

Positive allometry is likely with mate choice, competitive display and other functions

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Petrie (1988) argued that structures important in displaying competitive ability between individuals should be developed in a positively allometric manner in species where large animals usually win fights, with larger animals developing relatively larger structures, as with the frontal shield of the moorhen, *Gallinula chloropus*. Petrie's reasoning is that animals of low competitive ability have little to gain from paying the costs of developing a large structure because any structure advertising low ability will do little to reduce the number and/or intensity of contests. In contrast, characters important in mate choice are considered unlikely to be positively allometric. Referring to moorhen shields, Petrie said 'If shields were important in mate choice it is hard to see why they should be positively allometric, since it would pay all individuals to invest maximally in structures that advertise their quality as mates, and this would result in shields being isometric.'

In my view, positive allometry will often occur in characters used in mate choice or with various other functions, and is therefore not evidence that a character is used to display competitive ability. As animals grow, they will partition investment into both bodies and characters so that bigger animals have bigger characters. How much bigger they are will depend on both the costs and benefits of a larger body size, and the costs and benefits of a larger character. The key question is, as an animal acquires more resources to invest in growth, how much should it invest in the character and how much in body size? Positive allometry will result if the net benefit of larger characters increases faster than the net benefit of larger bodies. Negative allometry will result if the net benefit of larger characters increases more slowly. In other words, if the same resource investment into a character or body size brings a greater net benefit from the former, that is where investment will be concentrated, resulting in positive allometry. If, however,

a greater net benefit comes from the latter, negative allometry will result. This applies to characters with mate choice, competitive display or any other functions.

A character developed for mate attraction may be positively allometric for at least two reasons. First, smaller animals may be less able to obtain mates and so have little to gain from paying the costs of developing a large character that does little to increase the number of matings. This logic is similar to that used by Petrie (1988) for characters displaying competitive ability, and will apply whether body size influences mating success through intersexual competition or mate choice. There may be cases where competition between males prevents small males from gaining access to females, while females choose males with larger characters (e.g. in the pinyon jay, *Gymnorhinus cyanocephalus*, larger males are favoured through male–male competition, and males with brighter colours and larger testes are favoured by female choice, Johnson 1988). Alternatively, females may prefer both larger males and larger characters, or the female preference for the character itself may become relatively stronger as its size increases. There could be a threshold effect so that, below a certain size, larger characters will do nothing to increase mating success.

A second reason that a character for mate attraction may be positively allometric is that smaller males may be in a poorer phenotypic condition, e.g. having grown slowly because of low foraging success or a higher parasite load. Males will be selected to develop such characters in a phenotype-limited way, as the costs of a given character size are lower for a male in better condition (Andersson 1982; Parker 1982).

The continuous dorsal and tail crest of the male smooth newt, *Triturus vulgaris* (L.), is positively allometric and has a mate choice function. There is no fighting in either sex, no territoriality and no

Table I. Relationships between the logarithms of tail height (TH), tail length (TL), SVL and cube root of weight ($W^{1/3}$) in smooth newts

Y	X	Males ($N=70$)		Females ($N=57$)	
		LS slope	RMA slope	LS slope	RMA slope
log TH	log SVL	1.232	1.968***	0.358	1.924***
log TH	log $W^{1/3}$	1.402	2.131***	0.669	1.795***
log TH	log TL	0.954	1.690***	0.097	1.481*
log TL	log SVL	1.006	1.164*	1.007	1.299**
log TL	log $W^{1/3}$	1.055	1.261**	0.869	1.212
log $W^{1/3}$	log SVL	0.846	0.923	0.972	1.072

Slopes are calculated using the reduced major axis (RMA) and least squares regression (LS) techniques. LS slopes are biased (see text) and only RMA slopes are tested for significant deviation from 1.0. The standard error of the RMA slope is approximately equal to the standard error of the LS slope, and this is used to calculate a *t*-statistic with $df=N-2$. * $P<0.05$; ** $P<0.01$; *** $P<0.001$.

competitive displays over access to mates (Halliday 1977; Verrell 1984; Verrell & McCabe 1988). When two males are courting the same female, crest size, body length, tail length and weight have no influence on courtship access. When males deposit spermatophores, females make a choice and pick up a higher proportion of the spermatophores deposited by high crested males (Green 1991). I captured 77 males and 57 females from Ardley, Oxfordshire, between 9 April and 27 May 1987 and measured their snout-vent length (SVL), tail length and maximum tail height to the nearest 0.5 mm, and weighed them to the nearest 0.05 g. Maximum tail height is the most convenient measure of crest size.

If the relationship between body size and maximum tail height of male smooth newts were a simple linear one, there would be an isometric relationship and the slope of the regression of log of tail height versus log SVL would be one. Weight increases in proportion to the cube of SVL, and so in an isometric relationship the slope of log tail height versus log of cube root of weight would also be one. I conducted regressions to test whether there is a significant deviation from isometry for tail height. The usual least squares regression gives a biased value for the slope of *Y* on *X*, producing a flatter slope as the amount of error in *X* (from inherent variability and from measurement error) increases (Harvey & Mace 1982). Hence I calculated slopes using the reduced major axis analysis (Sokal & Rohlf 1981, page 550; Petric 1988) which assumes that there is similar variance due to error

in both axes. Males have positively allometric relationships between tail height and SVL, and between tail height and the cube root of weight as the slope of the regressions with logged variables were significantly greater than one (Table I).

Male tail height may be positively allometric because smaller males are less attractive to females. Smaller males will have less strength and probably generate weaker forces during the tail displays that provide mechanical stimulation to the females during courtship (whip and fan: Halliday 1974). In addition, their absolute tail height will inevitably be lower, and it is possible that female preference becomes relatively stronger as tail height increases. Alternatively, male tail height may be positively allometric because larger males are in better phenotypic condition. There is no evidence of this because larger males do not weigh relatively more (i.e. there is an isometric relationship between male SVL and the cube root of weight, Table I). However, this relationship is not necessarily an accurate index of phenotypic condition (e.g. an animal heavier for its size may be carrying more parasites).

Positively allometric relationships, unlikely to be explained by mate choice, also exist for tail length in male smooth newts, and for tail height and tail length in females (Table I). Positive allometry in tail dimensions increases the relative tail surface area in larger newts and may be an adaptation to counter their lower surface area to volume/weight ratio, raising the propulsive force from the tail during swimming. By the same argument, tail allometry may also counteract the lower potential for

cutaneous oxygen gain in larger newts. Many urodelan amphibians obtain oxygen from the water by cutaneous uptake (Ultsch 1976).

Various other functions are also likely to generate positively allometric characters. For example, the width of the atlas vertebrae of the caribou, *Rangifer tarandus*, is positively allometric in relation to other measurements because of the relatively greater volume and mass of muscles that have to be supported in larger animals (Hardy & Stroud 1981).

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