acta ethol (2003) 6:19–22
DOI 10.1007/s10211-003-0082-9

ORIGINAL ARTICLE

Monica N. Wymann · Martin J. Whiting

Male mate preference for large size overrides species recognition in allopatric flat lizards (*Platysaurus broadleyi*)

Received: 9 December 2002 / Revised: 5 May 2003 / Accepted: 1 August 2003 / Published online: 10 September 2003

Abstract Species recognition and mate preference both influence mate choice but can be in conflict with each other. In such cases the relative importance of the two functions depends on the costs of mating with heterospecifics and the frequency of such interactions. We tested whether male flat lizards (*Platysaurus broadleyi*) are able to discriminate between conspecific females and females of its allopatric sister species *P. capensis*. Given a simultaneous choice between equally sized females of both species, males courted conspecific females in 85% of trials. We then tested whether mate preference for large female body size can override species recognition. When offered a choice between a larger heterospecific female and a smaller conspecific, males showed no preference for conspecifics and courted larger heterospecific females in 58% of trials. Comparison of the two sets of trials showed a significant effect of female body size on male mate preference, supporting the hypothesis that mate quality can override species recognition.

Keywords Mate preference · Species recognition · Conflicting preference · Squamata · Cordylidae

Introduction

Species recognition and mate preference are both implied in the assessment of signals of potential mates and should be considered in the same framework (Ryan and Rand 1993). Species recognition avoids mating with heterospecifics, which may result in low to zero fitness due to genetic incompatibilities (but see Grant and Grant 1992; Arnold and Hodges 1995). Mate preference—the assessment of conspecific mate quality—promotes direct or indirect fitness (reviewed in Andersson 1994). Species recognition and mate preference can be in conflict (Ryan and Wagner 1987; Basolo 1990), which may arise when heterospecifics possess traits that exploit preexisting biases for novelties or supernormal stimuli, or that resemble high quality conspecifics (Ryan and Rand 1990; Ryan and Keddy-Hector 1992; Hankinson and Morris 2002). Heterospecific resemblance is likely to be most pronounced in recently diverged taxa, which use similar traits for mate recognition (Pfennig 1998). How such conflicts are resolved depends on the relative weighting of species recognition versus mate preference. This weighting relies on the cost-benefit ratio of mating with heterospecifics compared to conspecifics and the frequency ratio of interactions with heterospecifics compared to conspecifics (Reeve 1989; Pfennig 1998, 2000). When heterospecifics do not interact owing to allopatry, there is no possibility that signals used to assess mates will conflict with species recognition (Gerhardt 1994).

Platysaurus capensis and *P. broadleyi* are closely related allopatric species of cordylid lizard. They were formerly treated as a single species, but later separated into two species based on their allopatric distribution (100 km separation) and nonoverlap in morphological space, in addition to the presence of two autapomorphies (Branch and Whiting 1997). Recent molecular work has confirmed that the two taxa are sister species. The 3′ half of the ND4 gene and most of the flanking tRNA-HSL cluster were sequenced for the majority of *P. latysaurus* taxa and showed strong support for a *P. capensis-P. broadleyi* clade in which the two taxa are sister species. They showed a genetic divergence of 8.6–10.4% (Scott et al. 2003). Males and females are sexually dimorphic with females of both species appearing to be very similar to the human eye. However, males of the two species have distinct color patterns and therefore appear quite different

Communicated by K. Kotrschal

M. N. Wymann · M. J. Whiting (✉)
School of Animal, Plant and Environmental Sciences
,Communication & Behaviour Research Group,
University of the Witwatersrand,
Private Bag 3, Wits 2050, South Africa
e-mail: martin@gecko.biol.wits.ac.za
Tel.: +27-11-7176321
Fax: +27-11-4031429

Present address:
M. N. Wymann, Bachlettenstrasse 76, 4054 Basel, Switzerland

to the human eye (Branch and Whiting 1997). Both species are restricted to rocky outcrops in northern South Africa and Namibia, with the closest known populations of the two species being separated by 100 km (Branch and Whiting 1997). At Augrabies Falls National Park, male *P. broadleyi* establish territories at feeding sites to which females travel on a daily basis to feed. This results in large aggregations of lizards in which males encounter multiple females simultaneously (Whiting and Bateman 1999). Females move between male territories while feeding and so it may be adaptive for males to court females in proportion to their quality (Andersson 1994). *Platysaurus broadleyi* males evaluate females and strongly prefer large conspecific females to smaller ones (Whiting and Bateman 1999).

Because *P. capensis* and *P. broadleyi* are closely related species in which females appear to be extremely similar, we decided to test whether *P. broadleyi* are able to discriminate conspecific from heterospecific females using visual cues. On the basis that only one flat lizard species, *P. broadleyi*, occurs at our study site, we then tested the hypothesis that, in allopatry, males may weight mate preference over species recognition.

Methods

Fieldwork was conducted during November 2000 at Augrabies Falls National Park (hereafter Augrabies) (28°35′S, 20°20′E), Northern Cape Province, South Africa. We staged male mate preference trials in the field using male and female *P. broadleyi* from Augrabies and female *P. capensis* from Kamieskroon (30°09′S, 17°56′E), Namaqualand, South Africa. Twenty-seven female *P. broadleyi* were captured at least 500 m from test sites to prevent using females known to test-males. Females were housed for 1–4 days together in an aquarium supplied with water and food ad libitum, and released at the end of the study at their site of capture. Fifteen female *P. capensis* were from a captive population of flat lizards maintained at the University of the Witwatersrand, Johannesburg. They were originally collected during July–August 2000 at Kamieskroon. They were housed under identical conditions to the *P. broadleyi* females for the duration of the study. All females were weighed on an electronic scale to the nearest 0.01 mg and snout vent length (SVL) was measured to the nearest mm with a ruler. To ensure that only mature females were used, the minimum size for female subjects was 65 mm SVL (Van Wyk and Mouton 1996), with the largest females of both species measuring 78 mm SVL.

We conducted mate preference trials in the field by placing a test chamber containing a *P. capensis* and a *P. broadleyi* female within sight of a free-ranging male *P. broadleyi*. The test chamber was a plexiglas aquarium measuring 60×10×40 cm. Two plexiglas divisions divided the chamber into three equally sized compartments (following Whiting and Bateman 1999). Females were randomly allocated to the outer compartments. The middle compartment allowed clear separation of the females. The design allowed for minimal movement of females, which prevented them from moving about and we saw no evidence of any interaction between the two females or any reaction of females to approaching or courting males.

We conducted two sets of trials. In the first set, both females were of equal SVL and within 1 g in body weight. In the second set, *P. capensis* females were 5–6 mm longer than the *P. broadleyi* females. We used this size difference because Whiting and Bateman (1999) showed that male *P. broadleyi* could reliably distinguish between conspecific females that differed in SVL by 5 mm. A single test chamber was placed at sites of high lizard density where males were observed showing territorial and courtship behavior. Lizards at Augrabies are habituated to human observers due to frequent visitation of the park by tourists. They can be approached within 1–3 m before withdrawing to a crevice and reappear at their previous location within minutes after retreat of the human observer (personal observations). Lizard habituation allowed us to place the test chamber at the exact location where males had been observed and to withdraw about 10 m to observe the first interactions, which usually occurred within 5–10 min. We oriented the test chamber such that both females were equally visible to the test male. We recorded which female the male approached first and, if courtship occurred, which female he first courted. Courtship consists of a male lowering and raising his forebody while approaching and circling a female, and cannot be mistaken for any other behavior pattern. Each female was tested 1–2 times in trials with size-matched females and 1–3 times in trials with females of different sizes, but each female pair was used only once. To ensure that each male was tested only once, we performed tests each day at a different section along the Orange River and within each section we placed the test chamber at different localities. We conducted a total of 20 trials with size-matched females and 30 trials with females of different sizes.

We evaluated differences in preference within female size-matched trials and within trials with females of different sizes using binomial tests (two-tailed). For both sets of trials, we separately analyzed which female was approached first and which was courted first. Incidence of courtship was examined, not duration, because courtship was often terminated if a male contacted the plexiglas chamber. To control for type 1 errors due to multiple comparisons, we performed a sequential Bonferroni test (Rice 1989) for all four binomial tests. We also evaluated the influence of female body size on male mate preference by testing for significant differences between the two sets of trials using 2×2 chi-square tests.

Results

When females were size-matched, males first approached conspecific females in 16 trials whereas they first approached heterospecific females in 4 trials (Binomial test, P=0.005, Fig. 1) and courted the conspecific female first in 12 trials and the heterospecific female first in 2 trials (Binomial test, P=0.006, Fig. 2). Both P-values remained significant given our sequential Bonferroni procedure. When females were of different size, males preferred larger females but the relationship was not significant. They approached the conspecific female first in 13 trials and the heterospecific female first in 17 trials

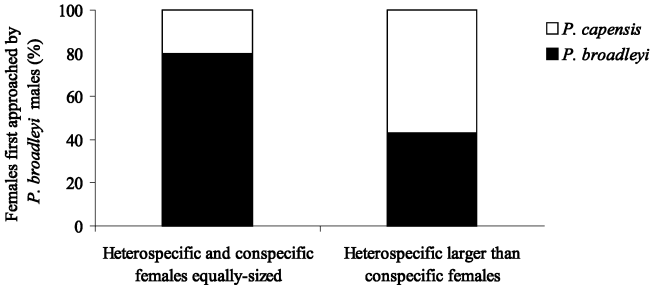

Fig. 1 Percentage of *Platysaurus capensis* to *P. broadleyi* females first approached by *P. broadleyi* males in trials with conspecific and heterospecific females of equal size (n=20) and in trials in which heterospecific females were larger than conspecific females (n=30)

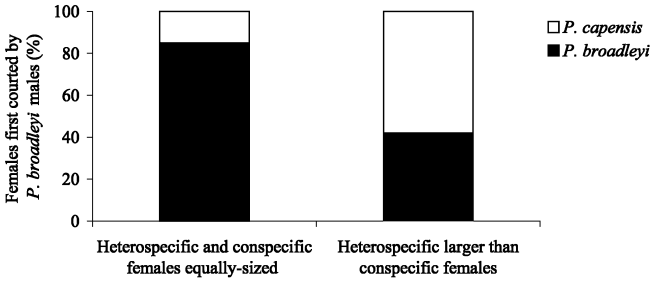

Fig. 2 Percentage of *Platysaurus capensis* to *P. broadleyi* females first courted by *P. broadleyi* males in trials with conspecific and heterospecific females of equal size (n=14) and in trials in which heterospecific females were larger than conspecific females (n=19)

(Binomial test, P=0.11, Fig. 1) and courted the conspecific female in 8 trials and the heterospecific female first in 11 trials (Binomial test, P=0.14, Fig. 2). Approaching males switched up to three times between females before initiating courtship with a single female. Comparing the two experiments, relative size of the heterospecific female had a significant effect on both frequency of approach (df=1, χ^2=6.49, P=0.01, Fig. 1) and courtship (df=1, χ^2=6.22, P=0.01, Fig. 2), both in favor of larger female body size.

Discussion

Platysaurus broadleyi males preferentially first approached and first courted conspecific females when given the choice between a conspecific and an equally sized heterospecific. This confirms the use of some species-specific visual cue used by males to discriminate between *P. capensis* and *P. broadleyi* females. However, male *P. broadleyi* also sometimes approached and courted heterospecific females first, implying that female *P. capensis* were still recognized as potential mates and that traits preferred by male *P. broadleyi* may overlap between females of the two species.

On the basis that male *P. broadleyi* preferred conspecific females when given the choice between a conspecific and a heterospecific of the same size and their preference for larger compared to smaller conspecific females (Whiting and Bateman 1999), we then tested whether assessment of cues was in favor of species recognition or mate quality assessment (body size). As hypothesized for an allopatric situation, our second experiment showed that preference for body size as a possible indicator for mate fecundity or longevity can override the preference for species-specific cues. Given the choice between a large heterospecific and a small conspecific female, the preference to first approach and court conspecific females was reduced. Furthermore, when the two experiments were evaluated together, the effect of body size was significant, in favor of large body size. A similar result was found in a study of pigmy swordtails (*Xiphophorus pygmaeus*) in which females showed a mate preference for large heterospecifics (*Xiphophorus cortezi*) over small conspecifics. They also exhibited a preference for barless versus barred males, but no preference when presented with both the species-specific and mate quality, cue (Hankison and Morris 2002).

But as in the swordtail study, our experimental design allowed only for visual cues and precluded chemical cues, and given that females remained motionless during the trials, any behavioral cues were likely negligible. Under natural conditions with males having access to all cues, this preference function may be altered, as is the case for swordtails, in which a preference for heterospecifics based on visual cues may be lost when chemical cues (Crapon de Caprona and Ryan 1990), or chemical and visual cues, are added (Hankison and Morris 2003).

By engaging in mate quality recognition, mates may increase their risk of misdirected matings and compromise species recognition. Likewise, by engaging in species recognition, any advantages from mate quality recognition may be confounded (Pfennig 1998). For example, to ensure conspecific matings, female spadefoot toads (*Scaphiopus multiplicata*) co-occurring with heterospecifics, trade-off the benefits of high-quality matings by reducing the preference for an extreme call character resembling that of heterospecific males (Pfennig 2000). Understanding conflicts of this nature and their interaction, particularly in fitness terms, could be a rewarding avenue of research.

Acknowledgements This study was supported by grants from the Josef and Olga Tomcsik-Foundation Basel, the Theodor Engelmann-Foundation Basel and the International Student Exchange Fund of the University of Basel to M.N.W. We are grateful to the National Parks Board and the staff at Augrabies Falls National Park, in particular Piet van Staden, for the permission to conduct this study in the Park and for logistical support. The University of the Witwatersrand Central Animal Services is acknowledged for husbandry and Anna Gsell and Manuel Rivera for field assistance. This study was approved by the Animal Ethics Screening Committee of the University of the Witwatersrand (clearance certificate number 2000 74 2a) and complied with current South African law.

References

Andersson MA (1994) Sexual selection. Princeton University Press, Princeton, N.J.

Arnold ML, Hodges SA (1995) Are natural hybrids fit or unfit relative to their parents? Trends Ecol Evol 10:67–71

Basolo AL (1990) Female preference predates the evolution of the sword in Swordtail Fish. Science 250:808–810

Branch WR, Whiting MJ (1997) A new *Platysaurus* (Squamata: Cordylidae) from the Northern Cape Province, South Africa. Afr J Herpetol 46:124–136

Crapon de Caprona MD, Ryan MJ (1990) Conspecific mate recognition in Swordtails, *Xiphophorus nigrensis* and *X. pygmaeus* (Poeciliidae): olfactory and visual cues. Anim Behav 39:290–296

Gerhardt HC (1994) Reproductive character displacement of female mate choice in the grey treefrog, *Hyla chrysoscelis*. Anim Behav 47:959–969

Grant PR, Grant BR (1992) Hybridization of bird species. Science 256:193–197

Hankison SJ, Morris MR (2002) Sexual selection and species recognition in the pygmy swordtail, *Xiphophorus pygmaeus*: conflicting preferences. Behav Ecol Sociobiol 51:140–145

Hankison SJ, Morris MR (2003) Avoiding a compromise between sexual selection and species recognition: female swordtail fish assess multiple species-specific cues. Behav Ecol 14:282–287

Pfennig KS (1998) The evolution of mate choice and the potential for conflict between species and mate-quality recognition. Proc R Soc Lond B 265:1743–1748

Pfennig KS (2000) Female spadefoot toads compromise on mate quality to ensure conspecific matings. Behav Ecol 11:220–227

Reeve HK (1989) The evolution of conspecific acceptance thresholds. Am Nat 133:407–435

Rice WR (1989) Analyzing tables of statistical tests. Evolution 43:223–225

Ryan MJ (1990) Sexual selection, sensory systems and sensory exploitation. Oxford Surv Evol Biol 7:157–195

Ryan MJ, Keddy-Hector A (1992) Directional patterns of female mate choice and the role of sensory biases. Am Nat 139:4–35

Ryan MJ, Rand AS (1993) Species recognition and sexual selection as a unitary problem in animal communication. Evolution 47:647–657

Ryan MJ, Wagner WE Jr (1987) Asymmetries in mating preferences between species: female swordtails prefer heterospecific males. Science 236:595–597

Scott IAW, Keogh JS, Whiting MJ (2003) Shifting sands and shifty lizards: molecular phylogeny and biogeography of African flat lizards (*Platysaurus*). Mol Phylogenet Evol (in press)

Van Wyk JH, Mouton FN (1996) The reproductive cycles of the oviparous lizards *Platysaurus capensis* and *P. minor*: evidence supporting a viviparity-oviparity reversal in the Cordylidae. Amphibia-Reptilia 17:115–129

Whiting MJ, Bateman PW (1999) Male preference for large females in the lizard *Platysaurus broadleyi*. J Herpetol 33:309–312