

This article was downloaded by: [Macquarie University]

On: 01 February 2012, At: 04:54

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office:
Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Ethology Ecology & Evolution

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tee20>

Are female tree agamas (*Acanthocercus atricollis atricollis*) turned on by males or resources?

L.T. Reaney^a & M.J. Whiting^a

^a Communication and Behaviour Research Group, School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag 3, Wits, 2050, South Africa

Available online: 19 May 2010

To cite this article: L.T. Reaney & M.J. Whiting (2003): Are female tree agamas (*Acanthocercus atricollis atricollis*) turned on by males or resources?, *Ethology Ecology & Evolution*, 15:1, 19-30

To link to this article: <http://dx.doi.org/10.1080/08927014.2003.9522687>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.tandfonline.com/page/terms-and-conditions>

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae, and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand, or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

Are female tree agamas (*Acanthocercus atricollis atricollis*) turned on by males or resources?

L.T. REANEY and M.J. WHITING¹

Communication and Behaviour Research Group, School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag 3, Wits 2050, South Africa

Received 13 December 2001, accepted 24 March 2003

We examined the relative importance of male and home range quality on female-male spatial overlap in the tree agama, *Acanthocercus atricollis atricollis*. Specifically, we asked whether males in good condition had the greatest spatial overlap with females, whether these same males have the best home ranges, or whether females are simply occupying areas with the best habitat and highest food abundance. Tree structure and prey abundance were used as measures of male home range quality, and male snout-vent length and male body condition were used as indices of male quality. Males had significantly larger home ranges compared to females and female-male overlap was common, while male-male overlap was marginal in a few cases ($n = 3$). Contrary to prediction, larger males did not occupy larger areas and home range size was not influenced by prey abundance. However, there was significant variation in prey availability between male areas. Female-male overlap was linked to prey abundance in male home ranges, possibly because of the direct influence it has on female fitness. However, several high quality males with high spatial overlap with females also had relatively high prey abundance. Male quality may well be linked to resource availability, but small sample size requires a cautionary interpretation.

KEY WORDS: female-male spatial overlap, home range quality, male quality, prey abundance, resources.

Introduction	20
Materials and methods	21
Results	23
Home range size and resource distribution	23
Are males or resources important for females?	25
Discussion	26
Male home range size and location	26
Female spatial distribution	27
Male quality and home range quality	28
Acknowledgements	28
References	29

¹ Corresponding author (E-mail: martin@gecko.biol.wits.ac.za).

INTRODUCTION

Many aspects of an animal's mating system and reproductive behaviour can be predicted on the basis of spatial and temporal distribution of resources (EMLEN & ORING 1977). Several studies have shown this for fish (e.g., JONES 1981, WARNER 1987), birds (e.g., ALATALO et al. 1986), lizards (e.g., HEWS 1993, WIKELSKI et al. 1996) and mammals (e.g., BARASH 1989, TRAVIS & SLOBODCHIKOFF 1993). Furthermore, variation in ecological factors such as food has been shown to influence individual reproductive success (DAVIES & LUNDBERG 1984, HEWS 1993). In polygynous systems, male distribution is strongly influenced by female distribution, which in turn is often linked to the spatial pattern of essential resources, such as food and nesting sites (EMLEN & ORING 1977, ANDERSSON 1994). By defending resources that are essential to females, males may increase their chances of mating with multiple females (EMLEN & ORING 1977).

In species with resource-defence mating systems, as in many lizard species (STAMPS 1983), territory characteristics often correlate with male mating success (CÔTÉ & HUNTE 1989). Factors determining territory quality may vary depending on the species and its reproductive needs. For example, food abundance is an important determinant of territory quality in the side-blotched iguanid lizard *Uta palmeri* (HEWS 1993), while habitat structure is more important than food in the tree lizard *Urosaurus ornatus* (M'CLOSKEY et al. 1990). In the Lake Eyre Dragon, *Ctenophorus maculosus*, males with larger territories had more females (OLSSON 1995). However, female mate choice could be based on the quality or quantity of the resources in the male's territory, or on the phenotypic characteristics of the male (ANDREWS 1985). Whether females use male traits such as size and colouration, or territory quality, for mate choice, has been the focus of many studies (e.g., ALATALO et al. 1986, WARNER 1987). Nevertheless, it has been difficult to evaluate the relative contributions of male traits and territory quality to female choice (HEWS 1990) because traits affecting competitive ability for territories can also be preferred by females (HEWS 1993). Furthermore, some studies have found that both territory and male quality were correlated with male pairing success and were further correlated with each other (PRICE 1984, ROITHMAIR 1994) and no conclusions on the relative importance of male and territory quality can therefore be reached (BART & EARNST 1999).

This study focuses on the influence of male and home range quality on female spatial patterns in the tree agama (*Acanthocercus atricollis atricollis*) in South Africa, during a single breeding season. *Acanthocercus a. atricollis* are large (maximum snout-vent length: males 167 mm, females 135 mm), diurnal, arboreal lizards, occurring throughout most of the African continent, ranging from Ethiopia in the north to coastal KwaZulu-Natal in the south (BRANCH 1998). Males are sexually dimorphic in both size (males have larger heads; REANEY & WHITING 2002) and colouration (males have blue heads; BRANCH 1998) and are territorial (BRANCH 1998). During the breeding season, sexually mature males have a bright blue head and throat, a broad yellow-green vertebral stripe, and a dark shoulder spot. The smaller females remain olive coloured with black marbling (BRANCH 1998).

As lizard copulations are rarely observed, an index of male mating success may be estimated from home range overlap by females (ABELL 1997). ABELL (1997) showed that measures of male-female home range overlap were significantly correlated with an estimate of male mating success (spatial proximity) in *Sceloporus virgatus*. A home range can be defined as the area that is habitually occupied, but not necessarily defended (SMITH 1985), although males typically defend a core area

within a home range (SCHOENER 1968). There are often high degrees of overlap between adjacent home ranges (SMITH 1985) and this is often more pronounced between males and females.

For arboreal lizards like *A. a. atricollis*, tree structure is of obvious importance for territory quality as trees provide foraging sites, nest sites and refuges from predators (COOPER 1993, COOPER & VITT 1994). Females usually prefer trees with greater surface area and complexity because they are more likely to contain these resources (COOPER 1993). Food availability is also one of the major factors determining spatial use by lizards (SIMON 1975). Experimental food manipulations have also shown that females shift their home ranges into supplemented areas which subsequently affects male mating opportunities (HEWS 1993).

We measured the extent of female-male spatial overlap of *A. a. atricollis* in relation to male quality (body condition and body size), tree quality, and prey abundance within male home ranges. We asked the following questions: (i) Do higher quality males have higher levels of female overlap on their home ranges? (ii) Do higher quality home ranges have higher levels of female-male overlap? and, (iii) Do higher quality males occupy higher quality home ranges?

MATERIALS AND METHODS

Study area and population

Field observations were conducted during the breeding season (September–November, 2000) in Mountain Sanctuary Park (25°50'S, 27°28'E), Magaliesburg, North-west Province, South Africa. The study area was a camping ground on a north-facing slope of the Magaliesberg Mountains, a continuous ridge running from Rustenburg in the west to Pretoria in the east. The habitat consisted of indigenous trees surrounded by low grass ground cover, kept short for camping purposes. Trees were labelled, identified to species, and plotted using a measuring tape and compass; a map of the area was then compiled. The study area was dominated by thorn trees (*Acacia* sp.), buffalo thorns (*Ziziphus mucronata*), common resin trees (*Ozoroa paniculosa*), mountain karree (*Rhus leptodictya*) and wild seringa (*Burkea africana*).

Acanthocercus a. atricollis were caught by noosing. Upon capture, lizards were measured for snout-vent length (SVL) and tail length (measured with a transparent ruler to the nearest mm), head length, width and height (measured to the nearest 0.01 mm using digital calipers) and mass (measured on a digital scale to nearest 0.1 g). We used both male SVL and male body condition ($\text{mass}^{1/3} / \text{snout-vent length}$ (log [base 10] transformed)) as indices of male quality.

A previous study determined that females reach sexual maturity at 96 mm SVL and males reach sexual maturity at 82 mm SVL (REANEY & WHITING 2002). Adult lizards were marked with a unique combination of coloured cable ties around the neck. Due to weight constraints, only 4 males were fitted with transmitters for the duration of the study. All 4 males had a mass that exceeded 100 g. The backpack, containing a transmitter (Heli-Trace; 2.5 g) with an external antenna, powered by either a 5.3 g or 3.9 g battery, was fitted according to the method described by RICHMOND (1998). Transmitter signals were received by an AR8000 receiver and antenna. When *A. a. atricollis* were caught and measured, they instantly lost their breeding colouration and exhibited a dark grey colour due to the stress of capture. All males fitted with backpacks regained their breeding colouration within a few minutes of release, and showed no physical signs of stress. Furthermore, there was no difference in the diurnal and nocturnal perch heights of males with backpacks and those without (REANEY & WHITING 2003), indicating that the backpacks did not affect the behaviour of the fitted males in any significant way.

Sampling protocol

Lizards were located by slowly walking through the study area several times a day and scanning the trees and ground. The census route took approximately 90 min and started at different locations each time to minimise any potential bias in the number of sightings per individual. Each sampling period was restricted to 90 min to prevent any tendency to spend more time in certain areas. The study area was censused during 08:30-17:00 hr. We recorded the location of each lizard and its nearest neighbour (within 10 m) to obtain a measure of female proximity to males. We also recorded any territorial behaviour, such as fighting or displaying, and courtship behaviour. We used only sightings separated by at least 2 hr to keep sightings as independent as possible. We observed lizards with binoculars from a distance to avoid disturbing their behaviour.

Spatial overlap

We used the plotted map of trees within the study site to determine home range size and spatial overlap. Home-range size of lizards was estimated using the minimum convex polygon method (ROSE 1982). This method is very accurate when the time intervals between sightings are short, such as daily intervals (ROSE 1982). We determined the number of males and females overlapped by each individual, as well as three measures of the extent of home range overlap between individuals of the same and opposite sex: percent overlap, overlap pressure and encroachment (for description of methods see ABELL 1998). Percent overlap can be defined as the percent of the focal individual's home range shared with one or more other individuals. The percent overlap measure is the most commonly used overlap measure of the three (ABELL 1998). Overlap pressure is the total area shared by the focal individual with each overlapped individual, divided by the home range area of the focal individual. The overlap pressure measure gives additional weight to space shared by more than two individuals. Encroachment represents the average percent of other lizards' home ranges overlapped by the focal individual. The encroachment measure provides an estimate of how much space the focal individual overlaps rather than how much of the focal individual's space is overlapped. Measures of female-male overlap give an indication of male access to females and may therefore serve as a rough indication of male mating success in lizards (M'CLOSKEY et al. 1990, HEWS 1993, ABELL 1997).

To determine the minimum number of sightings for accurate estimation of home range size, we performed a series of linear regressions (separately for each sex) with home range size as the dependent variable and number of sightings as the independent variable. For females, nine sightings or more were needed for an accurate home range measure (sightings ≥ 8 : $R^2 = 0.35$, $n = 20$, $P = 0.021$; sightings ≥ 9 : $R^2 = 0.20$, $n = 18$, $P = 0.108$). For males, 17 sightings or more were needed (sightings ≥ 16 : $R^2 = 0.63$, $n = 10$, $P = 0.033$; sightings ≥ 17 : $R^2 = 0.43$, $n = 7$, $P = 0.158$). We analysed female SVL (and not body condition) in relation to home range size because we could not account for any influence of reproductive condition which may affect body mass. For males, we analysed both SVL and male body condition in relation to home range.

Home range quality

For each male, home range quality was estimated by food availability and tree physical characteristics. Analyses of stomach contents indicated that insects dominate *A. a. atricollis*' diet (REANEY & WHITING 2002), with ants (Formicidae), beetles (Coleoptera) and orthopterans making up the greatest proportions. To quantify insect abundance within each male's home range, three trees were selected in the lizard's core home range area and sampled once each, with sticky traps (10 \times 10 cm), on different days within the study period. Twenty trees in

areas that did not contain resident males were also sampled to quantify prey abundance across the entire study site. Three sticky traps were placed in the tree canopy (approximately 1.5 m above ground) and on the ground 2 m from the base of each tree. Sticky traps were placed at 09:00 hr and collected at 17:00 hr. Prey items were counted and measured for length and width to obtain numerical and volumetric prey abundance. Prey volume was determined using the formula for a prolate spheroid (VITT et al. 1993):

$$\text{volume} = 4\pi/3 (\text{length}/2) \times (\text{width}/2)^2$$

To quantify tree quality within a male's home range, we measured and scored the following physical features: (1) tree height, by estimating the height of the tree and using 2–4 m and > 4 m categories; (2) the diameter of the base by measuring circumference (circumference = $2\pi r$, where diameter = $2r$) at 1 m above ground or before the main split; (3) canopy cover by measuring the maximum canopy width and the width 90° to that and using the formula: canopy cover = $\pi^2 [r = (\text{maximum width} + \text{width } 90^\circ / 2) / 2]$; (4) the presence of holes or loose bark large enough to accommodate lizards and (5) the presence of a parasitic plant species (*A. a. atricollis* have a preference for parasitised trees as this may decrease lizard conspicuousness or make lizards less vulnerable to predators; (REANEY & WHITING 2003). Indices 4 and 5 were quantified as the total percent of trees within a male's home range that contained either holes or a parasitic plant. All measurements were made to the nearest meter.

Statistical analysis

All analysis was performed on Statistica 5.5 (STATSOFT 1999). Means were reported \pm 1 SE. Differences were considered significant at $\alpha = 0.05$. Principle component analysis (PCA), using unrotated factor loadings, was performed on home range quality, male quality and female-male overlap, as estimates of male mating success. Before performing the PCA, all variables were standardized using the formula: raw score – mean/standard deviation (STATSOFT 1999). We used the first three components because they explained 84% of the variance and none of the remaining components were characterised by high loadings.

RESULTS

Home range size and resource distribution

Male home range size averaged $2114.85 \pm 480.73 \text{ m}^2$, while females averaged $186.39 \pm 31.52 \text{ m}^2$, and were significantly larger than female home ranges ($Z = 3.813$, $P < 0.0001$; $n = 7$ males with at least 17 sighting and $n = 18$ females with at least 9 sighting; Fig. 1). Female home range size was significantly negatively correlated with SVL ($r_s = -0.50$, $P = 0.034$, $n = 18$). However, there was no correlation between male home range size and male body condition ($r_s = -0.32$, $P = 0.482$, $n = 7$) or male SVL ($r_s = -0.21$, $P = 0.558$, $n = 7$). Prey abundance was also unrelated to male home range size (prey number; $r_s = -0.68$, $P = 0.094$; prey volume; $r_s = -0.14$, $P = 0.760$).

Female home ranges frequently overlapped those of males (78%, $n = 18$), while males maintained largely exclusive areas (except for males 1, 2, 7, which each slightly overlapped one other male; Fig. 1). Although we followed 18 females, we only had reliable spatial data for seven males. Of the 18 females, 8 (44%) overlapped three males and were relatively clumped (Fig. 1). The remaining females were not clumped. Four of these females did not overlap a male (but overlapped one other female); two overlapped single males in the absence of other females,

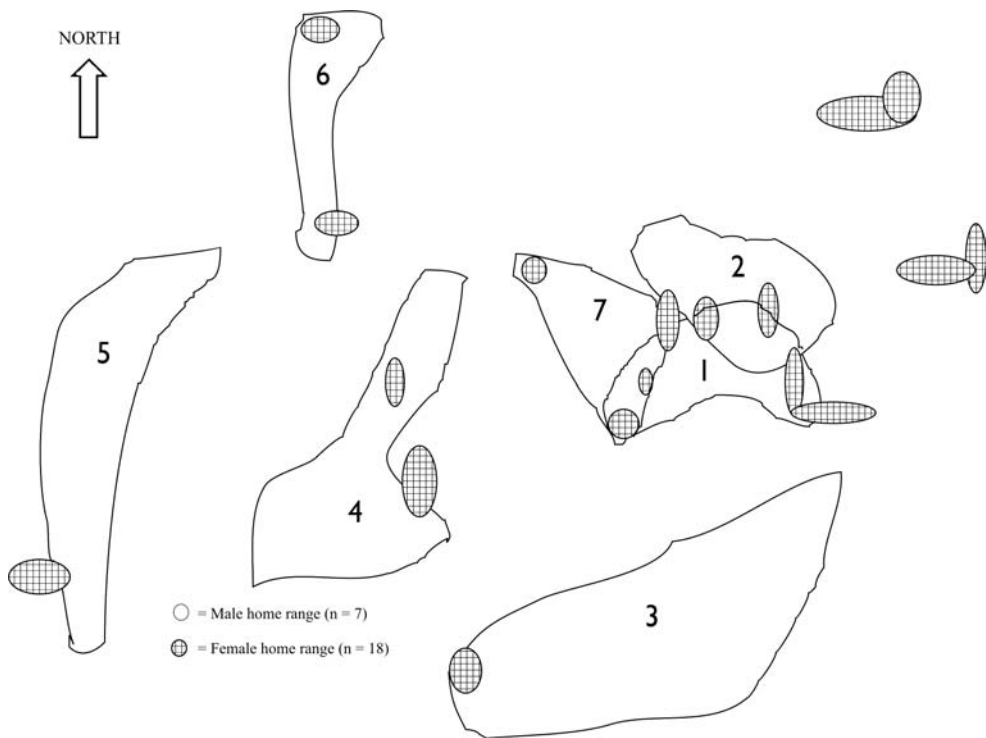


Fig. 1. — Schematic representation of study area, showing male 1-7 and female *Acanthocercus a. atricollis* home range distribution.

Table 1.

Measures of home range overlap in *Acanthocercus a. atricollis* for adult males with at least 17 sightings ($n = 7$) and females with at least 9 sightings ($n = 18$).

	Number overlapped mean \pm SE (n)	Percent overlap mean \pm SE (n)	Overlap pressure mean \pm SE (n)	Encroachment mean \pm SE (n)
♂ on ♀	1.37 \pm 0.11 (19)	0.64 \pm 0.12 (14)	1.03 \pm 0.20 (14)	0.05 \pm 0.01 (14)
♂ on ♂	0.57 \pm 0.30 (7)	0.37 \pm 0.18 (7)	0.37 \pm 0.18 (7)	0.26 \pm 0.14 (7)
♀ on ♂	3.14 \pm 0.80 (7)	0.17 \pm 0.06 (7)	0.19 \pm 0.07 (7)	0.60 \pm 0.12 (7)
♀ on ♀	0.45 \pm 0.15 (18)	0.05 \pm 0.03 (18)	0.05 \pm 0.03 (18)	0.05 \pm 0.02 (18)

and two pairs of females overlapped single males (males 4 and 6; Fig. 1). The highest levels of percent overlap and overlap pressure were for the presence of males on the home ranges of females, and the highest value for number individuals overlapping and encroachment were for females on male home ranges (Table 1). All three measures of overlap suggest extensive sharing of space, but specifically between females and males.

If the female aggregation was a result of an uneven distribution of important resources, these resources should vary significantly enough to influence female distribution. Tree height ($\chi^2_6 = 47.88$, $P < 0.0001$), percentage of trees containing holes ($\chi^2_6 = 47.16$, $P < 0.0001$) and parasitised trees ($\chi^2_6 = 58.32$, $P < 0.0001$) were all highly variable among the seven male home ranges. However, canopy cover ($H_{6, 103} = 10.35$, $P = 0.111$) and tree diameter ($H_{6, 103} = 11.05$, $P = 0.087$) did not show significant variation between the seven male home ranges. Although prey abundance (total prey number and volume) was not significantly different between areas without a male, and those areas frequented by a male (number: $U_{20,7} = 62$, $P = 0.658$; volume: $U_{20,7} = 47$, $P = 0.203$), mean prey abundance between male home ranges varied significantly both by number ($\chi^2_6 = 13.51$, $P = 0.036$) and volume ($\chi^2_6 = 293.08$, $P < 0.0001$). These results suggest that resources in male home ranges varied in both quality and quantity (Table 2).

Are males or resources important for females?

To separate variables (male characteristics and home range quality) explaining female distribution, we conducted a principal components analysis. In factor I, which explained 45.67% of the variation, tree height and canopy cover, prey number, male SVL, male body condition and all four measures of female overlap had high loadings (Table 3). The factor scores from the first component separated male 1, 2 and 7, who had the highest male quality, prey number and female overlap measures, from male 5, who had the lowest measures (Table 4, Fig. 2). Prey volume had the highest loading in factor II, which explained 22.31% of the variation (Table 3), with male 3 having the highest factor score reading (Table 4). Percentage of trees containing holes had the highest positive factor loading while home range size had the highest negative factor loading in Factor III, but neither prey abundance nor male quality had high loadings (Table 3). We were limited by male sample size, but our results suggest a link between male quality (SVL and condition), prey number, tree size, and female overlap.

Table 2.

Home range size and descriptive statistics (percentages and means [\pm SE]) of home range quality of seven *Acanthocercus a. atricollis* males. Home range quality was measured using physical tree characteristics and prey abundance.

Male ID	Home range size (m ²)	Physical tree characteristics					Prey abundance	
		% > 4 m	Diameter (m)	Canopy cover (m ²)	% holes	% parasitised	Total prey no.	Total prey vol. (mm ³)
1	1892	90	0.26 (0.03)	67.01 (13.90)	15	40	24.4 (6.0)	366.23 (115.61)
2	1472	93	0.32 (0.03)	80.56 (15.60)	13	33	17.3 (8.8)	234.23 (79.55)
3	4400	89	0.30 (0.04)	69.41 (15.82)	5	22	20.3 (10.2)	582.37 (484.13)
4	2680	100	0.35 (0.03)	71.96 (12.31)	20	40	15.3 (5.4)	228.70 (164.48)
5	2700	29	0.21 (0.04)	22.04 (10.31)	14	14	6.7 (2.9)	233.32 (105.25)
6	1000	60	0.33 (0.10)	48.27 (20.23)	40	0	25.7 (9.7)	401.86 (118.07)
7	660	82	0.29 (0.04)	64.40 (18.91)	36	45	25.3 (7.3)	327.18 (226.02)

Table 3.

Factor Loadings (unrotated) of the first three principle components of home range quality, male body size and condition, and female-male overlap measures for *Acanthocercus a. atricollis*. Variables with the highest loadings are in *italics*.

	Factor I	Factor II	Factor III
Height	<i>0.873</i>	0.132	– 0.311
Diameter	0.582	0.360	0.251
Canopy cover	<i>0.900</i>	0.104	– 0.276
% holes	0.055	– 0.185	<i>0.934</i>
% parasitised	0.521	– 0.453	– 0.468
Prey number	<i>0.745</i>	0.182	0.523
Prey volume	0.217	<i>0.817</i>	0.041
Male home range size	– 0.271	0.645	– 0.702
Male SVL (log)	<i>0.706</i>	0.420	0.178
Male body condition	<i>0.969</i>	0.175	0.116
Number of females	<i>0.708</i>	– 0.583	– 0.072
Percent overlap	<i>0.730</i>	– 0.584	– 0.108
Overlap pressure	<i>0.713</i>	– 0.571	– 0.146
Encroachment	<i>0.745</i>	0.630	– 0.036
Explained variance	45.67	22.31	15.58

Table 4.

Factor scores (unrotated) for the seven *Acanthocercus a. atricollis* males.

Male	Factor I	Factor II	Factor III
1	0.956	– 0.677	– 0.430
2	0.791	– 0.714	– 0.478
3	0.070	1.912	– 0.895
4	0.068	0.107	– 0.482
5	– 2.092	– 0.621	– 0.390
6	– 0.059	0.695	1.980
7	0.266	– 0.703	0.695

DISCUSSION

Male home range size and location

In polygynous systems, male home ranges typically exceed those of females because males attempt to overlap as many females as possible (POOLE 1989). Male *A. a. atricollis* had significantly larger home ranges than females, which is consistent with other studies of lizard spatial ecology (e.g., *Uta palmeri*, HEWS 1993; *Agama agama*, MADSEN & LOMAN 1987; *Sceloporus virgatus*, SMITH 1985). However, male quality and home range size were not significantly correlated, suggesting that prey was unevenly distributed. Prey availability was variable among male home ranges. However, prey number and prey volume were not correlated ($r = 0.71$, $P = 0.07$), making it difficult to evaluate the importance of prey availability. Further-

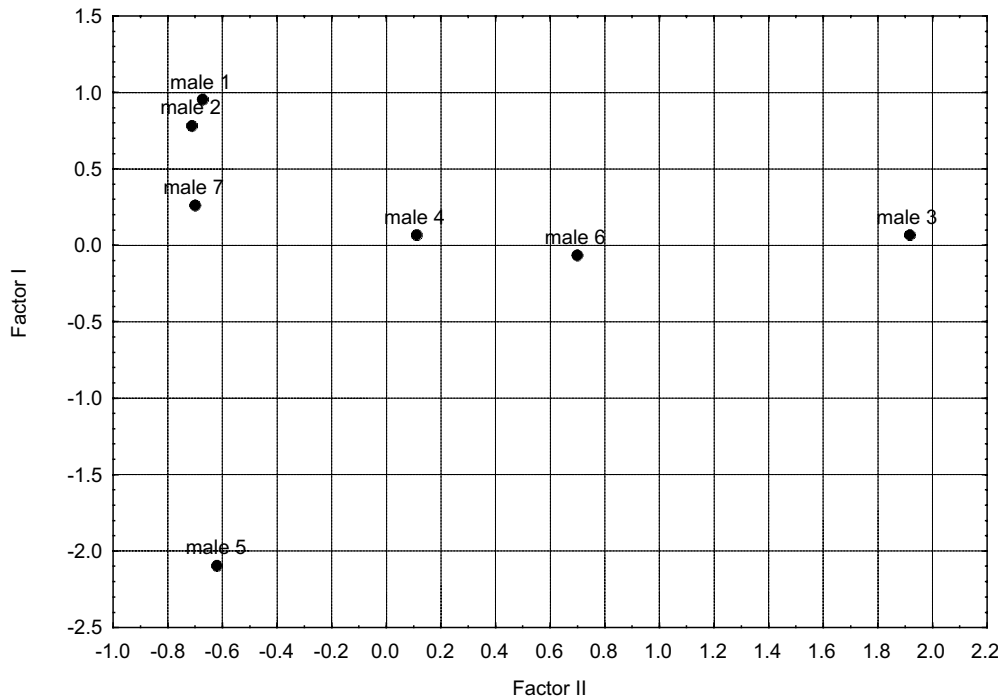


Fig. 2. — Separation of the seven *Acanthocercus a. atricollis* males, using the factor scores from the first two principal components.

more, males with larger home ranges and therefore, potentially greater energy expenditure, were not in significantly poorer condition.

We observed only a few male-male contests, possibly because male spacing patterns had already been established and because male density was relatively low. However, males maintained exclusive areas with only minor overlap among three males (Fig. 1), strongly supporting previous anecdotal reports of territoriality (BRANCH 1998).

Prey abundance did not increase significantly with home range size. Male home range size may be affected more by the number of females that they enclose than on any difference in the availability of ecological resources such as food (MARTINS 1983). A relatively small area contained eight females and was overlapped by three males, which also overlapped each other (Fig. 1). Because larger home ranges had neither more resources nor more females, male-female spatial patterns suggest an interaction with food availability (EMLEN & ORING 1977, SMITH 1985).

Female spatial distribution

The PCA revealed a link between prey number, tree size, and female overlap onto male home ranges. In arboreal lizards, physical features of trees, particularly larger trees, may be important for foraging success and refuge from predators

(COOPER 1993). Prey number, rather than tree size, varied significantly between male home ranges and by occupying areas where food abundance is high, females may gain the necessary energy requirements for egg development and thus increase their fitness (SEARCY 1979, M'CLOSKEY et al. 1990). Furthermore, sites rich in prey could facilitate hatchling growth and provide food for lipid storage before inactivity periods (M'CLOSKEY et al. 1990). Food resources commonly influence female distribution in other animals. For example, food supplements in both blue tits (SVENSSON & NILSSON 1995) and dunnocks (DAVIES & LUNDBERG 1984) resulted in a shift of female home ranges into these areas. In species where females directly gain resources, such as food, many studies have suggested that female mate choice is based primarily on male territory quality rather than male quality (JONES 1981, ALATALO et al. 1986, HEWS 1990). Attributes of territory quality have been argued to be more assessable than male quality (SEARCY 1979) and females should therefore be more influenced by resources because of the direct affect they have on female fitness (HOWARD 1978, SEARCY 1979). A manipulative study in this system would help distinguish the relative roles of male quality and food resources.

Male quality and home range quality

Although there was no relationship between male quality and home range size, higher quality males did occupy areas with higher levels of prey abundance. Similarly, the multivariate analysis revealed that female overlap was also linked to prey number, tree size, and male quality. If female choice was based primarily on home range quality, one would expect strong selection on males to succeed in contest competition for the best home range (SEARCY 1979), resulting in larger males aggressively displacing smaller ones for the best area (JONES 1981). Male *A. a. atricollis* exhibit characteristics such as large head size, aggressiveness, and conspicuous colouration that may be advantageous in male contests. We have previously shown that large male head size is best explained by selection as a result of male contest competition (REANEY & WHITING 2002). Given that larger males were occupying areas of relatively high prey abundance, resource defence could have important implications for fitness. Female choice should therefore be influenced both by the quality of the male and the area he is defending (EMLEN & ORING 1977).

In summary, there is an interaction between food resources and male quality that determines female distribution in tree agamas. Because males are territorial (BRANCH 1998) and maintain largely exclusive areas, defence of key resources (trees and food) likely results in high spatial overlap with females. Whether it is male contest success and territory placement that determines male reproductive success, or female choice for male traits such as body condition or colour, remains to be determined. Because traits affecting competitive ability for territories can also be preferred by females, evaluating the relative contributions of male traits and territory quality to female choice and reproductive success is problematic (HEWS 1990, 1993) and will require experimental manipulation of resources.

ACKNOWLEDGEMENTS

Our thanks to Owen Sutton (manager, Mountain Sanctuary Park) for accommodation and excellent support during this study. We are grateful to David Kirchhoffer, Alex Davison,

Simon Lailvaux and Andrew Muller for assistance with marking and mapping trees and field work in general. We also thank Jacky Galpin, Sarah Kramer and Chris Chimimba for providing useful statistical advice. This study was funded by grants to M.J. Whiting from the University Research Committee (University of the Witwatersrand) and the National Research Foundation. Clearance for this study was granted by the University of the Witwatersrand Animal Ethics Committee (clearance certificate number: 2000-86-2a). Permission to conduct the field study was granted by the North-west Province Parks Board (permit number: 833/2000 NW).

REFERENCES

- ABELL A.J. 1997. Estimating paternity with spatial behaviour and DNA fingerprinting in the striped plateau lizard, *Sceloporus virgatus* (Phrynosomatidae). *Behavioral Ecology and Sociobiology* 41: 217-226.
- ABELL A.J. 1998. Male-female spacing patterns in the lizard, *Sceloporus virgatus*. *Amphibia-Reptilia* 20: 185-194.
- ALATALO R.V., LUNDBERG A. & GLYNN C. 1986. Female pied flycatchers choose territory quality and not male characteristics. *Nature* 323: 152-153.
- ANDERSSON M. 1994. Sexual selection. *Princeton: Princeton University Press*.
- ANDREWS R.M. 1985. Mate choice by females of the lizard, *Anolis carolinensis*. *Journal of Herpetology* 19: 284-289.
- BARASH D.P. 1989. Marmots: social behaviour and Ecology. *Stanford: Stanford University Press*.
- BART J. & EARNST S.L. 1999. Relative importance of male and territory quality in pairing success of male rock ptarmigan (*Lagopus mutus*). *Behavioral Ecology and Sociobiology* 45: 355-359.
- BRANCH B. 1998. Field guide to snakes and other reptiles of Southern Africa. *Cape Town: Struik Publishers*.
- COOPER W.E. JR 1993. Tree selection by the broad-headed skink, *Eumeces laticeps*: size, holes and cover. *Amphibia-Reptilia* 14: 285-294.
- COOPER W.E. JR & VITT L.J. 1994. Tree and substrate selection in the semi-arboreal scincid lizard *Eumeces laticeps*. *Herpetological Journal* 4: 20-23.
- CÔTÉ I.M. & HUNTE W. 1989. Male and female mate choice in redlip blenny: why bigger is better. *Animal Behaviour* 38: 78-88.
- DAVIES N.B. & LUNDBERG A. 1984. Food distribution and a variable mating system in the dunnock, *Prunella modularis*. *Journal of Animal Ecology* 53: 895-912.
- EMLEN S.T. & ORING L.W. 1977. Ecology, sexual selection and the evolution of mating systems. *Science* 197: 215-223.
- HEWS D.K. 1990. Examining hypotheses generated by field measures of sexual selection on male lizards, *Uta palmeri*. *Evolution* 44: 1956-1966.
- HEWS D.K. 1993. Food resources affect female distribution and male mating opportunities in the iguanian lizard *Uta palmeri*. *Animal Behaviour* 46: 276-291.
- HOWARD R.D. 1978. The evolution of mating strategies in bullfrogs, *Rana catesbeiana*. *Evolution* 32: 850-871.
- JONES G.P. 1981. Spawning-site choice by female *Pseudolabrus celidotus* (Pisces: Labridae) and its influence on the mating system. *Behavioral Ecology and Sociobiology* 8: 129-142.
- MADSEN T. & LOMAN J. 1987. On the role of colour display in the social and spatial organization of male rainbow lizards (*Agama agama*). *Amphibia-Reptilia* 8: 365-372.
- MARTINS E.P. 1983. Phylogenetic perspectives on the evolution of lizard territoriality, pp. 117-144. In: Vitt L.J. & Pianka E.R., Edits. *Lizard ecology. Historical and experimental perspectives*. *New Jersey: Princeton University Press*.
- M'CLOSKEY R.T., DESLIPPE R.J., SZPAK C.P. & BAIA K.A. 1990. Tree lizard distribution and mating system: the influence of habitat and food resources. *Canadian Journal of Zoology* 68: 2083-2089.

- OLSSON M. 1995. Territoriality in Lake Eyre Dragons *Ctenophorus maculosus*: are males 'superterritorial'? *Ethology* 101: 222-227.
- POOLE J. 1989. Mate guarding, reproductive success and female choice in African elephants. *Animal Behaviour* 37: 842-849.
- PRICE T. 1984. Sexual selection on body size, territory, and plumage variables in a population of Darwin's finches. *Evolution* 38: 327-241.
- REANEY L.T. & WHITING M.J. 2002. Life on a limb: ecology of the tree agama, *Acanthocercus atricollis atricollis*. *Journal of Zoology* 257: 439-448.
- REANEY L.T. & WHITING M.J. 2003. Picking a tree: habitat use by the tree agama (*Acanthocercus atricollis atricollis*) in South Africa. *African Zoology* (in press).
- RICHMOND J.Q. 1998. Backpacks for lizards: a model for attaching radio-transmitters. *Herpetological Review* 29: 220-221.
- ROITHMAIR M.E. 1994. Male territoriality and female mate selection in the dart-poison frog *Epipedobates trivittatus* (Dendrobatidae, Anura). *Copeia*: 107-115.
- ROSE B. 1982. Lizard home ranges: methodology and functions. *Journal of Herpetology* 16: 253-269.
- SCHOENER T.W. 1968. Sizes and feeding territories among birds. *Ecology* 49: 123-141.
- SEARCY W.A. 1979. Female choice of mate: a general model for birds and its application to red-winged blackbirds (*Agelaius phoeniceus*). *The American Naturalist* 114: 77-100.
- SIMON C.A. 1975. The influence of food abundance on territory size in the iguanid lizard *Sceloporus jarrovi*. *Ecology* 56: 993-998.
- SMITH D.C. 1985. Home range and territory in the striped plateau lizard (*Sceloporus virgatus*). *Animal Behaviour* 33: 417-427.
- STAMPS J.A. 1983. Sexual selection, sexual dimorphism, and territoriality, pp. 169-204. In: Huey R.B. et al., Edits. *Lizard ecology*. Cambridge: Harvard University Press.
- STATSOFT INC. 1999. Statistica for Windows, version 6. Tulsa, Oklahoma.
- SVENSSON E. & NILSSON J. 1995. Food supply, territory quality, and reproductive timing in the blue tit (*Parus caeruleus*). *Evolution* 76: 1804-1812.
- TRAVIS S.E. & SLOBODCHIKOFF C.N. 1993. Effects of food resource distribution on the social system of gunnison's prairie dogs. *Canadian Journal of Zoology* 71: 1186-1191.
- VITT L.J., ZANI P.A., CALDWELL J.P. & DURTSCHKE R.D. 1993. Ecology of the whiptail lizard *Cnemidophorus deppii* on a tropical beach. *Canadian Journal of Zoology* 71: 2391-2400.
- WARNER R.R. 1987. Female choice of sites versus mates in a coral reef fish, *Thalassoma bifasciatum*. *Animal Behaviour* 35: 1470-1478.
- WIKELSKI M., CARBONE C. & TRILLMICH F. 1996. Lekking in marine iguanas: female grouping and male reproductive strategies. *Animal Behaviour* 52: 581-596.

Errata-Corrige

Are female tree agamas (*Acanthocercus atricollis atricollis*) turned on by males or resources?

L.T. REANEY and M.J. WHITING

Ethology Ecology & Evolution 15: 19-30, 2003

First column of Table 1* on page 24 should be read as follows:

Table 1.

Measures of home range overlap in *Acanthocercus a. atricollis* for adult males with at least 17 sightings (n = 7) and females with at least 9 sightings (n = 18).

	Number overlapped mean \pm SE (n)	Percent overlap mean \pm SE (n)	Overlap pressure mean \pm SE (n)	Encroachment mean \pm SE (n)
♂ on ♀	1.37 \pm 0.11 (19)	0.64 \pm 0.12 (14)	1.03 \pm 0.20 (14)	0.05 \pm 0.01 (14)
♂ on ♂	0.57 \pm 0.30 (7)	0.37 \pm 0.18 (7)	0.37 \pm 0.18 (7)	0.26 \pm 0.14 (7)
♀ on ♂	3.14 \pm 0.80 (7)	0.17 \pm 0.06 (7)	0.19 \pm 0.07 (7)	0.60 \pm 0.12 (7)
♀ on ♀	0.45 \pm 0.15 (18)	0.05 \pm 0.03 (18)	0.05 \pm 0.03 (18)	0.05 \pm 0.02(18)

* In online version Table 1 is correct