

# Consequences of paternal care on pectoral fin allometry in a desert-dwelling fish

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**Abstract** Positive static allometry is a scaling relationship where the relative size of traits covaries with adult body size. Traditionally, positive allometry is thought to result from either altered physiological requirements at larger body size or from strongly condition-dependent allocation under sexual selection. Yet, there are no theoretical reasons why positive allometry cannot evolve in fitness-related traits that are solely under the influence of natural selection. We investigated scaling and sexual dimorphism of a naturally selected trait, pectoral fin size, in comparison to a trait important in male–male combat, head width in natural populations of a fish, the desert goby *Chlamydogobius eremius*. Male desert gobies provide uniparental care and use their pectoral fins to fan the brood (often under hypoxic conditions); hence, larger fins are expected to be more efficient. Male pectoral fins do not appear to fulfil a signalling function in this species. We found that, for both pectoral fin size and head width, males exhibited positive allometric slopes and greater relative trait size (allometric elevation) than females. However, for head width, females also showed positive allometry, albeit to a lesser degree than males. Because fin locomotory function typically does not result

in positive allometry, our findings indicate that other naturally selected uses, such as paternal care, can exaggerate trait scaling relationships.

**Keywords** Allometry · Fish · Fin · Scaling · Natural selection · Sexual selection

The optimal allocation of resources to different traits is typically condition-dependent (Rowe and Houle 1996). While phylogenetic constraints may exist (Smith 1994), among the conspecifics of a certain developmental stage, the size of a trait in relation to body size (i.e. its static allometry) is generally thought to be adaptive. Much debate has centred on what can be inferred from such relationships, particularly whether traits that are relatively larger in large individuals (positive allometry) differ fundamentally from those that scale proportionally (isometry) or are relatively larger in small individuals (negative allometry) (Green 1992; Simmons and Tomkins 1996; Bonduriansky 2007a). Positive static allometry is found in both sexually selected traits and traits solely under natural selection. Differential growth in naturally selected traits may be necessary to accommodate the altered relative physiological requirements associated with increased body size. For example, the cross section of the human tibia is positively allometric because it determines torsional strength and should thus be under stabilising selection to increase with mass rather than height (Ruff 2000). However, most described cases of positive static allometry occur among sexual traits (Kodric-Brown et al. 2006). Given this bias, much attention has focussed on what characteristics of sexually selected traits lead to this type of scaling.

By their nature, sexual traits appear predisposed to evolve condition-dependent expression (Kotiaho 2000; Bonduriansky

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2007b and references therein). Ornaments and armaments are typically costly fitness-related traits under directional sexual selection (Green 1992; Kodric-Brown et al. 2006). Consequently, high-condition individuals prioritise allocation of excess resources to these traits (Andersson 1986; Emlen 1996; Tomkins et al. 2004; Bonduriansky 2007b). Positive allometry is thought to evolve only when large individuals receive greater net fitness returns by allocating excess resources to a trait rather than investing those resources into viability by increasing body size (Bonduriansky and Day 2003).

Bonduriansky and Day's (2003) conclusions regarding the requirements for the evolution of positive allometry are essentially neutral to the nature of selection acting on traits (i.e. natural or sexual). Theoretically, positive allometry can evolve in naturally selected traits under a mechanism similar to that seen in sexual traits. For example, Wickman and Karlsson (1989) suggested that positive allometry for abdomen size in female butterflies results from directional fecundity selection rather than physiological demands, since heavy females have proportionally greater fecundity but may suffer reduced flying ability (Karlsson and Wickman 1990). Indeed, some classes of naturally selected traits exhibit characteristics very similar to sexually selected traits. Life history traits, such as fecundity and viability, are often strongly fitness-related, subject to directional selection, costly, and exhibit condition dependence (Roff and Mousseau 1987; Rowe and Houle 1996). Naturally selected traits may also exhibit the exponential fitness functions required for the evolution of positive allometry (Schluter 1988). Although the parallels of such traits (e.g. parental care, fecundity) and sexually selected traits have previously been recognised (Ghiselin 1974), current theory does not address positive allometry under natural selection (Bonduriansky and Day 2003; Kodric-Brown et al. 2006).

Here, we examine trait scaling in the desert goby (*Glamydogobius eremius*), a small teleost that inhabits spring-fed pools and ephemeral waters in the arid regions of central Australia. During the breeding season, males establish nests under rock crevices and defend these against takeover attempts by rivals, with males using their enlarged heads to help them lock jaws, grapple and bite their opponents (Svensson et al. 2012). To entice females to spawn in the nest, male desert gobies perform elaborate courtship displays involving jerky body movements accompanied by the blackening and flaring of their dorsal and anal fins (Wong and Svensson 2009). Males provide exclusive parental care by defending the eggs and fanning the developing brood with their pectoral fins (Symons et al. 2011) which is likely to be energetically taxing (Jones and Reynolds 1999).

Specifically, we compared the allometry of a trait presumed to be under fitness-related natural selection (pectoral fin size) to a trait under sexual selection (head width). Desert goby habitats fluctuate widely in oxygen content (Glover

1982), suggesting that hypoxic conditions may exert strong selection on fanning ability. Greater fin size increases both maximum thrust (Blake 1979) and efficiency (Künzler and Bakker 2000), and fin size may be condition-dependent (Bakker and Mundwiler 1999). Male head size is sexually selected in gobies for the ability to win male–male conflict (Lindström 1992) and is thus expected to exhibit positive allometry. Although locomotory function appears to cause scaling with negative allometry or isometry in fins (Drucker and Jensen 1996; Baldauf et al. 2010), larger desert goby males possess conspicuously large pectoral fins. A recent experimental evolution study on guppy fins suggests that relative trait size (allometric elevation) shows greater evolvability than variability in the rate of allocation (allometric slope) (Egset et al. 2012). We thus expect a greater allometric elevation of pectoral fins in males than in females and, due to the potential fitness benefits of paternal care ability, expect positive allometry in males but not females.

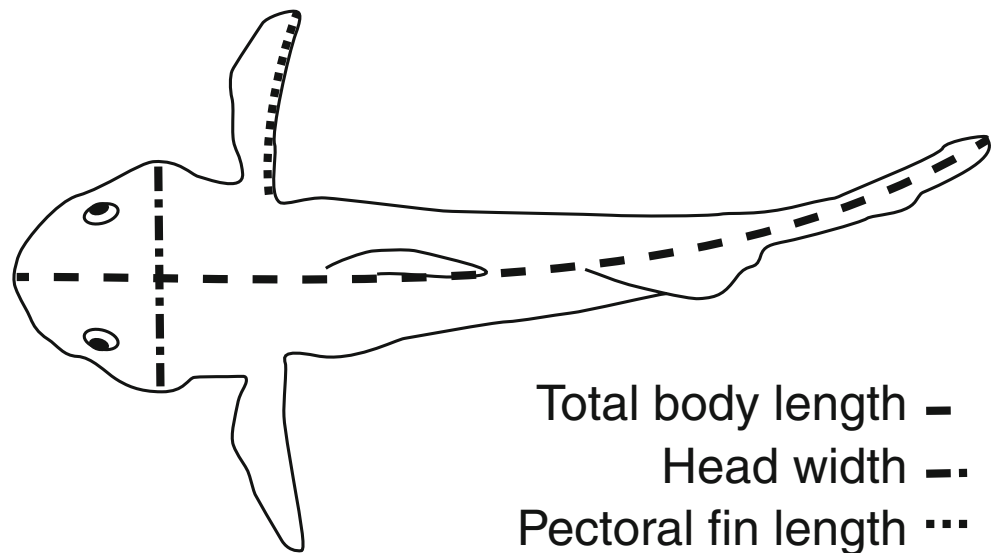
## Methods

In August 2007, 95 adult and 51 juvenile desert gobies were collected using dip and seine nets from three sites in the Lake Eyre basin in Central Australia (Neales River 27°53'54" S, 135°48'41" E; Ockenden Spring 27°50'33" S, 135°44'29" E; Peake Creek 28°2'6.59" S, 135°48'0.15" E). Back in the laboratory, sexually mature males, distinguishable by the colouration of their fins, were placed in individual aquaria, while juveniles and females were kept in communal tanks. All tanks were maintained at conditions similar to those at the collection site (24–26 °C, 5 ‰ salinity, 12-h light/dark cycle).

To minimise handling, morphological measurements were obtained by placing gobies in a beaker filled with water to a depth of 2–3 cm and digitally photographed from above (Nikon D80 camera, Micro Nikkor 60-mm f/2.8 lens). Resulting images were analysed with ImageTool 3.0 image analysis software (UTHSCSA, San Antonio, TX) using a 1-cm calibration grid placed on the bottom of the beaker. Three size measurements were obtained: total body length (measured from the tip of the snout to the visible end of the caudal fin over the medial axis); pectoral fin length (measured from the base of the pectoral fin to the tip of the longest visible ray); and maximum head width (Fig. 1).

Scaling relationships were modelled using the equation  $y = b \cdot x^\alpha$ , where  $x$  and  $y$  stand for body and trait size, and constants  $b$  and  $\alpha$  denote the allometric elevation and slope, respectively. While  $b$  describes trait size relative to body size,  $\alpha$  indicates whether relative trait size is constant for all body sizes ( $\alpha=1$ , 'isometry'), decreases with body size ( $\alpha<1$ , 'negative allometry') or increases with body size ( $\alpha>1$ , 'positive allometry'). After log-transformation of  $x$  and  $y$ , several

**Fig. 1** Dorsal view of an adult male desert goby. *Dashed lines* indicate morphological measures used in analyses



regression methods are available to estimate  $\alpha$  and  $b$ . Lines fitted using ordinary least squares regression minimise only error in the  $y$  variable, making this method appropriate for predictions given specific values of  $x$  (Warton et al. 2006). Intraspecific studies of static allometric relationships, however, aim to infer how individuals allocate resources between further growth in trait or body size, which is essentially a symmetric problem (Smith 2009). Standardised major axis (SMA, also known as reduced major axis) regression fits lines that minimise error in both  $x$  and  $y$ , making it preferred in studies of static allometry (Green 1999; Bonduriansky 2007b; Cuervo and Møller 2009). SMA assumes that the error variances in  $x$  and  $y$  are proportional to the variances in  $x$  and  $y$  respectively, and independent. The nonindependence of traits within species thus raises questions about the appropriateness of SMA in interspecific studies (Hansen and Bartoszek 2012). In our study, measurement error is similar for  $x$  and  $y$  since both were measured identically in the same images. We therefore conducted SMA regression using the package ‘smatr’ for analyses of allometry (Warton et al. 2012) by using R 2.15.1 (R Development Core Team 2012). Significance was tested using analysis of covariance (ANCOVAs) with population included as a fixed factor due to the limited number sampled. If interactions were not statistically significant, they were dropped (Engqvist 2005) and initial type III ANCOVAs were replaced with type II analyses.

## Results

Descriptive statistics for measured traits are presented by sex and age (Table 1). Neither pectoral fin length nor head width of adult fish differed among populations (Table 2). Sex and body length affected pectoral fin length (Table 2 and Fig. 2a). In contrast, the relationship between total body

length and head width depended on sex: male head width increased more strongly with body size (Table 2 and Fig. 2b). In both sexes, pectoral fin length and head width scaled with positive allometry (Table 2). Allometric slopes were similar in adult males and females for fin length (likelihood ratio, LR=0.04,  $p=0.85$ ) but showed sexual dimorphism for head width (likelihood ratio, LR=3.84,  $p=0.0499$ ). However, for both fin length and head width, adult males’ allometric curves had greater elevation than those of females (Wald tests, head width:  $W=184.6$ ,  $p<0.001$ ; fin length:  $W=9.01$ ,  $p=0.003$ ). Juvenile allometric slopes (Table 2) did not differ from adults’ of the same sex for both head width (likelihood ratios, male: LR=0.37,  $p=0.54$ ; female: LR=0.14,  $p=0.71$ ) and were not statically significantly lower for fin length (likelihood ratios, male: all LR=3.31,  $p=0.07$ ; female: LR=2.54,  $p=0.11$ ).

## Discussion

In desert gobies, male pectoral fin length, a trait involved in parental care, exhibits a similar degree of positive allometry as male head width, a trait important in male–male sexual competition. Apart from a sexual dimorphism in the allometric slopes of head width, this finding was, to a lesser

**Table 1** Sample sizes and means (standard errors) for measured traits by sex and age groups

Sex	Age	<i>n</i>	Body length	Pectoral fin length	Head width
M	Juvenile	28	43.14 (1.12)	7.73 (0.21)	7.69 (0.29)
	Adult	50	62.69 (0.57)	12.62 (0.15)	14.48 (0.21)
F	Juvenile	23	39.34 (0.59)	6.73 (0.10)	6.32 (0.13)
	Adult	45	52.23 (0.75)	9.32 (0.17)	8.88 (0.16)

**Table 2** ANCOVA results and SMA slopes for head width and pectoral fin length in adult desert gobies

	Pectoral fin length				Head width <sup>a</sup>		
ANCOVA	df	$\beta$	F	p	$\beta$	F	p
Sex	1	1.32	29.09	<0.001	-3.91	0.08	0.773
Body length	1	0.19	105.29	<0.001	0.19	101.95	<0.001
Population	2		0.02	0.982		2.72	0.071
Sex×body length	1			n.s.	0.12	4.13	0.045
Allometry	SMA slope (95 % CI)		SMA slope (95 % CI)				
Males	1.31 (1.08–1.60)**		1.57 (1.35–1.83)***				
Females	1.28 (1.06–1.55)*		1.29 (1.13–1.47)***				
Juvenile males	1.05 (0.92–1.21)		1.49 (1.34–1.65)***				
Juvenile females	0.98 (0.74–1.29)		1.35 (1.11–1.63)**				

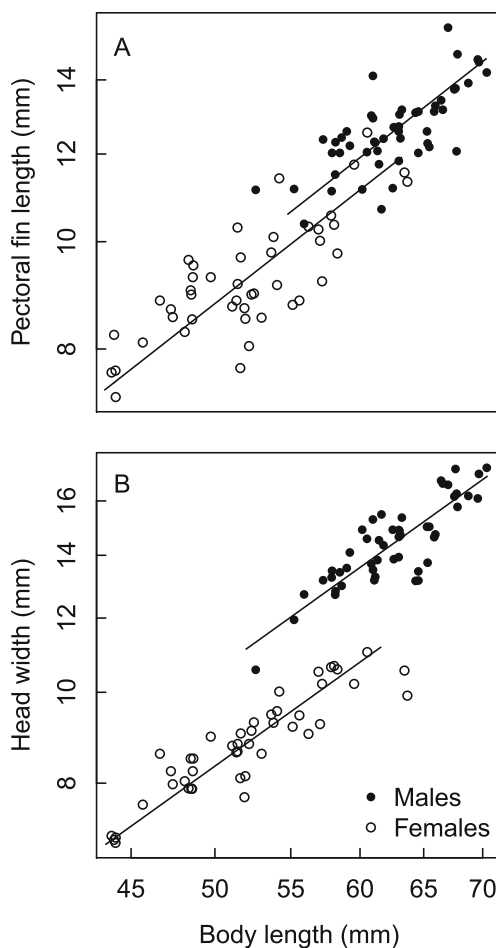
\* $p=0.05$ ; \*\* $p=0.01$ ;\*\*\* $p=0.001$  (significant difference from isometry)<sup>a</sup>Square root transformed to meet normality requirements

degree, also present in females, suggesting further naturally selected causes to positive allometry.

We show that pectoral fin length is positively allometric, but, contrary to initial predictions, both sexes exhibit this scaling relationship. Unlike head width, fin length is dimorphic

only in the allometric elevation, not the slope. Theoretically, positive allometry in linear locomotor traits might be expected because drag is proportional to the cross-sectional area of a fish (Vogel 1994). Yet, there is little empirical evidence to support such a relationship in fish fins. In fact, fins generally scale with negative allometry or isometry when solely under selection for locomotion (Drucker and Jensen 1996; Baldauf et al. 2010). Positive ontogenetic allometry in pectoral fins has previously been found in both sexes of a waterfall-climbing goby species, but not another (Maie et al. 2007). In contrast, desert gobies are bottom-dwelling fish that inhabit stagnant or slowly flowing shallow waters. The discrepancy between the allometric slopes for head width and fin length in males indicates that fin allometry is not merely a consequence of the increased drag associated with larger heads.

Positive allometry in fins is usually interpreted in terms of sexual selection. In sailfin mollies, for example, the degree of positive allometry of ornamental dorsal fins covaries to the within-species diversity in male alternative mating behaviours (Hankison and Ptacek 2007). Pectoral fin expression in three-spined sticklebacks is condition-dependent and reflects paternal care ability (Künzler and Bakker 2000). While stickleback males have a greater allometric elevation than females, both sexes exhibit isometry for pectoral fin size (Bakker and Mundwiler 1999). Male desert gobies similarly show greater proportional allocation (elevation) in pectoral fins than females. Courtship signalling involves chiefly the dorsal and anal fins, which are flared and blackened (Wong and Svensson 2009). It seems unlikely that female preferences for male parental ability target pectoral fins in this species. Specifically, in contrast to sand gobies, where paternal care is under sexual selection (Lindström et al. 2006), male desert gobies actually reduce their parental effort when presented with additional mating opportunities (Symons et al. 2011). Indeed, if females prefer higher fanning frequencies (Lindström et al. 2006), this should favour smaller, rather than larger, fins. Hence, our data suggest that pectoral fin allometry in desert gobies is, instead, shaped by natural selection on paternal care ability. Fin area is



**Fig. 2** Allometric scaling relationships for adult male and female **a** head width and **b** pectoral fin length. Fitted lines are slopes obtained from SMA analysis



directly related to maximum thrust and fanning efficiency (Blake 1979; Künzler and Bakker 2000). Hence, larger fins may allow males to better protect their broods against hypoxic conditions. Yet, the presence of positive allometry in females remains unexplained. Baldauf et al. (2010) showed that female pelvic fins in a cichlid with biparental care scale more positively than other fins but suggest that this was due to their use in signalling. There is no evidence for either male mate choice or female intrasexual conflict in desert gobies. A recent work on guppies showed genetic constraints preventing evolution in caudal fin allometric slopes subject to artificial selection (Egset et al. 2012). The absence of sexual dimorphism could indicate that pectoral fin allometric slopes in desert gobies are constrained by an intersexual genetic correlation for condition dependence (Bonduriansky and Rowe 2005).

We also found that both male and female adults show positive allometry for head width, but the allometric slope and elevation are greater among males. The occurrence of positive allometry among females indicates a naturally selected cause, either specific to females or common to both sexes, since there is no apparent evidence of either male mate choice for female head size or female intrasexual competition in this species. Assuming that expression in females is adaptive, this scaling relationship could derive from advantages in foraging or fighting. Head dimensions also scale with positive allometry in baleen whales due to their unique feeding method, although the foraging benefits of large gapes are offset by greater energetic demands (Goldbogen et al. 2010). Since metabolic rates typically scale with an allometric exponent of  $\sim 0.75$  (Farrell-Gray and Gotelli 2005), head allometry in desert gobies is also unlikely to result from a need for increasingly large prey with body size. The stronger exaggeration in males may relate to the male's need for armaments in nest site defence. Male–male interference over nest sites is a critical step in mate acquisition and a source of variance in reproductive success in fish (Klug et al. 2010). Mandible size influences intraspecific contest outcomes when fights involve biting (Lindström 1992), which occur among male desert gobies (PAS and BMW unpublished data). Yet, nest defence is likely to have additional naturally selected functions that are strongly fitness-related. Desert gobies are part of relatively simple food webs where predation of conspecific eggs is likely to represent an important potential source of nutrition. In small populations, the reduction of rival fitness should contribute substantially to a male's own fitness and could underlie exponential fitness returns on allocation to head size through natural selection.

This study shows positive allometry in traits that is unlikely to be accounted for by either sexual selection or physiological necessity. Our findings add to a limited number of studies arguing that disproportionate allocation may be expected in naturally selected traits closely tied to fitness

such as parental care ability (mayflies: Sweeney et al. 1986; butterflies: Wickman and Karlsson 1989; moths: Marshall 1990). Such findings are important, given that the presumed differences in allometry produced by natural and sexual selection remain a key device in theoretical efforts to explain trait scaling.

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**Ethical standards** The experiments comply with the current laws of the country in which they were performed.

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