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VARIATION IN DORSAL CREST MORPHOLOGY AND TAIL HEIGHT WITH AGE IN GREAT CRESTED NEWTS (*TRITURUS CRISTATUS*)

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Variation in dorsal crest morphology and tail height in males of a population of great crested newts (*Triturus cristatus*) was examined in relation to putative age. Newts were divided into three age classes according to the number of years that they had been recorded in the breeding population: first-year breeders, second-year breeders and long-term breeders. Crest morphology differed between the age classes, with a tendency for the crest's teeth to be more irregular in older males. We believe this is the first recorded evidence of age-dependent variation in a sexually selected, morphological character in an amphibian. However, it remains to be tested whether females distinguish between males on the basis of crest morphology. Body size (snout-vent length) and tail height, which is strongly correlated with crest size, also differed between the age groups: body size increased with age and males breeding for the first time had tails that were less tall than those of older animals.

Key words: great crested newt; *Triturus cristatus*; crest; sexual selection; age; courtship; behaviour

INTRODUCTION

Among urodeles, newts of the genus *Triturus* exhibit an unusually high degree of sexual dimorphism, and are unusual in lacking amplexus (Halliday, 1977; Duellman & Trueb, 1986). During the breeding season, males develop bold coloration, toe flaps, tail filaments, deep tail fins and, in most species, dorsal crests. The role of the crest of *Triturus* newts has a long history of attention (Darwin, 1871; Halliday, 1977; Green, 1989).

The dorsal and caudal crests of *Triturus cristatus* were noted by Darwin (1871) as examples of male ornamentation that have been sexually selected. The lack of amplexus in *Triturus* provides conditions under which such selection may occur through female choice (Halliday, 1977). Halliday's (1977) supposition that females select mates on the basis of crest size has been supported by experimental evidence: larger crests are associated with greater mating success in *T. cristatus* (Hedlund, 1990), *T. carnifex* (Malacarne & Cortassa, 1983) and *T. vulgaris* (Green, 1991; Gabor & Halliday, 1996). However, as Malacarne & Cortassa (1983) point out, such results can be ambiguous, as crest development is controlled by hormones that may also influence other, potentially confounding, factors such as courtship behaviour. For example, prolactin is involved in the development of the dorsal crest (Vellano, Mazzi & Sacerdote, 1970) and also in inducing courtship behaviour (Grant, 1966; Malacarne *et al.*,1982). Males with better-developed secondary sexual characters also spend longer displaying to females, which in turn increases sexual attractiveness (Malacarne & Cortassa, 1983). Although methodological problems exist in separating the role of crests from other aspects of newt courtship, the positive association between tail height (a measure of the caudal crest) and body condition in *T. cristatus* suggests that crest height potentially provides a reliable, fitness-related, cue (Baker, 1992).

The present study further investigates the crest of *T. cristatus* as an indicator of male quality by examining the relationship between crest traits and male age. Female preference for older males may be adaptive (Trivers, 1972; Halliday, 1978, 1983; Manning, 1985) and has been demonstrated in numerous species (Andersson, 1994; Kokko & Lindström, 1996; Kokko, 1998). In newts, males contribute only sperm to reproduction, so female choice can relate only to the acquisition of "good genes", as opposed to age-related male parental skills (e.g. Searcy, 1982). The argument that older males must have superior genotypes has been disputed by Hansen & Price (1995). They argue, for example, that genetic benefits associated with proven longevity will tend to be offset by deleterious age-related effects such as decreased male fertility and the accumulation of mutations in the male germ-line. Models developed by Kokko (1997, 1998), however, suggest that female preference for older males can be favoured by selection on the basis of a "good genes" effect. The present study examines the relationship between age and tail height, and between age and crest morphology, in *T. cristatus*, age being estimated from the number of years that individuals had been recorded in a breeding population.

MATERIALS AND METHODS

Great crested newts were captured at a pond on the campus of the Open University, Milton Keynes, England, during the course of an eight-year monitoring programme, from 1988 to 1995 (Baker, 1999). This programme entailed the annual registration of breeding adults to yield data on population dynamics. During the last year of the programme, 1995, the crest morphology of males captured between 4 April and 23 May was also recorded.

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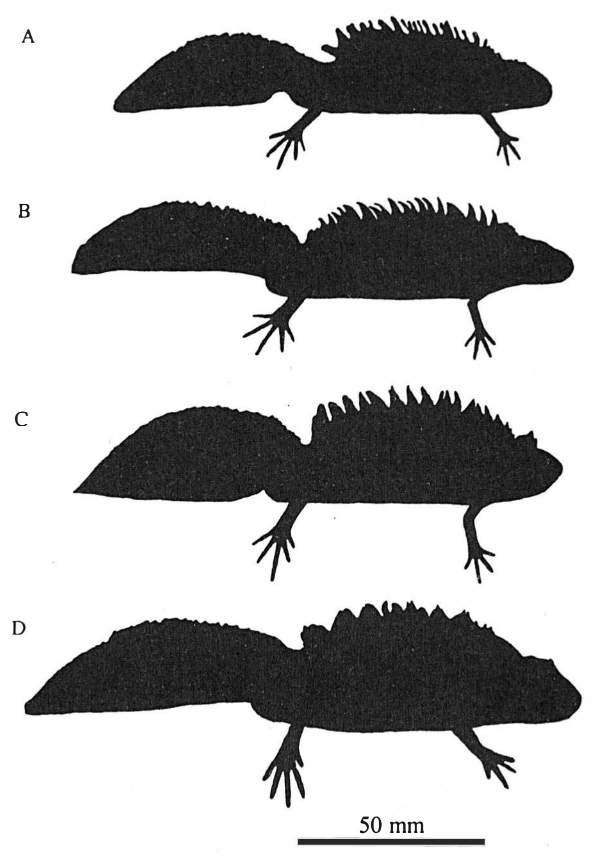

FIG. 1. Silhouettes of male *Triturus cristatus* showing variation in crest morphology. These illustrations were made by tracing the outlines of photocopied newts selected as representative of four different categories of crest shape. A, digitate; B, serrate; C, dentate; D, irregular. These males had been recorded in the breeding population for one, two, two and seven years, respectively.

Upon capture, each male was anaesthetized by immersion in a 1:1000 solution of MS222, placed on its side on a sheet of transparent plastic, and photocopied. The dorsal and caudal crests were laid flat with the aid of a small paintbrush. The lateral profiles of 112 males were recorded. The dorsal crest profiles were assigned to one of six categories on the basis of shape. The categories were defined as follows – (1) digitate: the projections of the crest form relatively regular, finger-like projections; (2) dentate: the projections of the crest form pointed, triangular-shaped projections; (3) serrate: the projections of the crest form relatively regular, sharp-pointed, backward-sloping teeth; (4) intermediate between digitate and dentate; (5) intermediate between serrate and either digitate or dentate; and (6) irregular: the crest profile consists of irregularly shaped projections. Fig. 1 illustrates some of the variation in crest morphology.

Snout-vent length (SVL) and the maximum tail height (TH) of anaesthetized newts were measured to the nearest 0.5 mm using a ruler with 1 mm graduations. SVL provided a measure of body size and TH was used as a measure of crest size. In *T. cristatus*, tail height, or the size of the caudal crest, is a more discrete character than that of the dorsal crest and hence more accurately measured. The sizes of the two crests are highly correlated (Baker, 1992).

Male great crested newts were assigned to one of three age classes as follows: (1) newts recorded in the breeding population for the first time, referred to as first-year breeders; (2) newts recorded in the breeding population for the second year in succession, referred to as second-year breeders; and (3) newts recorded in the breeding population for more than two years (3-8 years), referred to as long-term breeders. Males in the study population bred for the first time at two years of age (Baker, 1999); hence, first-year breeders were assumed to be two years old, second-year breeders three years old and the long-term breeders more than three years old.

Ageing newts on the basis of the number of years for which they were recorded in the breeding population makes the assumption that all males were captured each year. Although this was not always achieved, the numbers of newts captured as percentages of the estimated population size were high: 100%, 77% and 86% in 1993, 1994 and 1995, respectively. So, although the number of years for which some individuals had been in the breeding population may have been underestimated, the number of newts concerned was small and unlikely to have affected the overall pattern that emerged.

RESULTS

The distribution of the six categories of crest morphology across age groups (Table 1) was examined using a contingency table and χ^2 analysis. Data from the second-year and long-term breeders were combined to achieve sample sizes large enough for statistical analysis. There was a statistically significant difference in the distributions of the crest shapes between first-year breeders and second year- and long-term breeders (χ^2 with Yates' correction = 36.65, df=5, $P<0.001$). In the first-year breeders, 54% had digitate crests and the remainder were spread fairly evenly across the other five categories of crest morphology. Among the second-year breeders, there was no large group of newts with digitate crests; instead, all males were spread evenly over the remaining five crest morphology categories. Among the long-term breeders, there were no digitate

TABLE 1. The distribution of six categories of dorsal crest shape across three different age classes (1, first-year breeders; 2, second-year breeders; 3, long-term breeders). Crest morphology categories are: 1, digitate; 2, dentate; 3, serrate; 4, intermediate digitate/dentate; 5, intermediate serrate and either digitate or dentate; 6, irregular.

Age class	Category of crest morphology						*n*
	1	2	3	4	5	6	
1	41	10	9	6	8	2	76
2	1	4	3	5	8	6	27
3	0	0	1	0	1	7	9

TABLE 2. The snout-vent lengths and tail heights of male newts from three age classes. Note that the *n* value for the second-year breeders differs from Table 1 because a body size measurement was not made for one of the males photocopied.

Age class	Snout-vent length			Tail height			
	Mean	SD	Range	Mean	SD	Range	*n*
1	71.1	4.86	60.0-82.5	17.5	2.78	10-23.5	76
2	77.7	3.20	71.0-84.0	19.2	3.11	13.0-25.0	26
3	84.5	5.63	75.0-90.0	20.0	3.41	14.5-24.0	9

crests, but instead a preponderance of irregular crest profiles (category 6).

Snout-vent length and tail height were measured for 111 of the males (Table 2). One-way ANOVAs indicated that both SVL and TH varied between age classes ($F_{2,108}$=46.61, P<0.05 and $F_{2,108}$=5.073, P<0.05, respectively). Tukey multiple comparison tests indicate that there were significant differences (P<0.05) in SVL between all three age groups: the long-term breeders were larger than first-year breeders ($q_{108,3}$ =11.66) and second-year breeders ($q_{108,3}$=5.39), and second-year breeders were larger than first-year breeders ($q_{108,3}$ =8.92). Long-term breeders and second-year breeders tended to have taller tails than the first-year breeders ($q_{108,3}$=3.390 and 3.485, respectively), but there was no significant difference between the heights of tails of long-term breeders and second-year breeders ($q_{108,3}$=1.042). There was no evidence that relative tail height differed between the age classes. A one-way ANOVA of tail height as a fraction of snout-vent length was not statistically significant ($F_{2,108}$=0.244, P>0.05).

DISCUSSION

The data on crest morphology suggest that crest shape in this population of *T. cristatus* changed with the age of males. As age increased there was a progression from regularly shaped teeth to an irregular crest profile. If this is so, we believe it is the first reported case of age-dependent variation in a sexually selected, morphological character in amphibians. Older males were also larger than young males and had higher tails, although there was no evidence that tail height increased disproportionately to body size.

The observed differences in crest morphology may have been due to damage incurred as males aged. Longer-lived animals are likely to have sustained greater damage to their crests. In spite of the considerable regenerative abilities of newts (Smith, 1964), our observations on captive *T. cristatus* are that damaged dorsal or caudal crests do not regenerate completely, except in circumstances when the whole distal portion of the tail is lost. In *T. cristatus* in southern Britain, the dorsal crest is not completely resorbed outside of the breeding season, but persists in a much reduced form. Damage to the crest may thus persist between breeding seasons. Alternatively, the shape of the crest may change with age, irrespective of damage incurred. In either case, the shape of the dorsal crest in *T. cristatus* may provide a cue for discriminating between males of different ages.

Although crest morphology may provide cues pertaining to male age, it should be noted that the courtship of this species occurs in conditions under which subtle visual cues may be redundant: namely, at night (Zuiderwijk & Sparreboom, 1986; Green, 1989), and in ponds where water may be turbid. Under such conditions female discrimination between males may be based on more salient visual cues such as overall body size, or crest size, which would be consistent with data from a Swedish population (Hedlund, 1990). The present data indicate that such cues could allow age-related discrimination, as older males tend to be larger and have taller tails.

It is also possible that female *T. cristatus* do not rely on visual cues at all to discriminate between males. The courtship of *T. cristatus* also provides olfactory and mechanical stimulation (Green, 1989). Tail-fanning and lashing motions observed in this species may be detected by the female's lateral line organs (Green, 1989) or may deliver courtship pheromones (*sensu* Arnold & Houck, 1982) from the abdominal gland (Belvedere *et al*., 1988). Green (1989) has suggested that the dorsal crest of *T. cristatus* serves no visual function during courtship, but instead aids the direction of pheromone towards the female.

A further consideration is that newts' crests may have evolved in response to selection agents other than within-species female mate choice. Crests may be significant in species recognition (Smith, 1964; Halliday, 1977) or they may function as auxiliary respiratory surfaces (Czopek, 1959), increasing the length of time that displaying males can remain submerged (Halliday, 1977). Finally, crests may play a role in intrasexual signalling. Male *T. cristatus* have been observed to display to other males, possibly in defence of courtship sites within a pond (Zuiderwijk & Sparreboom, 1986; Hedlund & Robertson, 1989).

The precise role of the newt crest has not been fully established, and the possible functions listed above may not be mutually exclusive. However, Baker (1992) has shown that in *T. cristatus*, the caudal and, by inference, dorsal crests are condition-dependent characters. The present data suggest that crest morphology in this species provides information on the age of a male. Information concerning both age and condition is potentially useful to females choosing mates. Whether *T. cristatus* uses this information as the basis for mate choice remains to be determined.

Although crest morphology changed with age in the population studied, variation within each age class was too great to allow this cue to be used by a researcher wishing to precisely determine the ages of individuals. Nevertheless, it may be possible to gauge recent recruitment to a population by noting the proportion of males that have digitate crests.

An alternative explanation for the observed differences in crest morphology between age classes is that phenotypic differences between age cohorts reflected genotypic differences. For example, a newt with genes for a digitate crest may have contributed strongly to the cohort of first-year breeders. Although we cannot rule out such an explanation, on the basis of our observations we believe there is substantial evidence that crest shape in *T. cristatus* changes with age.

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