Field experiments on intersexual differences in predation risk and escape behaviour in the lizard *Platysaurus broadleyi*

Martin J. Whiting

Communication and Behaviour Research Group, School of Animal, Plant and Environmental Sciences,
University of the Witwatersrand, Private Bag 3, Wits 2050, South Africa
e-mail: martin@gecko.biol.wits.ac.za

Early evolutionary biologists had difficulty explaining the mechanisms underlying the evolution of seemingly costly, extravagant traits in males (Darwin, 1871). Sexual selection is normally invoked to explain the fitness advantage conferred to males with conspicuous, sometimes gaudy traits (Darwin, 1871; Andersson, 1994). Extravagant traits in males serve as components of signalling systems (Whiting et al., in press), but they also may attract predators and result in males suffering higher predation rates than females (Gwynne and O'Neill, 1980; Howard, 1981; Ward, 1986). Behaviour also may account for higher predation on males than females (e.g., Pitelka, 1957; Thornhill, 1978).

The Augrabies flat lizard, *Platysaurus broadleyi* (formerly *P. capensis* (part); Branch and Whiting, 1997), is a small cordylid lizard restricted to the Northern Cape Province, South Africa. *Platysaurus broadleyi* exhibits marked sexual dichromatism. Females are a drab gray-brown whereas males have brightly coloured front legs (orange, yellow, or a mix), blue heads, a lateral orange stripe, and a brightly coloured venter and throat (see Branch and Whiting (1997) for a detailed description and colour photograph), but bright colours on the less visible areas of the body, suggesting that bright colouration may be constrained by natural selection. Instances of predation on *P. broadleyi* have been rarely observed. Rock kestrels (*Falco tinnunculus*) have been observed provisioning offspring in the nest with *P. broadleyi* and may be the most significant predator of this lizard (A.J. van Zyl, pers. comm.). Sand snakes (*Psammophis* spp.) have also been seen eating *P. broadleyi* (W.D. Haacke, pers. comm.). Potential predators include mongooses and arthropods such as spiders and centipedes that may feed on small juvenile lizards.

Predation consists of the following phases: detection, pursuit, subjugation and consumption (Schwarzkopf and Shine, 1992; Endler, 1986). Most studies have addressed either prey detection (e.g., Olsson, 1993) or escape from predation (pursuit phase) (e.g., Bulova, 1994; Cooper, 1997), but rarely both (but see Schwarzkopf and Shine, 1992). Also, measurements of laboratory performance variables may have little relevance to the wild when prey detection is more important in determining a predation outcome than escape tactics (Schwarzkopf and Shine, 1992). Field-based experiments examining prey detection and escape tactics should be a more effective means of determining the effects of bright male colouration on predation. If male *P. broadleyi* are more conspicuous to predators, they may compensate behaviourally. Therefore, I first examined whether males were more conspicuous than females using stationary models painted to resemble male and female lizards. Second, I tested for intersexual differences in escape tactics to test the hypothesis that males compensate for bright colouration behaviourally. Also, if bright colouration in males is a survival disadvantage, a sex ratio among adults departing from 1:1 in favour of females should be predicted, under the assumption of a 1:1 sex ratio at hatching.

Field work was conducted at Augrabies Falls National Park (28°35′S, 20°20′E) (hereafter Augrabies), Northern Cape Province, South Africa. The area is xeric, and is characterised by hot summers (max: 42.9 °C) and cold winters (min: −2.9 °C) (Branch and Whiting, 1997). The xeric effect is, however, ameliorated by the presence of the Orange River, in which large numbers of *P. broadleyi*'s primary prey, the black fly (*Simulium* spp.), breed. Briefly, lizards are restricted to the granite banks and cliffs along the Orange River, although some individuals occur on granite away from the river. This habitat is devoid of vegetation, except for the occasional Namaqua fig tree (*Ficus cordata*). To the human observer, lizards are therefore quite conspicuous. For detailed descriptions of the study area, see Branch and Whiting (1997), Whiting and Greeff (1997), and Greeff and Whiting (2000).

A dead lizard (snout-vent length = 81 mm) was used as a template for a mould from which 20 identical epoxy models were made. Models were painted to resemble living lizards using acrylic paint. Male models were good enough to solicit challenges from living males, and female models were approached by males and in a few instances courted. Models were placed in typical lizard habitat in the field, secured to a rock by putty, and tied to a fixed object using fishing line. A small piece of smooth gray putty was attached to each side of the neck and predatory attempts were scored from marks on the putty. Five, 5-day trials were conducted in separate locations to negate the effect of any single predator making repeated strikes. Because rock kestrels have large activity ranges, it is unclear if changing location effectively reduced repeated strikes by the same individual. Some kestrels were therefore probably exposed to the same models in different areas. The low overall incidence of bird 'attacks' suggests that this was not a problem (see Results). Because resident males will challenge and bite an intruder, I obtained bite imprints from several living males in order to exclude such bite marks from predation attempts. In instances where several marks existed, I scored them as a single predatory attempt.

I approached solitary lizards in exposed positions with an unobstructed view of my approach path. More than 20 preliminary trials were conducted to work out protocol and attain a consistent approach speed (also facilitated by timed approaches over a known distance). When lizards moved at least 20 cm, I dropped a marker and continued walking to the point from which they fled. After 5 s, if the lizard was still moving, I took that as its final position. I recorded the following variables (in cm): (1) approach distance; (2) flight distance; (3) single long or many short movements; (4) distance to nearest crevice from lizard's initial position; and (5) whether the lizard was concealed (rock crevice or behind boulder) or visible at the end of the trial. If a lizard disappeared before I could record its final destination, I did not record flight distance. No lizard was tested more than once.

During 1995-97, lizards from the same study population were individually marked and these data used to establish the sex ratio. In 1996, an independent measure of the sex ratio was obtained by walking a 20 m transect 11 times, on different days, and visually scoring all males and females within 5 m.

Prior to application of parametric statistics, normality was tested for using rankit plots and associated Wilk-Shapiro statistics; equality of variance was tested for using an F-test. In the case of heteroscedasticity, a t-test for unequal variance was computed (Analytical Software, 1996). All tests were two-tailed, except for the test for effects of bird predation ('beak marks') on male versus female lizard models where I predicted a priori that male models would contain more beak marks because of increased conspicuousness. I performed a power test on the predation model data using the software GPower (Erdfelder et al., 1996). A power test was calculated only for predation attempts by birds because other predatory marks (such as bite marks from nocturnal animals) may not be biologically significant. Because of the restriction of colour to less conspicuous areas of the body in males, I hypothesised that predation was having a significant effect. Using GPower, I therefore set effect size (w) at 'large' (0.5). For comparison, I performed a second power analysis using 'medium' effect ($w = 0.3$). These conventions follow Cohen (1988) and are now widely used in power analysis (Erdfelder et al., 1996). Means are reported $\pm 1\ s_{\bar{x}}$, alpha was set at 0.05.

A male model was lost in trials 4 and 5, possibly carried off by either predators, baboons (*Papio ursinus*) or tourists to the park; these were not scored as strikes. A minimum of 28 predatory attempts were recorded from putty marks. Number of predatory attempts on male ($n = 15$) and female ($n = 13$) models were not significantly different ($\chi^2_1 = 1.16$, $P > 0.5$; table 1). Seven male models showed bite marks from conspecifics, whereas no females had similar bite marks (not included in analysis). Three males and two females had mammalian teeth marks (table 1). It is unclear if these marks were made by potential (diurnal) predators or by nocturnal mammals that chewed the models. I therefore separately analysed beak marks from avian predators, which also failed to reveal sexual differences ($\chi^2_1 = 1.23$, $P > 0.25$; power $= 0.6693$ for $w = 0.5$; power $= 0.3014$ for $w = 0.3$).

Difference in approach distance between males and females was not significantly different ($t_{163} = -0.03$, $P = 0.97$; table 2). Male and female flight distance was not significantly different ($t_{101.4} = 0.93$, $P = 0.36$; table 2) and males and females showed

Table 1. Predatory attempts on models painted to resemble male and female *Platysaurus broadleyi*.

Trial	Male models	Female models	Type of mark
1	4	3	beak marks
2	4	3	beak marks
3	2	4	beak marks, one with claw marks as well
4	3	1	2 males with beak & claw marks; a male & female had mammalian bite marks
5	2	2	all 4 models had mammalian bite marks; 1 female model had a beak mark
Total	15	13	

Table 2. Descriptive statistics of escape behaviour in *Platysaurus broadleyi*. Means are reported $\pm s_{\bar{x}}$, ranges are in parentheses. All measurements are to the nearest cm.

	Approach distance	Flight distance	Crevice distance
Males	481 ± 30.7 (120-1400) ($n = 79$)	198 ± 17.8 (25-600) ($n = 62$)	151 ± 25.2 (5-500) ($n = 37$)
Females	482 ± 27.9 (110-1360) ($n = 86$)	179 ± 10.6 (30-440) ($n = 76$)	185 ± 24.4 (15-500) ($n = 40$)

Table 3. Sex ratio of *Platysaurus broadleyi* for a single population at Augrabies Falls National Park, during 1995-97. For the combined data, individuals caught in multiple years were counted once.

Year	Males	Females	Ratio	χ_1^2	P
1995	118	60	1.97	18.9	<0.0001
1996	159	154	1.03	0.08	>0.5
1997	91	92	0.99	0.005	>0.9
Combined	346	296	1.17	3.894	<0.05

no significant difference in their tendency to make long or short movements when initially fleeing (long: 15.4% males ($n = 10$), 7.6% females ($n = 6$); short: 84.6% males ($n = 55$), 92.4% females ($n = 73$)) ($\chi_1^2 = 2.22$, $P > 0.1$). Distance to crevice and approach distance was unrelated for both males ($r = 0.03$, $P = 0.87$, $n = 37$) and females ($r = 0.08$, $P = 0.62$, $n = 40$; table 2). Males and females were equally likely to either remain visible after approach, or seek cover (visible: 35.1% males ($n = 27$), 43.8% females ($n = 35$); concealed: 64.9% males ($n = 50$), 56.3% females ($n = 45$); $\chi_1^2 = 1.226$, $P > 0.1$). Males and females showed no significant difference in their choice of final destination when directly approached ($\chi_2^2 = 2.958$, $P > 0.1$).

Sex ratio for trapped individuals was significantly male biased for 1995, but not for 1996 or 1997 (table 3). Because of the heavy male bias in 1995, the overall sex ratio for the three years combined was significantly in favour of males. The independent transect produced a mean of 42.1 ± 2.2 (31-52) males and 47.9 ± 2.8 (33-63) females; which was not significantly different from 1 : 1 ($\chi_1^2 = 0.376$, $P > 0.1$).

The use of models was designed to test for differences in conspicuousness between males and females. This experiment was not designed to test for differences in predation rates, because a multitude of factors besides conspicuousness determine predation success (Schwarzkopf and Shine, 1992). Results of power tests suggest that the number of trials performed were insufficient to detect small, but significant differences in conspicuousness. Also, there was no evidence that males were behaviourally compensating for conspicuousness. Alternatively, a lack of difference in conspicuousness among male and female flat lizards could be real.

If the data from this study revealed a significant departure from a 50 : 50 sex ratio, the result would be open to interpretation. In 1995, the sex ratio was significantly male biased and no significant difference in sex ratio existed for 1996-97. Given the absence of a female sex ratio bias, there was no evidence for increased male conspicuousness due to bright colour.

Current predation pressure therefore, does not appear to affect male relative to female survival. The question of whether predation is a selective agent driving colour evolution in flat lizards therefore remains equivocal and will require innovative experiments and possibly a large-scale field study using more models over a greater area. However, the restriction of bright colours to the venter and flanks of male *P. broadleyi* suggests that predation played an historic role in the evolution of bright male colouration.

Acknowledgements. This work was financially supported by the NRF and the University of Stellenbosch (grants awarded to J.H. van Wyk), and the Transvaal Museum. Permission to conduct work at Augrabies was granted by the National Parks Board and Nico van der Walt. The staff at Augrabies are thanked for support provided during this study. I am grateful to Ira Greeff and Stephanie Ritter for the painstaking construction and painting of the model lizards, to Anthony van Zyl for useful information on rock kestrels at Augrabies, and Axel Buchner for expert assistance with power test calculations using G*Power. Bill Cooper, Jonathan Losos, Mats Olsson, Anthony van Zyl and two anonymous reviewers are thanked for helpful comments on earlier versions of this manuscript.

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Received: January 3, 2001. Accepted: July 30, 2001.