 650 mm. Since lizard activity levels are typically higher during the breeding season, there may be a degree of seasonal bias in habitat use. The study area was situated in a campground on a north-facing slope of the Magaliesberg mountain range. The study area consisted of typical open savanna habitat (Branch 1998) comprising indigenous shrubs and trees, such as thorn trees (*Acacia* spp.), buffalo thorns (*Ziziphus mucronata*), common resin trees (*Ozoroa paniculosa*), and mountain karree (*Rhus leptodictya*), surrounded by low grass ground cover that was cut regularly. We mapped all 363 trees within the demarcated study area (51 515 m<sup>2</sup>) and identified them to species. Each tree was numbered to facilitate mapping of tree use by lizards.

### Sampling of lizards

*Acanthocercus a. atricollis* were caught by noosing and individually marked with colour-coded plastic collars (Insulok<sup>®</sup> cable ties). Reaney & Whiting (2002) determined that minimum size for reproduction for females is 96 mm snout-vent length (SVL) and males 82 mm SVL. Because most *A. a. atricollis* were first reproductive in excess of the minimum SVL, we considered individuals with an SVL < 100 mm to be juveniles. Juvenile lizards were dorsally marked with a silver, permanent marker pen because tagging juveniles with collars could obviously be detrimental during growth. A total of 12 males, 20 females and 10 juveniles were marked and habitat data were obtained by locating individually marked lizards and by radio-telemetry. Owing to weight constraints, only males that exceeded 100 g ( $n = 4$ ) were fitted with a transmitter (attached to a backpack) with an external antenna and battery (Richmond 1998). Transmitters weighed 2.5 g and batteries weighed either 5.3 or 3.9 g. An AR8000 receiver and antenna were used to receive transmitter signals.

Lizards were located by systematically walking through the study area and scanning trees and the ground. For each identified lizard, we recorded

tree number, perched height and time. Because spatial use by lizards was predictable, we sampled all individuals relatively uniformly. The number of observations for individual lizards ranged from 10–25. Lizards were located between 09:00–16:00 daily, and less often during 19:00–21:00 for night retreats. At night, we located only lizards with transmitters, using a receiver and a flashlight. We noted whether lizards were partially concealed by overhead vegetation (leaves) or if they were completely exposed.

### Sampling of trees

Tree structure of 84 randomly selected trees that were not used by lizards was quantified by estimating the height of the main trunk using 2–4 m and >4 m categories and determining the percentage in each category. Trunk diameter was determined by measuring the circumference of the main trunk 1 m above ground or at the main split if below 1 m and using the formula: circumference =  $2\pi r$ , where diameter =  $2r$ . The maximum canopy length and the width 90° to the trunk were measured by standing under the tree and measuring the length and width of the overhead tree foliage at its maximum point. Canopy cover was determined using the formula: canopy cover =  $\pi r^2$  ( $r$  = maximum length + width 90°/2)/2. All measurements were made to the nearest 1 m. We also noted the presence of holes or loose bark that we considered large enough to accommodate lizards, and whether the tree was infected with a hemiparasitic plant (*Viscum* spp.).

### Statistical analysis

A chi-square analysis was used to determine significant differences in tree species selected in relation to available trees. A  $3 \times 10$  contingency table was used to detect lizard age or sex differences in tree species selected. After data for the five tree variables were square-root transformed to approximate normality, discriminant function analysis (DFA) was performed to examine the separation of groups (trees selected and not selected; lizard age and sex classes). A box modification of Bartlett's test was used to evaluate the homogeneity of variances among groups. Hole measures were left out of the multivariate analysis due to the high degree of unequal variances. We also performed MANOVA on tree physical characteristics for trees selected and not selected by lizards. We tested for significant differences between age–sex classes in diurnal perch height

**Table 1.** Frequency (%) of tree species used by *Acanthocercus a. atricollis*.

| Tree species (%)                               | Total trees<br>( <i>n</i> = 363) | Trees selected<br>( <i>n</i> = 129) | Males<br>( <i>n</i> = 93) | Females<br>( <i>n</i> = 68) | Juveniles<br>( <i>n</i> = 18) |
|--|----------------------------------|-------------------------------------|---------------------------|-----------------------------|-------------------------------|
| Sweet thorn ( <i>Acacia karroo</i> )           | 33.5                             | 45.8                                | 51.6                      | 54.5                        | 44.4                          |
| Common hook-thorn ( <i>Acacia caffra</i> )     | 4.6                              | 2.3                                 | 2.1                       | 2.9                         | 5.5                           |
| Brack thorn ( <i>Acacia robusta</i> )          | 3.9                              | 6.2                                 | 5.4                       | 4.4                         | 11.1                          |
| Buffalo-thorn ( <i>Ziziphus mucronata</i> )    | 18.2                             | 7                                   | 7.5                       | 4.4                         | 0                             |
| Common sugarbush ( <i>Protea caffra</i> )      | 9.5                              | 10.1                                | 9.5                       | 11.8                        | 0                             |
| Common resin bush ( <i>Ozoroa paniculosa</i> ) | 7.4                              | 7.7                                 | 6.6                       | 7.4                         | 5.6                           |
| Mountain karree ( <i>Rhus leptodictya</i> )    | 9.2                              | 4.8                                 | 4.3                       | 4.4                         | 0                             |
| Wild seringa ( <i>Burkea africana</i> )        | 4.6                              | 4.5                                 | 4.3                       | 3                           | 5.6                           |
| Dead trees                                     | 3.3                              | 8.5                                 | 6.5                       | 4.4                         | 27.8                          |
| Other*   | 5.8                              | 3.1                                 | 2.2                       | 2.8                         | 0                             |

\*Other = large-fruited bushwillow (*Combretum zeyheri*), live-long (*Lannea discolor*), Highveld cabbage tree (*Cussonia paniculata*), common wild pear (*Dombeya rotundifolia*).

using one-way ANOVA, followed by a Tukey HSD post hoc comparison of means and Mann-Whitney *U* tests for adult nocturnal perch heights. All tests were two-tailed with  $\alpha = 0.05$ . For the multiple univariate comparisons  $\alpha$  levels were adjusted using sequential Bonferroni procedures to reduce Type I errors (Rice 1989). Means are reported  $\pm 1$  S.E.

## RESULTS

### Tree selection

We observed *Acanthocercus a. atricollis* on 129 (36%) of the 363 total number of trees in the study area. Of the trees used by *A. a. atricollis*, 59 (46%) were *Acacia karroo* (Table 1). The proportion of tree species selected by *A. a. atricollis* did not reflect the proportion of tree species available in the study area ( $\chi^2_9 = 25.52, P < 0.0025$ ; Table 1). *Acanthocercus a. atricollis* appears to have a preference for *Acacia karroo*, *A. robusta*, and dead trees, and avoided *Ziziphus mucronata* and *Rhus leptodictae*. The

species of tree selected by lizards was unrelated to lizard age or sex ( $\chi^2_{18} = 24.10, P > 0.05$ ; Table 1).

### Physical characteristics of trees: univariate analysis

When tree variables were compared separately, trees used by *A. a. atricollis* had significantly larger diameter ( $U_{129,84} = 3947, P < 0.001$ ) and a higher percentage had holes ( $\chi^2_1 = 7.80, P = 0.0052$ ) compared with unused trees. However, after  $\alpha$  levels were adjusted, trees selected by *A. a. atricollis* did not have more canopy coverage ( $U_{129,84} = 4474.5, P = 0.032$ ) or parasites ( $\chi^2_1 = 5.120, P = 0.024$ ) and were not significantly taller ( $\chi^2_1 = 1.12, P = 0.29$ ) than unused trees. When trees use by male, female and juvenile tree agamas were compared, there were no significant differences in any of the tree variables measured (height:  $\chi^2_2 = 0.450, P > 0.05$ ; diameter:  $H_{2,179} = 1.686, P = 0.43$ ; canopy cover:  $H_{2,179} = 0.581, P = 0.75$ ; holes:  $\chi^2_2 = 5.685, P > 0.05$ ; parasites:  $\chi^2_2 = 0.883, P > 0.05$ ; Table 2).

**Table 2.** Means ( $\pm 1$  S.E.) and frequency of physical characteristics of trees selected and not used by *Acanthocercus a. atricollis*.

| Variable                       | Trees selected<br>( <i>n</i> = 129) | Trees not used<br>( <i>n</i> = 84) | Males<br>( <i>n</i> = 93) | Females<br>( <i>n</i> = 68) | Juveniles<br>( <i>n</i> = 18) |
|--------------------------------|-------------------------------------|------------------------------------|---------------------------|-----------------------------|-------------------------------|
| Height (%)                     |                                     |                                    |                           |                             |                               |
| 2–4 m                          | 20.16                               | 27.38                              | 17.2                      | 17.65                       | 11.11                         |
| > 4 m                          | 79.84                               | 72.62                              | 82.8                      | 82.35                       | 88.89                         |
| Diameter (m)                   | 0.276 (0.011)                       | 0.232 (0.015)                      | 0.282 (0.013)             | 0.303 (0.015)               | 0.296 (0.026)                 |
| Canopy cover (m <sup>2</sup> ) | 50.021 (4.280)                      | 35.261 (3.358)                     | 55.457 (5.341)            | 56.592 (5.725)              | 49.966 (10.480)               |
| Holes (%)                      | 20.93                               | 6                                  | 13.98                     | 19.11                       | 44.44                         |
| Parasites (%)                  | 27.13                               | 13.1                               | 29.03                     | 33.82                       | 38.89                         |

**Table 3.** Loading of variables on function I from discriminant function analyses of trees selected and those not used by *Acanthocercus a. atricollis* based on four tree variables.

| Variables    | Function | P-value |
|--------------|----------|---------|
| Height       | 0.104    | 0.710   |
| Diameter     | -0.607   | 0.015   |
| Canopy cover | -0.581   | 0.034   |
| Parasites    | -0.560   | 0.027   |
| Eigenvalue   | 0.084    |         |
| % explained  | 100      |         |

### Physical characteristics of trees: multivariate analysis

Variances for the three groups (trees used by male, female and juvenile lizards) were equal (Bartlett's test:  $M = 40.50$ ,  $\chi^2_{30} = 37.66$ ,  $P = 0.159$ ), however the variances for the two groups (trees selected and not selected) were unequal (Bartlett's test:  $M = 27.014$ ,  $\chi^2_{10} = 26.43$ ,  $P = 0.003$ ). The latter result indicates that the groups exhibited different patterns of variation with respect to the four variables examined. Variation in habitat variables are often analysed using MANOVA and DFA (Rienert 1984a,b). Both assume equal variances, meaning that groups respond in a similar way to the variables measured. However, this violation is often ignored due to the unrealistic nature of this assumption and the heuristic value of the test (Green 1971; Rienert 1984a,b).

An overall MANOVA for the four variables and two groups (i.e. trees selected and not selected) showed significant differences among the habitat measures ( $\lambda = 0.923$ ,  $F_{4,208} = 4.36$ ,  $P < 0.002$ ; - Table 3). Although the univariate analysis showed that selected trees only tended to have greater canopy cover and parasite infections, the DFA showed that the separation of the two groups was based significantly on diameter, canopy cover and parasite infection, but not height (Table 3). The overall MANOVA for the four habitat variables (Table 3) was not significantly different for the three age-sex groups (i.e. males, females, and juveniles) ( $\lambda = 0.979$ ,  $F_{8,346} = 0.460$ ,  $P < 0.884$ ); similarly, the DFA failed to show any significant difference among age-sex groups in the habitat variables measured, indicating that male, female and juvenile *A. a. atricollis* were using similar habitats (Table 4). The multivariate analysis of trees selected by different age and sex classes therefore produced the same pattern as the univariate analysis.

**Table 4.** Loading of variables on functions I and II from discriminant function analyses of trees selected by male, female and juvenile *Acanthocercus a. atricollis* based on four tree variables.

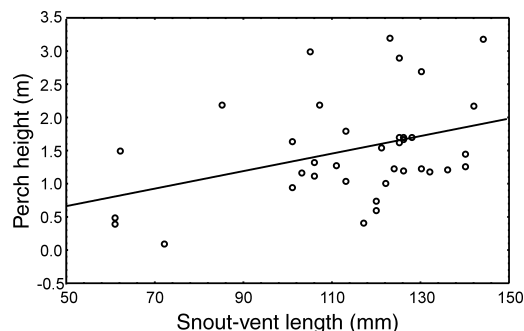
| Variables    | Function | P-value |
|--------------|----------|---------|
| Height       | 0.068    | -0.906  |
| Diameter     | 1.068    | 0.144   |
| Canopy cover | -0.609   | 0.850   |
| Parasites    | 0.844    | 0.169   |
| Eigenvalue   | 0.014    | 0.007   |
| % explained  | 67.21    | 32.79   |

### Diurnal perch heights

Male diurnal perch height for males with transmitters ( $n = 4$ ) versus those without ( $n = 8$ ) was not significantly different and was therefore combined ( $t_{10} = -0.793$ ,  $P = 0.446$ ). Male ( $n = 12$ ) perch height averaged  $1.81 \text{ m} \pm 0.48$ , females ( $n = 20$ ) averaged  $1.47 \text{ m} \pm 0.13$  and juveniles ( $n = 10$ ) averaged  $0.92 \pm 0.19 \text{ m}$ . Perch height for males, females and juveniles was significantly different ( $F_{2,39} = 4.51$ ,  $P = 0.017$ ). Using a Tukey HSD test, perch height for adult males and females were not significantly different ( $P = 0.385$ ), nor were adult female and juvenile perch height ( $P = 0.116$ ). Male perch height was, however, significantly higher than juvenile perch height ( $P = 0.013$ ). When male, female and juvenile perch heights were combined, larger individuals had significantly higher perch heights ( $r_s = 0.343$ ,  $P = 0.038$ ; Fig. 1).

### Nocturnal perch heights

Males with and without transmitters selected similar nocturnal perch heights ( $U_{4,3} = 5.5$ ,  $P = 0.860$ ); these data were therefore combined. Male ( $n = 7$ ) and female ( $n = 4$ ) nocturnal perch height was not significantly different ( $U_{7,4} = 6.00$ ,  $P = 0.131$ ), although females did have a lower mean



**Fig. 1.** Relationship between mean perch height (m) and snout-vent length (mm) for all age and sex classes of *Acanthocercus a. atricollis*.

perch height than males (males:  $3.5 \pm 0.465$  m; females:  $2.3 \pm 0.358$  m). Both adult male and female nocturnal perch heights were higher than their diurnal perch heights (males:  $U_{7,12} = 8.5$ ,  $P = 0.0046$ ; females:  $U_{4,20} = 14.5$ ,  $P = 0.048$ ). When all night observations were combined, *A. a. atricollis* spent 67% of their time in night retreats that provided partial cover (under leaves) and 33% totally exposed. All individuals were observed on branches and none were found in holes, although 21% of the trees selected by *A. a. atricollis* had holes large enough for occupation. We also observed two males and one female returning to their same individual nocturnal retreat sites for several nights.

## DISCUSSION

*Acanthocercus a. atricollis* appear to be selectively occupying some tree species over others. *Acacia karoo* was the most commonly selected tree species, verifying anecdotal observations that *A. a. atricollis* are found in close association with *Acacia* trees (Branch 1998). Their preference for *Acacia* and dead trees may be explained by any number of unexamined variables including prey availability, enhanced performance in relation to crypsis and escape from predation, or some physical aspect of tree structure that enhances signaling.

We identified three physical characteristics important for tree selection by *A. a. atricollis*: tree diameter, foliage cover and the presence of holes. *Acanthocercus a. atricollis*' association with trees containing holes may simply be an artifact of larger/older trees containing more holes. We found no evidence that lizards were using holes as refuges or night-retreat sites. *Acanthocercus a. atricollis* bury their eggs below ground, suggesting that tree holes do not serve as nesting sites. Furthermore, night-time observations showed that holes were not important retreat sites. Both adult male and female lizards were observed sleeping exposed, on branches, although often under foliage. However, Branch (1998) reported tree agamas to use hollow branches and loose bark as night-retreat sites and this tendency may vary geographically. Tree size is therefore presumably important for increasing foraging area while canopy cover could aid in crypsis.

Although tree height was not important, *A. a. atricollis* showed a preference for trees with large diameters and canopy coverage. Foliage cover is an important selection factor for arboreal lizards for the obvious benefit that it provides cover and

thus reduces the likelihood of detection by predators (Cooper 1993). *Acacia* spp. were frequently parasitised by *Viscum* spp. which seems to provide extra foliage cover in early summer before leaves were abundant (pers. obs.), which may explain the lizard's association with parasitised trees. Tree size has been shown to be an important factor for habitat choice in many arboreal lizards (e.g. *Eumeces laticeps*, Cooper 1993; *Mabuya striata*, Cooper & Whiting 2000), with individuals exhibiting strong preferences for larger trees. *Acanthocercus a. atricollis*' preference for trees with large diameter and canopy cover is therefore not surprising because larger trees are more complex and provide greater refuge from predators and have increased foraging surfaces and potential invertebrate prey for arboreal lizards (Cooper & Whiting 2000).

Adult male and female tree agamas forage in a similar fashion (Reaney & Whiting 2002), and our study failed to find any sex-related differences in habitat use. Similarly, there were no age-related differences in habitat use; both adults and juveniles occupied similar trees. However, adult males perched higher above ground than juveniles, as is the case for many other lizard taxa (reviewed in Chandler & Tolson 1990; Clark & Gillingham 1990). Interestingly, adults perched significantly higher above ground at night compared to during the day. Differences in diurnal versus nocturnal habitat use have been reported for several lizard taxa (e.g. Chandler & Tolson 1990; Clark & Gillingham 1990). Several plausible explanations exist for this relationship, the most likely of which include thermal preferences (Christian *et al.* 1983; Goto & Osborne 1989), social constraints (Chandler & Tolson 1990), and antipredatory tactics (Chandler & Tolson 1990; Clarke & Gillingham 1990; Vitt *et al.* 2002). Of these, predation pressure may be the strongest selective force driving nocturnal habitat selection in lizards. For example, *Anolis trachyderma* sleep higher off the ground at night and when disturbed, drop to the forest floor and remain immobile, relying on crypsis to avoid detection by predators (Vitt *et al.* 2002). Similarly, Puerto Rican *Anolis cristatellus* select short, thin branches, infrequently used by their primary predator (the boa *Epicrates monensis*) and sleep at the branch's extremity (Chandler & Tolson 1990). In *A. a. atricollis*, it is unlikely that social interactions influenced perch height selection because lizards were relatively dispersed and used trees with multiple branches that would allow several lizards to occupy different parts of the same tree at

the same height. Furthermore, adult perch height selection was not significantly different for males and females although a significant correlation existed between body size and perch height. Tree agamas are territorial (Branch 1998; pers. obs.) and it is therefore possible that some males excluded rivals from particular trees. However, we found no differences in tree selection among males, females and juveniles and any given tree species was abundant enough to exclude bias in tree selection through social interactions. Thermal influence on perch height is also questionable because trees were relatively open and therefore unlikely to have much of a thermal gradient. Furthermore, if any thermal gradient exists, temperature and tree height should be inversely related, such that lizards perching higher in a tree would experience lower temperatures. Snakes, feral cats, and various birds all feed on *A. a. atricollis* (pers. obs.). Whether selective pressures from these predators have driven nocturnal retreat site selection in *A. a. atricollis* remains an interesting, but unresolved problem.

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The third column heading of Table 4 should read as follows:

**Table 4.** Loading of variables on functions I and II from discriminant function analyses of trees selected by male, female and juvenile *Acanthocercus a. atricollis* based on four tree variables.

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| Variables    | Function<br>I | Function<br>II |
|--------------|---------------|----------------|
| <hr/>        |               |                |
| Height       | 0.068         | -0.906         |
| Diameter     | 1.068         | 0.144          |
| Canopy cover | -0.609        | 0.850          |
| Parasites    | 0.844         | 0.169          |
| Eigenvalue   | 0.014         | 0.007          |
| % explained  | 67.21         | 32.79          |

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