change by flexible-shelled eggs of painted turtles (*Chrysemys picta*). Physiol. Zool. 54:165–178.

RICKLEFS, R. E., AND J. BURGER. 1977. Composition of eggs of the diamond-back terrapin. Amer. Midl. Natur. 97:232–235.

TRIVERS, R. A. 1972. Parental investment and sexual selection. *In* B. G. Cambell (ed.), Sexual Selection and Descent of Man, pp. 136–179. Aldine, Chicago.

———. 1985. Social Evolution. Benjamin and Cummings Publishing Co., Menlo Park, California.

TROYER, K. 1983. Post-hatching yolk energy in a lizard: utilization pattern and interclutch variation. Oecologia (Berlin) 58:340–344.

WILHOFT, D. C. 1986. Eggs and hatchling components of the snapping turtle *Chelydra serpentina*. Comp. Biochem. Physiol. 84A:483–486.

WILLIAMS, G. C. 1966. Adaptation and Natural Selection. Princeton Univ. Press, Princeton, New Jersey.

YARON, Z. 1985. Reptilian placentation and gestation: structure, function, and endocrine control. *In* C. Gans and F. Billet (eds.), Biology of the Reptilia, Vol. 15, Development B, pp. 527–604. John Wiley and Sons, New York.

Accepted: 7 January 1999.

Journal of Herpetology, Vol. 33, No. 2, pp. 309–312, 1999
Copyright 1999 Society for the Study of Amphibians and Reptiles

Male Preference for Large Females in the Lizard *Platysaurus broadleyi*

MARTIN J. WHITING[1,2] AND PHILIP W. BATEMAN[3], [1]*Department of Zoology, University of the Witwatersrand, Johannesburg, Private Bag 3, Wits 2050, South Africa and* [2]*Department of Herpetology, Transvaal Museum, P. O. Box 413, Pretoria 0001, South Africa. E-mail: martin@gecko.biol.wits.ac.za* [3]*Department of Zoology and Entomology, University of Pretoria, Pretoria, Pretoria 0002, South Africa.*

Darwin (1859, 1871) noted that many sexual inequalities between males and females cannot be explained by natural selection alone. For example, in many species (particularly those lacking parental care) males mate with as many females as possible, whereas females may exert qualitative choices due to the greater energetic and survival costs of reproduction (Bateman, 1948; Trivers, 1972; Krebs and Davies, 1993). Conversely, where parental investment is greater in males, where sperm competition is high, or where female quality is variable, males may be more selective (Sargent et al., 1986; Schwagmeyer and Parker, 1990; Olsson, 1993). Mate choice is therefore often complex, and may be further confounded in territorial species in which male-male competition influences access to mates (Andersson, 1994).

Platysaurus broadleyi is a territorial cordylid lizard with a polygynous mating system (MJW, unpubl. data). Males are therefore expected to mate with as many females as possible, while females are expected to be discriminating. However, given a simultaneous choice between two females of variable quality, it may be adaptive for a male to choose the higher quality female.

Fecundity is an important aspect of female quality that may be evaluated by males (Trivers, 1972). Clutch size in *P. broadleyi* is fixed at two (van Wyk and Mouton, 1996). However, egg size can reasonably be expected to positively correlate with maternal body size, as has been reported for many lizard species with fixed clutch size (e.g., Andrews and Rand, 1974; Vitt, 1986; Doughty, 1997). This in turn may give larger offspring a competitive advantage (Lack, 1954; but see Sinervo et al., 1992). Based on this assumption, we tested the hypothesis that given a choice, males choose larger females.

Platysaurus broadleyi (formerly *Platysaurus capensis* [part]; Branch and Whiting, 1997) is endemic to the Gordonia-Kenhardt districts of the Northern Cape Province, South Africa. Adult snout-vent length (SVL) ranges from 64–84 mm, and males are larger than females (Branch and Whiting, 1997). We conducted field work during September (the height of the breeding season [MJW, unpubl. data]) 1996, at Augrabies Falls National Park (hereafter Augrabies) (28°35′S, 20°20′E), Northern Cape Province, South Africa. Details of the study area are given in Branch and Whiting (1997) and Whiting and Greeff (1997).

Females were collected ca. 700–1200 m from the males, reducing the likelihood of prior contact (*P. broadleyi* have small home ranges, the longest axis is generally <300 m; MJW, unpubl. data). We conducted staged trials in the field by placing a test chamber containing a large and small female within sight of a free-ranging male. The test chamber was a glass aquarium measuring 30 × 10 × 50 cm. Two glass divisions were inserted to create three equally sized chambers. Females differing by at least 5 mm SVL were randomly allocated to the outer chambers. (The middle chamber permitted a clear separation of females and therefore allowed the observer to accurately score choice.) Five mm was arbitrarily selected as a minimum SVL at which females were readily distinguished on the basis of size. After placing the females in a position easily visible to the male, the observer withdrew to a location (ca. 10 m from chamber) that would not distract the male, and remained still. We scored which female the male courted first. Courtship consists of a male raising and lowering his fore-body as he approaches or circles a female, and can not be mistaken for any other behavior. No female combination was used more than once, and no female was used in more than two trials (Table 1); a total of 17 trials were conducted. During trials, females generally remained stationary and did not respond to the male's presence. Males were tested once only.

Data are reported as mean ±1 SE. Differences in body size (SVL, mass) were evaluated using Mann-Whitney tests (one-tailed) while differences in choice were evaluated using a binomial test (one-tailed). Differences were considered significant at alpha = 0.05.

The 14 large females had a mean SVL of 74.86 ± 0.53 (72–78 mm) and a mean mass of 8.69 ± 0.43 (7.2–10.6 g; N = 8); the 10 small females had a mean SVL

[1] Address for correspondence.

TABLE 1. Mate choice trials for large versus small females. Snout-vent lengths (mm) are given in parentheses, following individual identity numbers. Two females (indicated by asterisk) were approached first, but not courted.

Large female #	Small female #	Female body length ratio	Outcome
26 (77)	23 (65)	0.84	large
27 (73)	23 (65)	0.89	large
33 (78)	30 (73)	0.94	large
20 (78)	30 (73)	0.94	large
20 (78)	41 (73)	0.94	small
25 (75)	9 (68)	0.91	small
22 (75)	9 (68)	0.91	large
5 (73)	32 (68)	0.93	large*
42 (73)	16 (68)	0.93	large
11 (73)	16 (68)	0.93	large
38 (74)	15 (69)	0.93	large
34 (75)	15 (69)	0.92	small
31 (77)	8 (71)	0.92	large
31 (77)	18 (70)	0.91	large
3 (72)	33 (67)	0.93	large
11 (73)	33 (67)	0.92	large*
34 (75)	18 (70)	0.93	large

of 69.2 ± 0.81 (65–73) and a mean mass of 7.07 ± 0.47 (4.8–8.6; N = 7, three females were not weighed); these differences were significant (SVL: Z = 3.72, P = 0.0001; mass: Z = 2.03, P = 0.02).

In two trials, the male approached the larger of the two females, but did not court her (Table 1). Overall, males approached the larger female first significantly more often than the smaller (P = 0.0064, N = 14 larger [82%], N = 3 smaller). Males courted the larger female first significantly more often than the smaller (P = 0.018; N = 12 larger, N = 3 smaller) (Table 1), and tended to ignore the second female, although the trials were not of sufficient duration to properly examine this. Of the 10 trials, nine males courted only one female (nine large, one small; P = 0.011), while the larger female was approached but not courted in the remaining trial.

A number of hypotheses have been posited for the evolution and mechanisms of mate choice in animals (Kirkpatrick and Ryan, 1991; Andersson, 1994; Eberhard 1996; Ryan, 1997). Much of this debate has centered on female choice as an outcome of sexual selection. Conversely, male mate choice has received little attention, particularly for the Squamata (Olsson, 1993). Currently, male mate choice has been examined experimentally for one lizard (*Lacerta agilis*; which is nonterritorial and mate guards), in which males preferred large females (Olsson, 1993), and a snake, *Thamnophis sirtalis parietalis* (Aleksiuk and Gregory, 1974). Inferential evidence for male mate preference for large females exists for another mate guarding lizard, *Eumeces laticeps*. In *E. laticeps*, clutch size is positively correlated with female SVL, and males mate-guard larger females resulting in positive size-assortative mating (Cooper and Vitt, 1997). Two studies (Fitzgerald, 1982; Rostker, 1983) have also provided evidence for a male preference for large females. Rostker (1983) showed that large male *Crotaphytus collaris* tended to consort with large females, while Fitzgerald (1982) found that males in several species of *Sceloporus* chose larger females in simultaneous two-choice trials in the lab.

Male *P. broadleyi* showed a strong preference for larger females. In the two instances where males did not court either female, they still approached the larger female. Traditionally, it has been assumed that males that only have genes to contribute will show little discrimination among females and conform to a "hit-and-run" strategy (Dewsbury, 1982). This appears true for many polygynous species including *P. broadleyi*, in which males court multiple females in a short space of time, including juveniles that are female-like (MJW, unpubl. data). Given a simultaneous choice of two or more females, it may be adaptive to court the larger female, particularly if the other females move away in the interim.

It may be argued that female interactions could influence male mate choice. However, females in the chambers did not appear to notice each other, often faced opposite directions, and were sufficiently separated to prevent interaction.

Extreme size (and therefore energetic) differences between sperm and eggs have been regarded as fundamental to the evolution of anisogamy (Parker et al., 1972; Birkhead and Parker, 1997). Costs of egg production have traditionally been compared to the costs of individual sperm production, leading to the misconception that sperm production is cheap and unlimited (Dewsbury, 1982; Nakatsuru and Kramer, 1982). A more appropriate unit of comparison is the ejaculate, which may contain millions of gametes (Dewsbury, 1982). In this context, males may be more selective if (1) ejaculate production is limited (Nakatsuru and Kramer, 1982), (2) fertilization success is lowered because the female recently mated with another male (sperm competition) (Erickson and Zenone, 1976; Schwagmeyer and Parker, 1990; Birkhead and Parker, 1997), or (3) female quality (e.g., fecundity or parental care) is variable, and/or if males can mate with only a limited number of females (Verrell, 1986; Olsson, 1993; Ryan, 1997). To our knowledge, ejaculate production has not been reported as costly for any lizard (but see Olsson et al., 1997). The sperm competition model is not supported because males were exposed to novel females and excluded from chemical contact, precluding information on the female's mating history. During courtship, males frequently nudge the female's cloacal opening (pers. obs.), although assessment of female mating history by this means remains to be demonstrated. The sperm competition model is possible if males mate as frequently as possible without assessing female mating history. Egg size has been demonstrated to be heritable and responsive to natural selection for at least one lizard (*Uta stansburiana*) (Sinervo and Doughty, 1996). Last, if larger offspring have a survival advantage, it would be adaptive for males to choose larger females. Male *P. broadleyi* did show a preference for larger females and this therefore best suits the fecundity model.

Alternatively, large female body size could correlate with some other maternal trait related to offspring growth and survival, regardless of egg size. A number of factors (both genetic and environmental) affect offspring quality and hence, survival (Sinervo et al., 1992;

Olsson et al., 1996; Sinervo and Doughty, 1996). For example, individuals with genes that code for slightly longer gestation periods have larger offspring that grow faster (Olsson et al., 1996). Phenotypic factors such as maternal nutritional condition and allocation to developing embryos may also influence offspring survival (Olsson et al., 1996). Therefore, evolution of a male preference for large female size may have been driven by better offspring survival due to egg size, either through environmental or genetic sources of variation.

In general, male assessment of females entails visual or chemical cues. Verrell (1985, 1986) demonstrated that male newts of both *Notopthalmus viridescens* and *Triturus vulgaris* prefer large fecund females, and assess size using visual and/or chemical cues. Male *P. broadleyi* frequently tongue-flick females during courtship. Because vomerolfaction in squamates is mediated through tongue-flicking and chemical transfer to the vomeronasal system (Halpern, 1992; Cooper, 1994), males may gain information on reproductive condition by tongue flicking. However, in our experiment, males were effectively prevented from doing so by the experimental chamber. Also, male *P. broadleyi* began courtship during approach when only visual contact was possible. This does not preclude the use of olfactory cues in nature, but does confirm the use of visual cues for size assessment.

Acknowledgments.—For financial support M. J. W. thanks the FRD (grant awarded to J. H. van Wyk), the University of Stellenbosch (grant awarded to J. H. van Wyk), and the Transvaal Museum. P. W. B. was supported by a Datalake post-doctoral grant and the Transvaal Museum. We are grateful to the National Parks Board, Nico van der Walt, and the staff at Augrabies Falls National Park for permission to conduct this study and for various logistical support and encouragement. For constructive comments on early drafts, we thank Bill Cooper and Jaco Greeff.

Literature Cited

ALEKSIUK, M., AND P. T. GREGORY. 1974. Regulation of seasonal mating behaviour in *Thamnophis sirtalis parietalis*. Copeia 1974:681–689.

ANDERSSON, M. 1994. Sexual Selection. Princeton Univ. Press, Princeton, New Jersey.

ANDREWS, R. M., AND A. S. RAND. 1974. Reproductive effort in anoline lizards. Ecology 55:1317–1327.

BATEMAN, A. J. 1948. Intra-sexual selection in *Drosophila*. Heredity 2:349–368.

BIRKHEAD, T. R., AND G. A. PARKER. 1997. Sperm competition and mating systems. *In* J. R. Krebs and N. B. Davies (eds.), Behavioral Ecology: an Evolutionary Approach, 4th ed., pp. 121–145. Blackwell Scientific Publ., Oxford.

BRANCH, W. R., AND M. J. WHITING. 1997. A new *Platysaurus* (Squamata: Cordylidae) from the Northern Cape Province, South Africa. African J. Herpetol. 46:124–136.

COOPER, W. E., JR. 1994. Chemical discrimination by tongue flicking in lizards: a review with hypotheses on its origin and its ecological and phylogenetic relationships. J. Chem. Ecol. 20:439–487.

———, AND L. J. VITT. 1997. Maximizing male reproductive success in the broad-headed skink (*Eumeces laticeps*): preliminary evidence for mate guarding, size assortative pairing, and opportunistic extra-pair mating. Amphibia-Reptilia 18:59–73.

DARWIN, C. 1859. On the Origin of Species by Means of Natural Selection. The Modern Library, New York.

———. 1871. The Descent of Man, and Selection in Relation to Sex. The Modern Library, New York.

DEWSBURY, D. A. 1982. Ejaculate cost and male choice. Amer. Natur. 119:601–610.

DOUGHTY, P. 1997. The effects of "fixed" clutch sizes on lizard life-histories: reproduction in the Australian velvet gecko, *Oedura lesuerrii*. J. Herpetol. 31: 266–272.

EBERHARD, W. G. 1996. Female Control: Sexual Selection by Cryptic Female Choice. Princeton Univ. Press, Princeton, New Jersey.

ERICKSON, C. J., AND P. G. ZENONE. 1976. Courtship differences in male ring doves: avoidance of cuckoldry? Science 192:1353–1354.

FITZGERALD, K. T. 1982. Mate selection as a function of female body size and male choice in several lizard species. Unpubl. Ph.D. Diss., Univ. Colorado, Boulder.

HALPERN, M. 1992. Nasal chemical senses in reptiles: structure and function. *In* C. Gans and D. Crews (eds.), Biology of the Reptilia, Vol. 18, pp. 423–523. Univ. Chicago Press, Chicago, Illinois.

KIRKPATRICK, M., AND M. J. RYAN. 1991. The evolution of mating preferences and the paradox of the lek. Nature 350:33–38.

KREBS, J. R., AND N. B. DAVIES. 1993. An Introduction to Behavioural Ecology, 3rd Ed. Blackwell Scientific Publications, Oxford.

LACK, D. 1954. The Natural Regulation of Animal Numbers. Clarendon Press, Oxford.

NAKATSURU, K., AND D. L. KRAMER. 1982. Is sperm cheap? Limited male fertility and female choice in the lemon tetra (Pisces: Characidae). Science 216: 753–755.

OLSSON, M. 1993. Male preference for large females and assortative mating for body size in the sand lizard (*Lacerta agilis*). Behav. Ecol. Sociobiol. 32:337–341.

———, A. GULLBERG, R. SHINE, T. MADSEN, AND H. TEGELSTRÖM. 1996. Paternal genotype influences incubation period, offspring size, and offspring shape in an oviparous reptile. Evolution 50:1328–1333.

———, T. MADSEN, AND R. SHINE. 1997. Is sperm really so cheap? Costs of reproduction in male adders, *Vipera berus*. Proc. R. Soc. London B 264:455–459.

PARKER, G. A., R. R. BAKER, AND V. G. F. SMITH. 1972. The origin and evolution of gamete dimorphism and the male-female phenomenon. J. Theor. Biol. 36:529–553.

ROSTKER, M. A. 1983. An experimental study of collared lizards: effects of habitat and male quality on fitness. Unpubl. Ph.D. Diss., Oklahoma State Univ., Stillwater.

RYAN, M. J. 1997. Sexual selection and mate choice. *In* J. R. Krebs and N. B. Davies (eds.), Behavioral Ecology: an Evolutionary Approach, 4th Ed., pp. 179–202. Blackwell Scientific Publications, Oxford.

SARGENT, R. C., M. R. GROSS, AND E. P. VAN DEN BER-

GHE. 1986. Male mate choice in fishes. Anim. Behav. 34:545–550.

SCHWAGMEYER, P. L., AND G. A. PARKER. 1990. Male mate choice as predicted by sperm competition in thirteen-lined ground squirrels. Nature 348:62–64.

SINERVO, B., P. DOUGHTY, R. B. HUEY, AND K. ZAMUDIO. 1992. Allometric engineering: a causal analysis of natural selection on offspring size. Science 258:1927–1930.

———, AND P. DOUGHTY. 1996. Interactive effects of offspring size and timing of reproduction on offspring reproduction: experimental, maternal, and quantitative genetic aspects. Evolution 50:1314–1327.

TRIVERS, R. L. 1972. Parental investment and sexual selection. *In* B. Campbell (ed.), Sexual Selection and the Descent of Man 1871–1971, pp. 136–179. Aldine, Chicago.

VAN WYK, J. H., AND P. LE F. N. MOUTON. 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.

VERRELL, P. A. 1985. Male mate choice for large, fecund females in the red-spotted newt, *Notopthalmus viridescens*: How is size assessed? Herpetologica 41:382–386.

———. 1986. Male discrimination of larger, more fecund females in the smooth newt, *Triturus vulgaris*. J. Herpetol. 20:416–422.

VITT, L. J. 1986. Reproductive tactics of sympatric gekkonid lizards with a comment on the evolutionary and ecological consequences of invariant clutch size. Copeia 1986:773–786.

WHITING, M. J., AND J. M. GREEFF. 1997. Facultative frugivory in the Cape flat lizard, *Platysaurus capensis* (Sauria: Cordylidae). Copeia 1997:811–818.

Accepted: 7 January 1999.

Journal of Herpetology, Vol. 33, No. 2, pp. 312–315, 1999
Copyright 1999 Society for the Study of Amphibians and Reptiles

The Tadpole of *Physalaemus santafecinus*, with Comments on Buccopharyngeal Morphology

MARÍA G. PEROTTI[1,3] AND JORGE A. CÉSPEDEZ[2] [1], *CONICET—Instituto de Herpetología, Fundación Miguel Lillo, Miguel Lillo 251, (4000) Tucumán, ARGENTINA. E-mail: gperotti@crilar.com.ar,* [2]*Facultad de Ciencias Exactas y Naturales y Agrimensura de la Universidad Nacional del NordEste, 9 de Julio 1449, (3400) Corrientes, ARGENTINA. E-mail: cespedez@unefcen.edu.ar*

Of the 38 species in the genus *Physalaemus* (Duellman, 1993; Lobo, 1993), the tadpoles of 13 have been described. Argentine species in the *Physalaemus biligonigerus* group include *P. biligonigerus*, *P. nattereri*, and *P. santafecinus*. Larvae of the first two species have been described by Vizzotto (1967) and Fernandez and Fernandez (1921) respectively. We present data on the external morphology and buccopharyngeal features of the tadpole of *Physalaemus santafecinus* and provide comparisons with the larvae of the other species of the *P. biligonigerus* group.

Ten tadpoles in Stages 35–40 (Gosner, 1960) were collected in humid shrub forest of the chacoan region near Corrientes, Argentina (October, 1995; Universidad Nacional del NordEste, Corrientes CHC-UNNE 02242). Terminology of the description follows Johnston and Altig (1986) and Lavilla (1988), and measurements (ocular grip and caliper, 0.01 mm; Table 1) follow Lavilla and Scrocchi (1986). Some tadpoles were reared through metamorphosis to confirm their identity. The description and illustration of the external morphology were based on larvae in Stage 38, and we examined the buccopharyngeal morphology of two larvae of *Physalaemus biligonigerus* in Stage 38 for comparisons. Buccopharyngeal structures stained with methylene blue were observed with a dissecting microscope and described using the terminology of Wassersug (1976, 1980).

The body of the tadpole of *Physalaemus santafecinus* is ovoid, slightly depressed, SVL = 24.04 mm (SD = 1.70, N = 4) at Stage 38. Maximum width of body is greater than width at eye level; eyes dorsolateral; snout rounded in dorsal and lateral views (Fig. 1A, B); oral disc subterminal, with marginal papillae in single row and wide rostral gap; row of intramarginal papillae in infraangular area (Fig. 1D); labial teeth strongly keratinized and pigmented with serrated free margins; upper beak wider than high and curved; lower beak V-shaped; tooth row formula 1, 1-1/1-1, 1; nostrils dorsal, oval, and separated by a distance of 0.66 times interocular distance; spiracle sinistral with opening directed dorsally; diameter of opening is less than tube diameter; venter transparent (Fig. 1C).

Tail length 66% of total length. Dorsal fin originates at tail-body junction; ventral fin originates on abdominal region; dorsal fin higher than ventral fin; tip of tail slightly curved; anal tube dextral, opening in line with ventral fin.

In preserved specimens, dorsum lightly pigmented brown with major concentration of pigments in interocular zone, near nostrils, and covering epaxial musculature up to origin of dorsal fin; fins and remainder of tail lightly pigmented; limbs pigmented dorsally.

Buccopharyngeal surface features in *Physalaemus santafecinus* are: buccal roof rectangular, slightly longer than wide (Fig. 2A); two pairs of infrarrostral pustulations forming a semicircular arch with median notch in the prenarial arena; choanae positioned at about 25% of the distance from oral disc to esophagus; internarial distance less than 50% of long axis of choana; nares obliquely oriented; anterior narial wall pustulate; posterior narial wall flap-like and twice as wide as high; postnarial arena narrow and triangular with four papillae; center pair of papillae anterior, large, wide, and each with pustulate anterior margin; lateral pair of papillae posterior, and situated beneath the lateral-ridge papillae, short, thick, and with pustulate anterior margin; both pair of papillae obliquely oriented from lateral-ridge papillae; median ridge

[3] Present Address: CRILAR (CONICET-UNLaR), Mendoza y Entre Ríos, (5301) Anillaco, La Rioja, ARGENTINA.