

Large male crests, an honest indicator of condition, are preferred by female smooth newts, *Triturus vulgaris* (Salamandridae) at the spermatophore transfer stage

ANDY J. GREEN

Wildfowl and Wetlands Trust, Slimbridge, Gloucester GL2 7BT, U.K.

(Received 12 October 1989; initial acceptance 28 November 1989;
final acceptance 25 August 1990; MS. number: SC-583)

Aquatic smooth newts are sexually dimorphic. Only the male has a dorsal crest, which begins behind the head and extends backwards as a vertical tail extension. Darwin (1871) proposed that the crest functions to attract females, but this has never been demonstrated. Malacarne & Cortassa (1983) and Hedlund (1990) found correlations between crest height of *Triturus cristatus* and the number of spermatophores picked up by females, but this may have been caused by high-crested males producing more spermatophores. My aim in this study was to investigate the role of the smooth newt's crest in various female choice decisions.

From March to June 1987, newts were collected from seven Oxfordshire ponds, and the sexes kept separately in tanks of 62 × 31 × 38 cm deep at 13–14°C. They were kept on a natural light schedule and fed with *Tubifex* and chopped earthworms. Daily, 18 h before observations, I placed six males in pairs in separate observation tanks. From 1700 to 2000 hours, I observed courtship in each tank in turn for 30 min. A female was introduced and a commentary of all behaviour recorded onto VHS tape, with a visual stopwatch. The behaviour patterns were later transcribed to the nearest 0.1 s. I removed the newts and measured their snout–vent length, tail length and maximum tail height (most practical measure of the crest). I observed 61 triads of two males and one female, using each individual once. I divided encounters into 'sessions' of courtship, separated by inactivity. Sessions begin with the first male Static Display act (Whip, Wave or Fan; Halliday 1974, 1975) and end when the pair separate, usually by a female withdrawal. I used GLIM and Statview statistical packages.

There is no aggression between males, although sexual interference occurs by males mimicking females (Verrell 1984). In 53 triads with males from the same population, neither tail height nor snout–

vent length had significant effects on competition for courtship access to the female (measuring the number of sessions initiated, matched-paired *t*-tests, NS). Hence the crest has no role in competition between males. When courtship begins with Static Display, the female's first major decision is whether or not to enter Retreat Display by consistently approaching the male. Females do this only when willing to attempt spermatophore transfer (Teyssedre & Halliday 1986). To analyse the effects of male traits, I excluded encounters in which both males did more than two display acts, since the female's decision to enter Retreat Display may have been influenced by both males. Of 49 triads, 25 had Retreat Display. Whether Retreat Display occurred or not was made the dependent variable in a logistic regression, with binomial error. Tail height, snout–vent length and tail length of the male were predictors. Because the three measurements are highly correlated, their partial effects and combined effect were considered. Other predictors were the populations from which the female and male were drawn, the date and the number of days the female spent in a stock tank. Tail height and other male traits had no effects (Table I).

A second major female decision is the duration of Static Display before she enters Retreat Display. A male who persuades females to enter Retreat Display rapidly will have a higher mating success, because separations in between Static Display sessions are likely to become permanent in the field, and longer sessions are more likely to attract rival males that interfere with courtship. Total Static Display duration(s) before Retreat Display was entered was made the dependent variable in a multiple linear regression with the same predictors as above. No male traits had an effect (Table I).

Retreat Display is followed by Spermatophore Transfer. The male enters a Creep, then stops to

Table I. Multiple regressions of three female choice parameters in *Triturus vulgaris*

Dependent variables†	Predictor variables‡				N§
	Tail height	Snout-vent length	Tail length	Snout-vent length + tail height + length	
Retreat Display or not	-0.93	+0.17	-0.22	(-)1.86	49
Static Display time	+0.55	-1.44	+2.12	(+)1.99	25
Spermatophore pick-up	+11.46**	+1.67	-1.84	(+)14.05*	26

†Whether or not the female enters Retreat Display; duration of Static Display before Retreat Display is entered; proportion of deposited spermatophores that females pick up.

‡For details of other predictors, see text. χ^2 values are given for logistic regressions (Retreat Display and Spermatophore pick-up); t values are given for the linear regression (Static Display). The partial effects of each variable are shown, with + and - denoting the sign of the regression slope. The combined effect of snout-vent length and tail height and length is also given, with (+) and (-) denoting its direction.

* $P < 0.01$; ** $P < 0.001$.

§Sample size for the regression.

Quiver his tail. The female approaches and gives a Tail-touch, eliciting spermatophore deposition. The male advances and stops in Brake, then the female follows and gives another Tail-touch. She may now pick up the spermatophore in her cloaca. Whether to pick up a male's sperm is a third female decision. Only 51% of spermatophores were picked up, the others adhering to the female's body or the substrate. From Brake, courtship continues with another sequence of Retreat Display and Spermatophore Transfer. One to four sequences are conducted. Halliday (1974) found that females are more likely to pick up later spermatophores, but I did not. The number of spermatophores each male had picked up was made the dependent variable in a logistic regression, with total spermatophores deposited as binomial denominator (i.e. a male who deposits four spermatophores and has two picked up registers as two out of four). Predictors were the date, the number of days the female spent in a stock tank, female snout-vent length, and male tail height, snout-vent length and tail length. There were highly significant partial effects of the time the females spent in stock tanks ($\chi^2 = 12.55$, $P < 0.004$), female snout-vent length ($\chi^2 = 16.14$, $P < 0.0001$) and male tail height (Table I). A higher proportion of spermatophores were picked up when males had higher tails. When tail height was added without controlling for snout-vent length or tail length, the effect was even more significant ($\chi^2 = 12.18$, $P < 0.0005$). Adding the population from which the female or male was drawn had no influence on the

effects of these variables. Females with long bodies were less likely to pick up spermatophores because males move one snout-vent length after depositing, when they Brake. When the female approaches, if her body is longer than his, her cloaca will not reach the spermatophore. Females are less likely to pick up spermatophores when they have been kept in isolation from males for longer. This is surprising, since it means that females who have had more time to run out of sperm are less likely to pick up.

This clear evidence of a female preference for a high crest at spermatophore pick-up is the first demonstration of female choice for exaggerated morphological traits in the Amphibia. The mechanism for this effect is unknown. Tail height is not correlated with duration or the number and rate of tail displays in Retreat Display. It is correlated with the time taken for the female to follow the male and give a Tail-touch when he begins to Quiver after the first Retreat Display ($\bar{X} \pm SD = 3.34 \pm 2.31$ s, $r = -0.43$, $P < 0.04$). This correlation is not the result of males with higher tails crawling less far away from the female during Creep. There is no correlation between tail height and Creep duration. Females may take less time to approach high-crested males in Quiver because their Retreat Display is more stimulating. The crest may enhance the directional strength of water currents generated during tail displays (Green 1989). Females respond to each Retreat Display act with an approach, after a variable delay. The duration of this delay is not correlated with tail height, but it is highly variable

from one act to the next, suggesting that it is not a good indicator of the display's effectiveness. If the crest is a visual stimulus to females, Spermatophore Transfer is an ideal time for assessment. In Brake, the male is stationary in a perpendicular position to the female, with his tail folded along the facing flank. This contrasts with the roughly parallel position of the male throughout Static and Retreat Display, and gives the female a good view of both dorsal and tail crest. A deep tail may alternatively present a better visual stimulus during Quiver, when it is concertinaed and held just in front of the female, although the dorsal crest is probably not visible.

By exerting a preference for high crests, females are not gaining any non-genetic resources such as improved oviposition sites or better paternal care, as males only provide females with spermatophores (Verrell & McCabe 1988). However, female choice may provide genetic benefits. In 1988, I did an experiment showing that crest height is correlated with recent food intake. I measured and weighed 14 freshly caught males and two females. They were assigned to two groups of seven males and one female, kept in similar, adjacent tanks. Only one group was fed (twice daily on *Tubifex* and chopped earthworms). After 6 days, the fed males were then moved to the tank previously occupied by the starved males, and vice versa. After 12 days, each group of males had spent the same amount of time in each tank and with each female. When remeasured, the starved males had lost more of their tail height than the fed males (one-tailed two-sample *t*-test, $t = 2.41$, $P = 0.017$). Crest height also correlates with male condition in the field. In 70 males from one population in 1987, multiple regression showed that, for a given snout-vent length, heavier males had a higher tail (partial $r = 0.245$, $df = 65$, $P < 0.05$). Crest height is thus an honest indicator of phenotypic vigour and recent foraging intake, and, if these are heritable, females may gain genetic benefits for their offspring by preferring the spermatophores of high-crested males. This is compatible with various 'viability indicator' theories of intersexual selection (Bradbury & Andersson 1987). However, the female preference could have evolved for different reasons that could still select for males to develop crests according to phenotype (e.g. a self-reinforcing Fisher runaway;

intrinsic biases; selection to avoid hybridization with other species; selection to minimize the costs of finding a mate). If female preference for large crests arose for any reason, due to the costs of this character, only healthy males are likely to have one. This range of possibilities illustrates that it is not possible to establish how female preferences were selected by studying their effects on male traits (Kirkpatrick 1987).

This work was conducted at the Department of Zoology, Oxford and financed by a Christopher Welch Scholarship from the University of Oxford. I am indebted to Alan Grafen and Tim Halliday for supervision, and to those people who helped me catch newts.

REFERENCES

- Bradbury, J. W. & Andersson, M. B. (eds) 1987. *Sexual Selection: Testing the Alternatives*. Chichester: John Wiley.
- Darwin, C. D. 1871. *The Descent of Man and Selection in Relation to Sex*. London: Murray.
- Green, A. J. 1989. The sexual behaviour of the great crested newt, *Triturus cristatus* (Amphibia: Salamandridae). *Ethology*, **83**, 129–153.
- Halliday, T. R. 1974. Sexual behaviour of the smooth newt, *Triturus vulgaris* (Urodela: Salamandridae). *J. Herpetol.*, **8**, 277–292.
- Halliday, T. R. 1975. An observational and experimental study of sexual behaviour of the smooth newt, *Triturus vulgaris* (Amphibia: Salamandridae). *Anim. Behav.*, **23**, 291–322.
- Hedlund, L. 1990. Factors affecting differential mating success in male crested newts, *Triturus cristatus*. *J. Zool., Lond. (A)*, **220**, 33–40.
- Kirkpatrick, M. 1987. The evolutionary forces acting on female mating preferences in polygynous animals. In: *Sexual Selection: Testing the Alternatives* (Ed. by J. W. Bradbury & M. B. Andersson), pp. 67–82. Chichester: John Wiley.
- Malacarne, G. & Cortassa, R. 1983. Sexual selection in the crested newt. *Anim. Behav.*, **31**, 1256–1257.
- Teyssedre, C. & Halliday, T. 1986. Cumulative effect of male's displays in the sexual behaviour of the smooth newt *Triturus vulgaris* (Urodela, Salamandridae). *Ethology*, **71**, 89–102.
- Verrell, P. A. 1984. Sexual interference and sexual defense in the smooth newt, *Triturus vulgaris* (Amphibia, Urodela, Salamandridae). *Z. Tierpsychol.*, **66**, 242–254.
- Verrell, P. & McCabe, N. 1988. Field observations of the sexual behaviour of the smooth newt, *Triturus vulgaris* (Amphibia: Salamandridae). *J. Zool., Lond. (A)*, **214**, 533–545.