Received: 1 June 2021 | Accepted: 26 October 2021
DOI: 10.1111/1365-2435.13968

Functional Ecology
BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

The stabilising impact of natural selection on the allometry of sexual ornaments: Fish that escape locomotor constraints exhibit extravagant ornamentation

Thomas C. Summers | Terry J. Ord

Evolution and Ecology Research Centre, and the School of Biological, Earth and Environmental Sciences, University of New South Wales, Kensington, NSW, Australia

Correspondence
Terry J. Ord
Email: t.ord@unsw.edu.au

Funding information
Australian Research Council, Grant/Award Number: DP120100356

Handling Editor: Cristina Tuni

Abstract

1. Positive allometry has been considered a hallmark of sexual selection whereby larger males of superior condition develop disproportionately larger ornaments for their body size compared to smaller males of poorer condition.
2. Yet many structures known to be sexually selected often exhibit other allometric patterns. This has led to controversy over the utility of allometry in adequately capturing the signature of sexual selection, particularly if static (within population) and evolutionary (across species) allometries are functionally constrained by stabilising natural selection.
3. To investigate this, we evaluated the allometries of ornamental head crests and dorsal fins across multiple species of blenny fish. In particular, we compared species that occupied an aquatic environment—where swimming performance was expected to have constrained ornament size—with species that have transitioned onto land where such biomechanical constraints on ornament size have been removed.
4. Static allometries of both head crest and dorsal fin ornaments were found to be positive in males, but less so in females, across all species examined. This was consistent with the allometric theory of sexual selection that predicts positive allometry specifically in male ornamentation. Nevertheless, male allometric exponents were constrained in aquatic species whereas males of terrestrial species were free to exaggerate the size of their ornaments. Natural selection therefore appears to limit the evolution of ornament size in aquatics, and probably because of the biomechanical constraints associated with swimming. These differences in within-population static allometry between aquatic and terrestrial species in turn manifested in a greater across-species evolutionary allometric elevation, but not exponent, for terrestrial species relative to aquatic species.
5. These findings indicate that the study of ornament allometries can provide useful insights into the role of sexual selection on ornament elaboration and also help reveal the presence of opposing natural selection that might result in alternative allometric patterns. The relationship between static and evolutionary allometries remains complex, and our results caution against the interpretation of

evolutionary allometry in the absence of a clear understanding of the underlying static allometries associated with it.

KEYWORDS
amphibious fishes, Blenniidae, condition-dependent ornamentation, evolutionary allometry, selection trade-off, sexual selection, static allometry

1 | INTRODUCTION

How morphological characteristics scale with body size—allometry—has a long history of study (Cheverud, 1982; Cock, 1966; Gould, 1966; Huxley, 1924, 1932). Recently, there has been a resurgence of interest in allometry following the proposition that scaling patterns can be used to infer the extent to which large morphological structures are the target of sexual selection (Kodric-Brown et al., 2006). For example, females often use the size of a morphological ornament to assess aspects of male quality because only males in good condition can incur the costs of developing and maintaining a large ornament (Andersson, 1982; Grafen, 1990; Kotiaho, 2001; Kotiaho et al., 1998; Moller, 1996; Zahavi, 1975, 1977). Bigger males are usually those in better condition and this should lead to a general trend of larger males within a population developing disproportionately larger sexual structures, or positive 'static allometry' (Green, 1992; Petrie, 1988). More specifically, the size of a morphological characteristic should exhibit a scaling exponent in a power function with body size of 1.5 or greater, which seems to be typical for characteristics known to be sexually selected (Kodric-Brown et al., 2006). The same prediction has also been used to interpret the average size of morphological characteristics as a function of average body size across populations or species, or 'evolutionary allometry' (e.g. Lemaitre et al., 2014; Plard et al., 2011). Here, the evolutionary exponent is generally viewed as a reflection of evolutionary change in gross ornament size relative to body size. The difficulty, however, is the functional relationship between within-population static allometry and across species evolutionary allometry is not entirely clear.

The basic assumption is that, as the relative strength of sexual selection on gross ornament size increases across taxa, the evolutionary exponent will become increasingly steeper as well. This would occur, for example, if sexual selection within taxa produces an increase in the static allometric exponent that in turn drags up the mean size of the ornament for the taxon as a whole and is similarly associated with a mean increase in overall taxon body size (e.g. females prefer larger ornaments on larger males; static exponent → evolutionary exponent). This is at least broadly consistent with several comparative studies reporting differences in static exponents among closely related taxa (e.g. Hosken et al., 2005; Simmons & Tomkins, 1996; Tomkins & Simmons, 1996; see also Kodric-Brown et al., 2006; Voje & Hansen, 2013). Yet laboratory and field studies have shown that selection seems to have a greater influence on the elevation of the static allometry line (its intercept) than its exponent (Bolstad et al., 2015; Egset et al., 2011, 2012; Pelabon et al., 2013; Tobler & Nijhout, 2010). A positive evolutionary exponent would therefore only occur if differences in the intensity of sexual selection among taxa promote changes in static elevations as a function of mean body size (i.e. static elevation → evolutionary slope). While it seems intuitive to link changes in static exponents or static elevations with changes in overall mean size of ornaments, the factors that might cause a concomitant change in mean body size across taxa are likely to be complex and hard to predict. It is therefore not obvious whether the interpretation of positive evolutionary allometry in sexual characteristics across species can be reasonably extrapolated from the same processes argued to generate positive static allometries within those species (sensu Kodric-Brown et al., 2006).

Nevertheless, both static and evolutionary allometries found to exhibit positive scaling in a putative sexually selected ornament (or weapon; e.g. McCullough et al., 2015) have been used to confirm the presence of sexual selection (e.g. Clutton-Brock et al., 1980; Green, 2000; Kawano, 2000; Ord & Hsieh, 2011; Tomkins et al., 2010; Voje & Hansen, 2013). The magnitude of the computed allometric exponent has also been used to gauge the likely strength of sexual selection acting on males within a given population, which can be difficult to measure directly in natural settings. Concerns have been raised over making such inferences because, in addition to the apparent limited sensitivity of static exponents to selection (see previous paragraph), morphological characteristics that do not function as sexual ornaments can also exhibit positive allometry, while known sexually selected ornaments can exhibit isometric (exponents ≈ 1) or even negative (exponents < 1) allometries (Bonduriansky & Day, 2003; reviewed by Bonduriansky, 2007; Eberhard et al., 2018; Voje, 2016). It is possible that sexual ornaments might exhibit isometric or negative static exponents because males with larger ornaments are often exposed to stronger opposing natural selection in the form of increased predation (Andersson, 1982; Klomp et al., 2016; see also Kotiaho, 2001; Zuk & Kolluru, 1998) or locomotion constraints (Barbosa & Moller, 1999; Basolo & Alcaraz, 2003; Swallow et al., 2000). The outcome of this trade-off could reduce the observed allometric exponent in those ornaments (Eberhard et al., 2018). In order to correctly interpret the allometric exponent in this context, the strength of opposing natural selection would have to be explicitly derived, which is often as difficult as measuring the relative strength of sexual selection in natural settings.

To tease apart the influences of natural and sexual selection on ornament allometries, and the functional relationship between static and evolutionary allometry more generally, a natural system in which closely related species are known to vary in the extent environmental constraints impact ornament size would be particularly informative. A remarkable system that meets these requirements is the marine intertidal fishes of the family Blenniidae (the blennies). In these fishes, males employ conspicuous displays centred on the presentation of a large prominent head crest and dorsal fin for attracting females (Bhikajee & Green, 2002; Morgans et al., 2014; Ord & Hsieh, 2011; Shimizu et al., 2006; Figures 1 and 2a). The optimal size of these ornamental structures is also likely to be constrained by these same structures needing to avoid drag or be directly functional for swimming (e.g. sunfish: Borazjani, 2013, Drucker & Lauder, 2001; trout: Standen & Lauder, 2007). For example, large morphological structures elaborated in fishes by sexual selection (i.e. ornaments) can result in increased drag during swimming (Webb, 2002; e.g. swordtails: Basolo & Alcaraz, 2003; see also related work on blennies: Laporte et al., 2016). Similarly, reducing the size of male ornamental dorsal fins has been linked to improve overall swimming performance (e.g. guppies: Karino et al., 2011; gobies: Robitzch et al., 2021). That is, while sexual selection might increase the size of the head crest and dorsal fin, natural selection can be expected to constrain the size of these structures to lie within the bounds that are functional for effective swimming.

What makes blennies unique is that some species have left the aquatic environment for a life on land (Ord & Cooke, 2016) and in the process have presumably escaped the locomotor constraints on ornament size. Out of the water, these 'terrestrial' blennies continue to respire through the gills and skin (Martin, 1995; Martin & Lighton, 1989) but must remain moist to avoid asphyxiation. This limits the fishes to a narrow band of habitable terrestrial habitat within

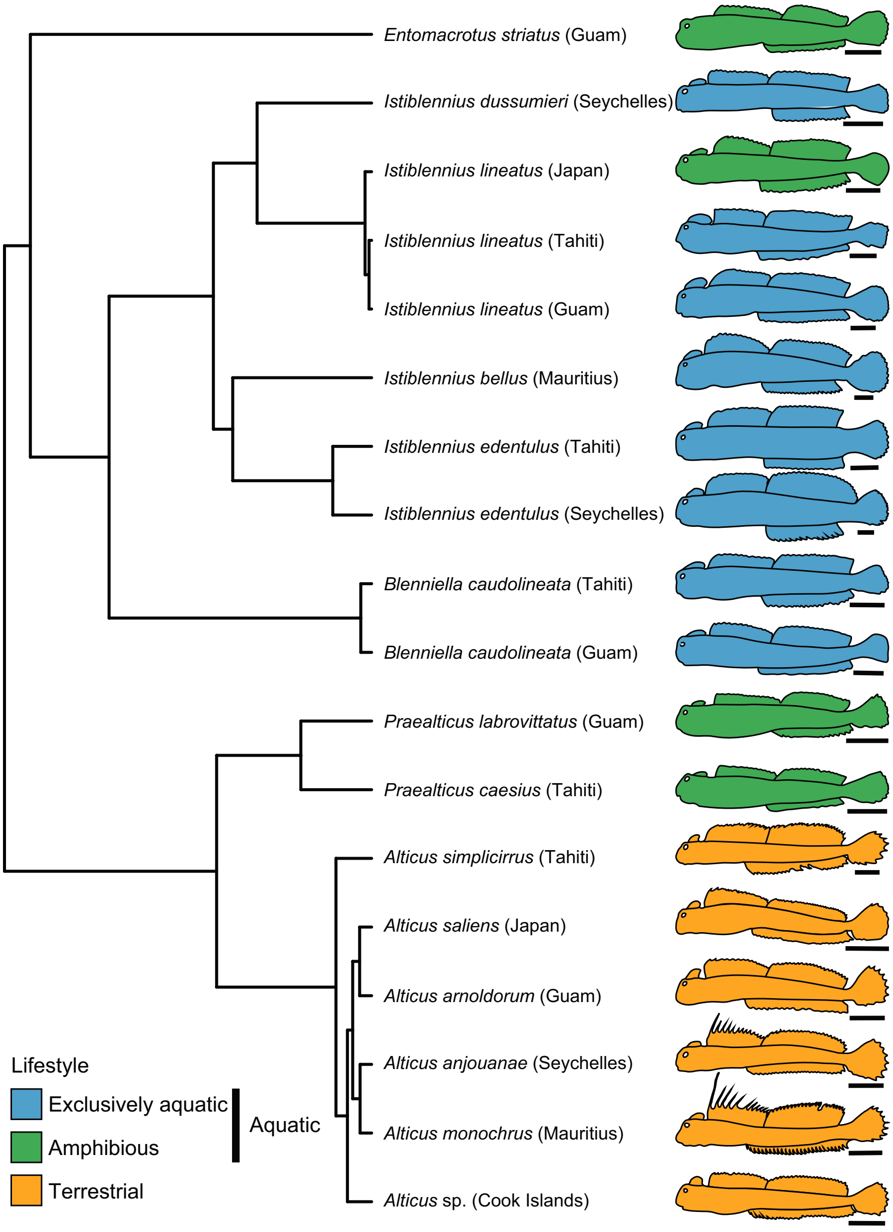

FIGURE 1 Phylogenetic relationships (taken from Ord & Cooke, 2016) and representative morphological profiles of males for each species sampled. Aquatic and amphibious taxa were grouped together for analyses because these taxa were expected to experience the same biomechanical constraints on morphology associated with swimming in water. Scale bar = 1 cm. Statistical analyses implemented across species explicitly controlled for the clustering of terrestrial species in a single monophyletic clade

the splash zone. The fishes are highly agile on land with locomotion consisting of crawling, hopping and jumping (Hsieh, 2010). Males continue to use the head crest and dorsal fin in the courtship of females (Morgans et al., 2014; Ord & Hsieh, 2011), indicating these structures remain strong targets of sexual selection out of water. These fishes therefore provide an excellent opportunity to quantify allometric changes in ornamentation between environments—aquatic and terrestrial—that likely vary in the degree natural selection has constrained the size of ornament expression. We studied multiple species of aquatic and terrestrial Blenniid fishes from a range of Pacific and Indian Ocean tropical islands (13 species for static allometry and 18 species for evolutionary allometry; Figure 1). First, we estimated separate static allometries for both males and females for each species for the size of the head crest, dorsal fin and ventral fin. The ventral fin was included as a control region because it was unlikely to be the target of sexual selection given the benthic lifestyle of blennies limits its visibility to conspecifics during social interactions. Second, the evolutionary allometry of these three morphological traits, for each sex, was computed by regressing the species mean size of each trait on the species mean body length across species.

We expected that only male head crest and dorsal fin size would exhibit static allometries with exponents ≥ 1.5 (following Kodric-Brown et al., 2006). Furthermore, the steepest exponents for these characteristics should generally occur among males of terrestrial species because these males no longer face the constraints on ornament size that might be imposed in water. The extent to which the gross (mean) size of head crests and dorsal fins should vary among species was less clear. Evolutionary allometry is expected to be similar to within-population static allometries if directional selection on body size accompanies proportional increases in ornament size across species (e.g. females prefer larger ornaments on larger males). In which case, we would expect male head crest and dorsal fin size to exhibit evolutionary allometries with exponents ≥ 1.5, under the assumption that the intensity of sexual selection varies across species independently of whether species occupy terrestrial or aquatic environments. The magnitude of that evolutionary exponent should nevertheless be steeper across terrestrial species than aquatics because the opposing natural selection on ornament size has been removed in terrestrial species. In the absence of concomitant changes in mean body size of males across species, there is no expectation that sexual selection within species that generates positive static allometries in ornaments will have any influence on evolutionary exponents across those species.

2 | MATERIALS AND METHODS

2.1 | Data

The range of body sizes, number and sex of fish sampled for each species, as well their collection locations, are provided in Table A1. Aquatic specimens were collected by snorkel using hand nets and small weighted drop nets. Terrestrial species were sampled along exposed rocks within the splash zone using hand nets. Once caught, fish were placed in opaque plastic containers with fresh seawater and kept in a sheltered shady area. All specimens were photographed within 30 min of capture, with the majority released back at the approximate point of capture, excluding a small number that were kept to obtain tissue samples in order to develop a phylogeny as part of a separate study (Ord & Cooke, 2016). Special effort was taken to obtain a range of adult body sizes for every species to ensure accurate estimates of head crest and dorsal fin allometries (allometry exponents tend to be influenced by the lower and upper ends of the size distribution). Blenniidae are relatively short-lived fishes and adults were easy identified in the field because juveniles were substantially smaller than adults (i.e. there is little overlap in size ranges between juveniles and adults; Bhikajee et al., 2006). Identification of species was facilitated using keys from Aizawa (2002). Any individuals for which species or age could not be verified were not included in this study.

Specimens were classified into aquatic or terrestrial lifestyles based on a strict categorisation scheme developed by Ord and Cooke (2016). To ensure consistent and accurate categorisation of fish lifestyle behaviour, the same person verified categorisations of each specimen from verbal descriptions given by the collector of the behaviour of fish during capture. Species exhibited one of three broad lifestyles: exclusively terrestrial, amphibious and exclusively aquatic (Figure 1). Amphibious blennies generally leave water at high tide as a means of avoiding the influx of predatory fishes, but are otherwise found in water at most other times (Ord et al., 2017). We have not observed any obvious social behaviour in amphibious blennies when on land, which implies that males likely court females primarily in the water. For the purposes of our study, we therefore grouped amphibious and aquatic species together into a single aquatic category, and based on the additional assumption that any species spending time underwater will be exposed to the same constraint on ornament size likely to be imposed by swimming.

High-resolution digital photographs of specimens were taken following Morgans et al. (2014) using a EOS 7D digital SLR with an EFS 15–85 mm, f/3.5-5.6 IS USM zoom lens. Photographs from Morgans et al. (2014) were also used to supplement data for *Alticus arnoldorum*, *Entomacrotus striatus*, *Praealticus labrovittatus*, *Istiblennius lineatus* and *Blenniella caudolineata*. Fish were placed in a small clear zip-lock bag with the air removed and just enough seawater to facilitate full erection of the dorsal and ventral fins by gently pressing on the surface of the bag. The bag was then placed beside a ruler and multiple photos were taken of the lateral side of the fish to ensure images of the head crest, dorsal fin, ventral fin and body length were flat against the background. From these images, measurements of the area of fins and length of the body—specifically standard length (see below)—were made using ImageJ version 1.47 (Rasband, 1997–2016; NIH) and calibrated to millimetres based on the ruler included in each photograph.

The standard length (mm) of the body was measured from the anterior tip of the snout to the posterior end of the last vertebra (caudal peduncle). The area (mm^2) of the male head crest was measured by tracing around its outer edge and following a straight line where it connected with the head (see Figure A1). Both the first dorsal and ventral fins areas (mm^2) were measured by tracing an outline along its length of the body and across the tips of each fin ray (see Figure A1 and Morgans et al., 2014). Fin rays were included in the estimate of fin area because in the case of the dorsal fin, these rays were greatly exaggerated in some species and presumably targeted by sexual selection given the way in which dorsal fins were presented to females during courtship (Bhikajee & Green, 2002; Ord & Hsieh, 2011). That is, females likely assess the collective size of the dorsal fin encompassed by the extension of the rays, and it is the preference of females for large dorsal fins (rays and all) that is the mechanistic basis that is anticipated to produce the positive allometry in ornament size. Measurements were made by a single researcher (TCS) and were replicated three times for each trait using separate photographs. These three measures were then averaged to obtain a single estimate of body length or crest/fin area. When computing evolutionary allometries, averages for individual fish were averaged a second time across individuals to obtain a species mean value for each trait.

2.2 | Computing allometries

All analyses were implemented in R version 3.2.4 (R Development Core Team, The R Foundation for Statistical Computing). Area measurements were first linearised using a square-root transformation (see Bonduriansky, 2007). All data were then natural-log transformed, which allowed linear regressions to be applied that were statistically equivalent to a power function, that is,

$$\text{ornament size} = \alpha(\text{body size})^{\beta},$$

converted to

$$\ln(\text{ornament size}) = \ln(\alpha) + \beta(\ln,\ \text{body size}).$$

Here, the intercept of the allometry line corresponds to the allometric elevation (α), while the slope corresponds to the allometric exponent (β), with positive allometry indicated by $\beta > 1$, isometry (one-to-one changes in ornament size with body size) $\beta = 1$ and negative allometry $\beta < 1$.

To evaluate the sensitivity of allometric parameters to sample size, allometric regressions were computed across a range of samples sizes by resampling data on head crest area for male *Alticus monochrus* (a species with one of the largest sample sizes; Table A1). These sensitivity analyses showed that 10 individuals or more would generally provide a reasonable estimate of ornament allometry (Figure A2). Thirteen species were either above or close to this number and were used in ordinary least squares (OLS) regressions of morphological areas on standard length to estimate static allometries using the 'ols' function in the 'RMS' package version 5.1-0 (Harrell, 2017). Interpretation of species static exponent (slope) values were the primary focus of this paper, while static elevations were not assessed because of significant differences among species in static exponents and lack of size range overlap among many of the species examined (see Introduction). For comparison, static allometries were also computed using reduced major axis regression (RMA) using the 'sma' function in the 'SMATR' package version 3.4-3 (Warton et al., 2012). Results for RMA regressions are presented in the Appendix (Table A2). The conclusions from these analyses were qualitatively identical to those obtained from OLS regressions and are not discussed further.

The static exponents computed for each of the 13 species using OLS regressions were then entered into a phylogenetic regression to examine the extent to which living on land versus in an aquatic environment contributed to an increase in static exponent. To do so we applied a phylogenetic generalised least squares regression (PGLS) using 'APE' version 3.5 (Paradis et al., 2004) and the phylogeny developed by Ord and Cooke (2016; also shown in Figure 1). The environment occupied by species was coded as 0 for aquatic/amphibious and 1 for terrestrial species. Phylogenetic covariance was incorporated into the regression using λ (Pagel, 1999). Note that the phylogenetic regression not only controls for the phylogenetic relationships among species but also the clustering of terrestrial species in a single monophyletic clade (Figure 1).

Phylogenetic generalised least squares regressions were also used to compute estimates of the evolutionary exponent and elevation. These analyses included an additional five aquatic species that had too few sampled individuals to reliably compute static allometries (see above; Table A1; Figure 1), but still provided a reasonable approximation of the likely species mean value. To evaluate the extent to which the evolutionary exponent and elevation might differ between aquatic and terrestrial species, we applied a second set of analyses with the addition of environment coded as 0 or 1 (aquatic or terrestrial respectively).

3 | RESULTS

3.1 | Static allometry

Across all species, male head crest and dorsal fins had static exponents that approached 1.5 (mean static exponent across all species, with 95% confidence interval range (CI): head crest, 1.36, 1.24–1.47; dorsal fin, 1.32, 95% CI 1.18–1.46; see also Table A2), whereas static exponents for male ventral fins—that were unlikely to be targets of sexual selection—were consistently found to have the shallowest exponents (ventral fin: 1.18, 95% CI 1.12–1.24; see also Figure A3a). Similarly, all female dorsal and ventral fin static exponents were equally low (dorsal fin: 1.16, 95% CI 1.03–1.29; ventral fin: 1.02, 95% CI 0.86–1.17; see also Figure A3b). Female head crest exponents were not calculated as they were either absent or miniscule in size and effectively absent.

Static exponents for male head crests did not differ statistically between aquatic and terrestrial species (Table 1a), but there

TABLE 1 Changes in static exponents between aquatic and terrestrial species estimated for ornament and non-ornament morphological structures exhibited by (a) male and (b) female blenny fish. Phylogenetic ANOVAs (PGLS) were implemented using Pagel's λ, which is reported here with the range of values within two AIC units of the maximum likelihood estimate. Intercept values correspond to the phylogenetic mean of static exponents across aquatic species, while the variable 'environment' reflects the mean difference in static exponents in terrestrial species relative to those aquatic species

Sex, morphological characteristic	λ (lower, upper AIC credibility range)	Parameter (±1 *SE*)	*t*	*p*
(a) Males				
Head crest	0.00 (0.00, 0.70)			
Intercept (aquatic species)		1.22 (0.11)	10.83	<0.001
Environment (difference in terrestrial species)		0.27 (0.16)	1.72	0.115
Dorsal fin	0.00 (0.00, 0.40)			
Intercept (aquatic species)		1.14 (0.06)	19.29	<0.001
Environment (difference in terrestrial species)		0.41 (0.09)	4.67	0.001
Ventral fin	0.00 (0.00, 0.95)			
Intercept (aquatic species)		1.22 (0.04)	29.57	<0.001
Environment (difference in terrestrial species)		−0.07 (0.06)	−1.14	0.279
(b) Females				
Dorsal fin	0.70 (0.00, 0.90)			
Intercept (aquatic species)		1.00 (0.14)	7.17	<0.001
Environment (difference in terrestrial species)		0.38 (0.22)	1.71	0.119
Ventral fin	0.90 (0.30, 1.00)			
Intercept (aquatic species)		0.94 (0.20)	4.66	<0.001
Environment (difference in terrestrial species)		0.01 (0.33)	0.03	0.979

was a general trend for steeper estimates of head crest exponents in terrestrial species compared to aquatic species (Figure 2b, inset). Static exponents for male dorsal fins were significantly greater among terrestrial species than aquatic species (Table 1a; Figure 2c). Furthermore, only the terrestrial species were computed to have static male dorsal fin exponents consistently equal to or above 1.5. Static exponents for male ventral fins did not differ between aquatic and terrestrial species (Table 1a; Figure 2e).

There was no statistical difference in static exponents for female dorsal or ventral fins between aquatic and terrestrial species (Table 1b; Figure 2d,f), but dorsal fins did exhibit a tendency towards steeper values in terrestrial species (Figure 2d, inset).

3.2 | Evolutionary allometry

Male evolutionary exponents were steeper than those of females (Figure 3). Only the male dorsal fin had an evolutionary exponent that converged on 1.5 (1.47, 95% CI 1.10–1.84). In contrast, the evolutionary exponent for the male head crest was effectively isometric (1.05, 95% CI 0.86–1.24), and much lower than the male ventral fin (1.23, 95% CI 1.13–1.34). Evolutionary exponents were not found to vary between aquatic and terrestrial species (interaction terms were initially considered in analyses but were not found to contribute statistical effects and were subsequently dropped from all models; Table 2).

Evolutionary elevations—the intercepts of the allometry trend lines—were not found to differ between aquatic and terrestrial species for male head crest or ventral fin (Table 2a; Figure 3a,d), but were significantly higher for terrestrial species for male dorsal fin size (Table 2a; Figure 3b).

The evolutionary exponent for female dorsal fin was <1.5 (1.18, 95% CI 0.95–1.40), as was the female ventral fin evolutionary exponent (1.11, 95% C 0.89–1.33; Table 2; Figure 3) and did not differ among aquatic and terrestrial species (Table 2a,b; NB: interaction terms were not statistically significant and dropped from models). Evolutionary elevations for female dorsal fins were also statistically indistinguishable between aquatic and terrestrial species (Table 2b; Figure 3c), but terrestrial female species were found to have slightly higher ventral fin evolutionary elevation (Table 2b; Figure 3e).

4 | DISCUSSION

Our study indicates that the study of allometry—and specifically static allometry—can offer useful insights into the selection pressures that might be operating on morphological structures within species, but with important caveats. Within species of blenny, all male structures used in courting females exhibited static exponents within or close to the expected range for structures targeted by sexual selection (Kodric-Brown et al., 2006). However, non-sexually selected morphological characteristics can also exhibit positive static allometries (Voje, 2016), so any inference of sexual selection must be made with appropriate benchmarking (Bonduriansky, 2007). For example, static exponents of putative sexually selected characteristics

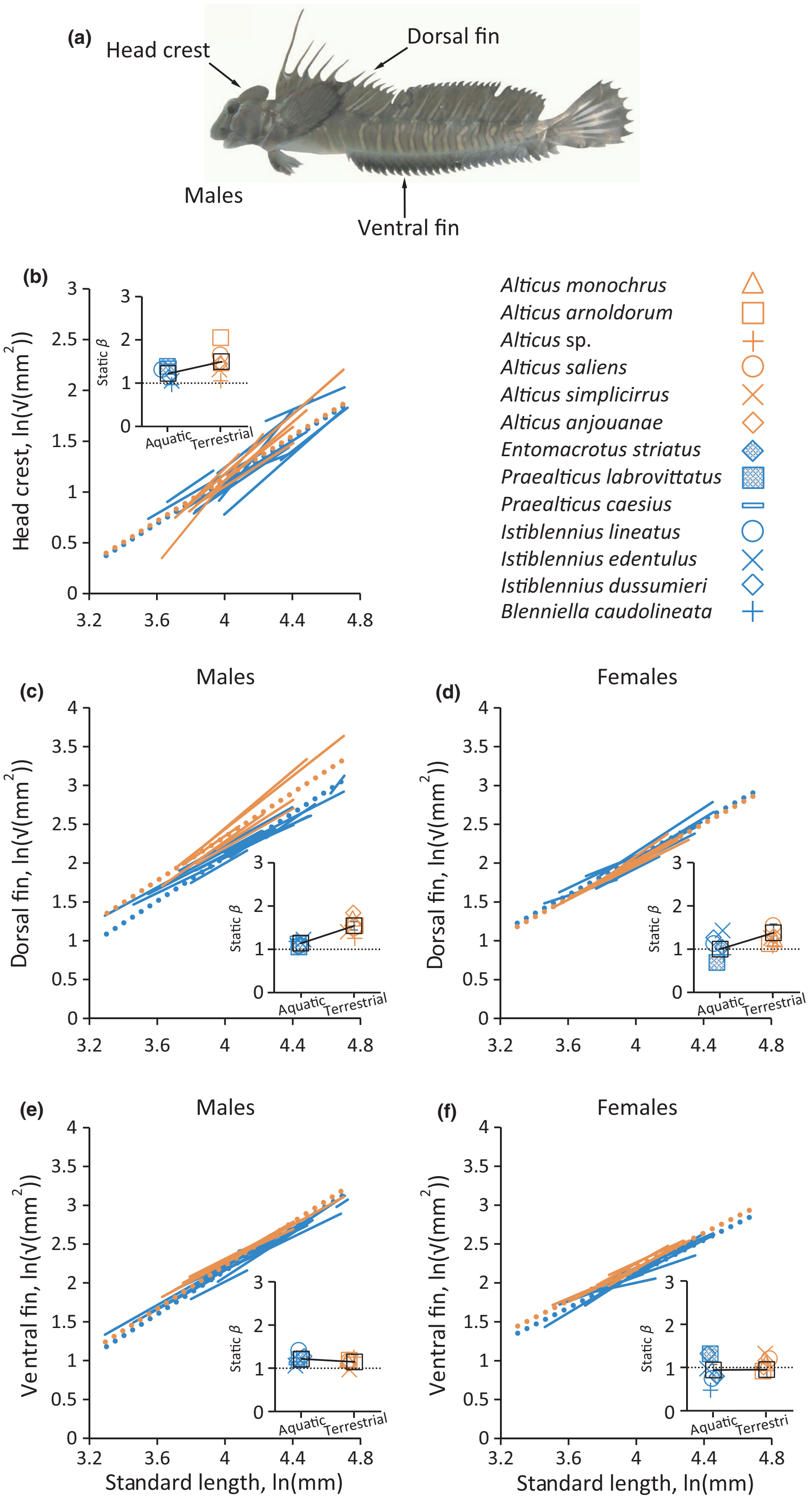

FIGURE 2 Static allometries of ornament and non-ornament morphological structures in blennies. Shown in (a) is a representative male *Alticus monochrus*, a terrestrial blenny from Mauritius, that illustrates the prominent head crest and exaggerated dorsal fin. The remaining panels show the estimated static allometries (solid lines) for each species for the (b) male head crest, (c) male dorsal fins, (d) female dorsal fins, (e) male ventral fins and (f) female ventral fins. The evolutionary allometries (dotted lines) are also illustrated and correspond to those depicted in Figure 3. Aquatic/amphibious species are shown in blue, while terrestrial species are shown in orange. Inset plots show the computed static exponents (β) compared between aquatic/amphibious and terrestrial species and relative to isometry (dashed line)

should be steeper in the sex for which ornamentation is expected to convey fitness benefits (here, male blennies) and steeper compared to static exponents of morphology unlikely to be targets of sexual selection (here, male ventral fins). In blennies, females lacked a prominent head crest altogether, which was consistent with the exclusive function of the head crest for courtship in males, and static exponents of dorsal fin size were generally steeper in males than females. Furthermore, the static exponents of both the head crest

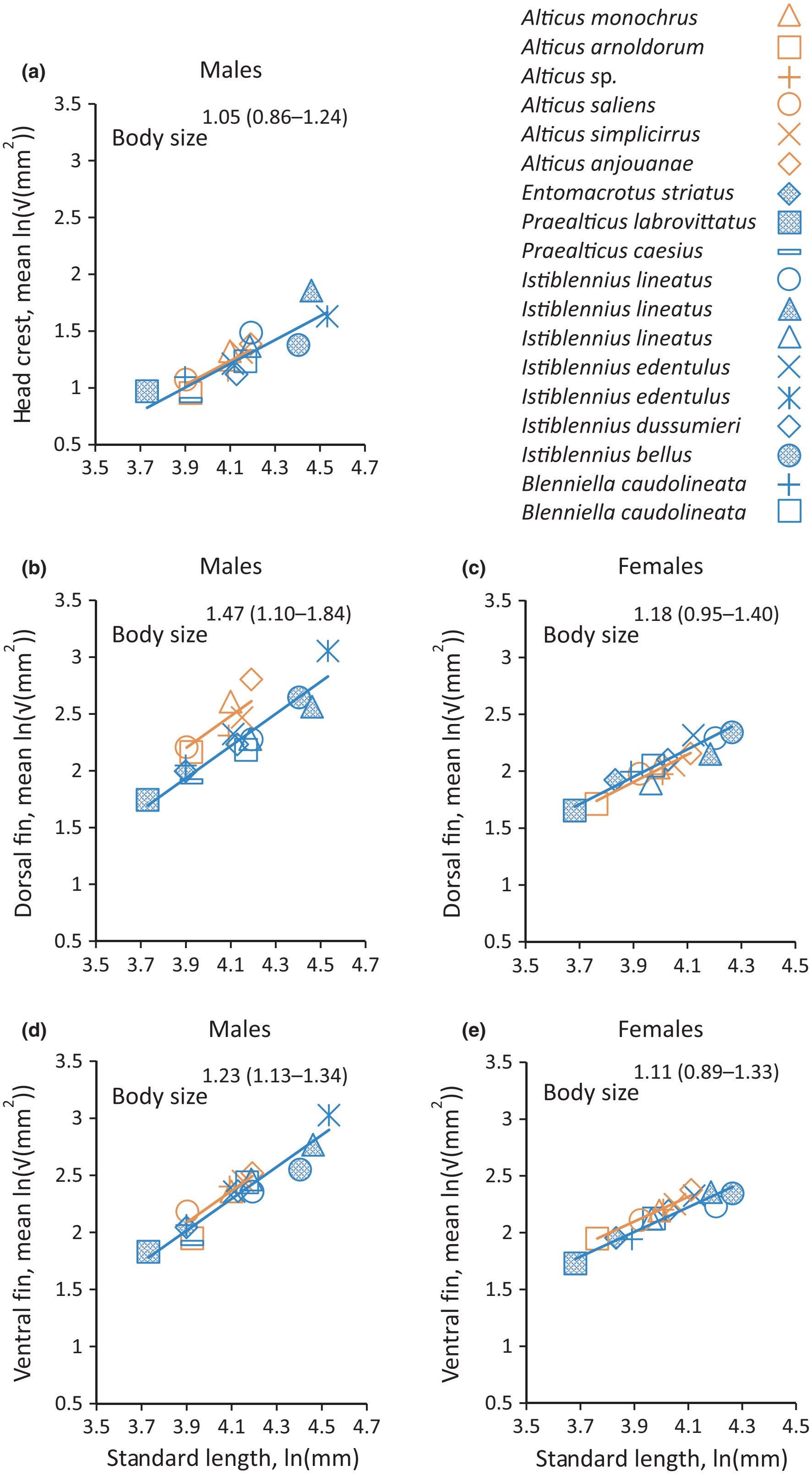

FIGURE 3 Evolutionary allometries of ornament and non-ornament morphological structures in blennies. Symbols represent species mean values and are given for (a) male head crest, (b) male dorsal fins, (c) female dorsal fins, (d) male ventral fins and (e) female ventral fins. The evolutionary exponents are also given (with 95% confidence limit) as computed by a phylogenetic generalised least squares regression across all species (irrespective of environment). Aquatic/amphibious species are shown in blue, while terrestrial species are shown in orange

and dorsal fin of males were steeper than those of the ventral fin, a control region that would not normally be visible to females during courtship. These findings show that selection operating on the size of condition-dependent morphologies can lead to changes in static exponents in nature (see also Morgans et al., 2014), despite experimental studies in laboratory settings implying that static elevations are more (or exclusively) responsive to selection than static exponents (e.g. Egset et al., 2012; Tobler & Nijhout, 2010; Tsuboi et al., 2016). Nevertheless, the magnitude of static exponents computed for male sexual characteristics in blennies was clearly not the

TABLE 2 Differences in the evolutionary allometry exponent (β) and elevation (α) between aquatic and terrestrial species estimated for ornament and non-ornament morphological structures exhibited by (a) male and (b) female blenny fish. See Table 1 legend for other details. Phylogenetic regressions (PGLS) were implemented using Pagel's λ, which is reported here with the range of values within two AIC units of the maximum likelihood estimate. Intercept values indicate the evolutionary allometric elevation for aquatic species, the slope value of standard length (body size) is the evolutionary allometric exponent across all species, and the variable 'environment' indicates the mean difference in elevation across terrestrial species relative to aquatic species. All models initially included an interaction term between standard length and environment that tested for a difference in the evolutionary exponent between aquatics and terrestrial species, which was found to be indistinguishable from zero in all cases and subsequently dropped

Sex, morphological characteristic	λ (lower, upper AIC credibility range)	Parameter ($\pm$1 *SE*)	*t*	*p*
(a) Males				
Head crest	0.75 (0.00, 0.95)			
Intercept (α, aquatic species)		−3.08 (0.71)	−4.34	0.001
Standard length (β, all species)		1.05 (0.17)	6.06	<0.001
Environment (α, difference in terrestrial species)		0.02 (0.11)	0.18	0.862
Dorsal fin	0.00 (0.00, 0.70)			
Intercept (α, aquatic species)		−3.59 (0.60)	−6.03	<0.001
Standard length (β, all species)		1.42 (0.14)	9.87	<0.001
Environment (α, difference in terrestrial species)		0.26 (0.06)	4.24	0.001
Ventral fin	0.00 (0.00, 0.70)			
Intercept (α, aquatic species)		−3.42 (0.44)	−7.72	<0.001
Standard length (β, all species)		1.40 (0.11)	13.04	<0.001
Environment (α, difference in terrestrial species)		0.07 (0.05)	1.50	0.155
(b) Females				
Dorsal fin	0.70 (0.00, 0.95)			
Intercept (α, aquatic species)		−2.75 (0.48)	−5.73	<0.001
Standard length (β, all species)		1.21 (0.12)	9.89	<0.001
Environment (α, difference in terrestrial species)		−0.05 (0.08)	−0.62	0.543
Ventral fin	0.00 (0.00, 0.55)			
Intercept (α, aquatic species)		−2.24 (0.34)	−6.51	<0.001
Standard length (β, all species)		1.09 (0.09)	12.72	<0.001
Environment (α, difference in terrestrial species)		0.09 (0.03)	3.36	0.005

sole product of sexual selection, and evolutionary allometry across species cannot be interpreted through a simple extrapolation of processes expected to be operating on static allometries within those species.

The steepest static exponents generally belonged to males from terrestrial species, and especially so for the dorsal fin (Table 1a; Figure 2c). This was consistent with the expectation that the dorsal fin probably has a greater impact on swimming performance than the head crest (see Introduction). The size of the dorsal fin should therefore be subjected to a high level of stabilising selection in aquatic species. The tendency for natural selection to reduce the observed static exponents of sexually selected characteristics in this way is likely to be common in many animals. For example, large sexual ornaments have been frequently linked to reduced locomotor abilities and increased predation risk (guppy fish: Egset et al., 2011; rhinoceros beetles: Kojima et al., 2014; lizards: Klomp et al., 2016). Selection trade-offs might consequently account for many of the irregularities reported in the literature on the scaling patterns of ornament allometries (instances of isometric and negative static exponents: Bonduriansky, 2007; Bonduriansky & Day, 2003; Voje, 2016). Therefore, the utility of static allometry for inferring the presence and magnitude of sexual selection will not only depend on appropriate within species benchmarking (previous paragraph), but accounting for the presence and magnitude of potential opposing natural selection as well.

Interpretations of evolutionary allometry remain problematic. For example, the positive static exponents within species did not translate into a positive evolutionary exponent across species for the head crest, but did so for the dorsal fin. Yet even in the case of the dorsal fin, the large differences in static exponents between terrestrial and aquatic species failed to diverge the evolutionary exponents of these two groups. Instead, it appears the steeper static exponents of terrestrial blennies has increased the overall mean size of the dorsal fin, with no concomitant changes in mean body size. The result has been a shift in the elevation of the evolutionary allometry of dorsal fin size, not its exponent. The few previous investigations that have examined static and evolutionary allometric exponents in the same system have similarly reported a mixed relationship between the two levels of allometry (e.g. Voje & Hansen, 2013; Voje et al., 2014). The standard interpretation has been that the evolutionary exponent will tend to match the mean of the static exponents among species, unless selection for larger body size causes additional forms of selection to operate on ornament size (Lande, 1979; Tidiere et al., 2017; Voje et al., 2014). In our study, it appears the effect of opposing natural selection operating on aquatic blennies did not influence evolutionary exponents in the same way as it did within-species static exponents, with a particularly noticeable difference observed for the head crest (mean static exponent among species = 1.36 vs. an evolutionary exponent = 1.05). The question remains, then, of what the evolutionary exponent functionally reflects, but our data suggest it is not a simple translation of factors operating upon static exponents.

5 | CONCLUSIONS

There has been recent debate over the extent to which allometric scaling parameters of ornament (or weapon) size can be interpreted in the context of sexual selection (Bonduriansky, 2007; Voje, 2016). In general, we caution against making direct comparisons of static exponents among closely related species in order to gauge the relative strength of sexual selection experienced by those species. In many cases, static exponents will reflect a trade-off between positive sexual selection and negative natural selection on ornament size, with a balance that likely varies among species (e.g. as a function of habitat). Nevertheless, interpretations can be made when static exponents are compared between the sexes for a dimorphic characteristic and in relation to appropriate control regions of morphology that can be reasonably expected not to be the target of sexual selection (Bonduriansky, 2007). Such benchmark comparisons can in turn help qualify the interpretation of differences in static exponents among closely related species as well (e.g. this study). Understanding the potential cause of species differences in static exponents would be further informed by correlations across those species with some index of sexual selection (e.g. sex ratios; Morgans et al., 2014) or measure of a potential confounding variable (e.g. locomotor performance or predation risk). The study of static allometry would be especially useful as a tool for directing future empirical study and experimentation (e.g. to determine whether or in which species to measure female preferences, or the condition dependence of seemingly costly structures). However, the manner in which sexual selection is expected to produce positive static allometries in sexual characteristics (Green, 1992; Kodric-Brown et al., 2006; Petrie, 1988) does not seem to readily translate to evolutionary allometry. Using evolutionary allometry alone to draw any conclusions on the presence of sexual selection, or its magnitude, remains questionable.

ACKNOWLEDGEMENTS

This work was supported by an Australian Government Research Training Program Scholarship to T.C.S., and a Discovery Project grant (DP120100356) from the Australian Research Council to T.J.O. The work followed protocols described in the University of New South Wales Animal Care and Ethics Committee applications 11/36B and 13/21B approved on 10 March 2011, and 4 March 2013 respectively. Collection of specimens was conducted under permits issued by: the Cook Island Research Committee, the Office of the Prime Minister (#27/12); Protocole D'Accueil (10/10/2013), Moorea and Tahiti, French Polynesia; Secretary to Cabinet and Head of the Civil Service, Prime Minister's Office, Mauritius (permission granted on 27/09/2012); and Seychelles Bureau of Standards (#A0157). We wish to thank Georgina Cooke, Sammy Goyen and Courtney Morgans for assistance in the field, and Russel Bonduriansky for discussions on allometry.

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHORS' CONTRIBUTIONS

T.C.S. and T.J.O. conceived the study and collected the data; T.C.S. analysed the data; T.C.S. and T.J.O. wrote the paper.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.70rxwdbzp (Summers & Ord, 2021).

ORCID

Thomas C. Summers https://orcid.org/0000-0002-8743-1545
Terry J. Ord https://orcid.org/0000-0002-2608-2150

REFERENCES

Aizawa, M. (2002). Blenniidae. In T. Nakabo (Ed.), *Fishes of Japan with pictorial keys to the species* (2nd ed., pp. 1090–1119). Tokai University Press.

Andersson, M. (1982). Sexual selection, natural selection and quality advertisement. *Biological Journal of the Linnean Society*, *17*, 375–393. https://doi.org/10.1111/j.1095-8312.1982.tb02028.x

Barbosa, A., & Moller, A. P. (1999). Aerodynamic costs of long tails in male barn swallows *Hirundo rustica* and the evolution of sexual size dimorphism. *Behavioural Ecology*, *10*, 128–135. https://doi.org/10.1093/beheco/10.2.128

Basolo, A. L., & Alcaraz, G. (2003). The turn of the sword: Length increases male swimming costs in swordtails. *Proceedings of the Royal Society of London B: Biological Sciences*, *270*, 1631–1636. https://doi.org/10.1098/rspb.2003.2388

Bhikajee, M., & Green, J. M. (2002). Behaviour and habitat of the Indian Ocean amphibious blenny, *Alticus monochrus*. *African Zoology*, *37*, 221–230.

Bhikajee, M., Green, J. M., & Dunbrack, R. (2006). Life history characteristics of *Alticus monochrus*, a supratidal blenny of the southern Indian Ocean. *African Zoology*, *41*, 1–7.

Bolstad, G. H., Cassara, J. A., Marquez, E., Hansen, T. F., van der Linde, K., Houle, D., & Pelabon, C. (2015). Complex constraints on allometry revealed by artificial selection on the wing of *Drosophila melanogaster*. *Proceedings of the National Academy of Sciences of the United States of America*, *112*, 13284–13289.

Bonduriansky, R. (2007). Sexual selection and allometry: A critical reappraisal of the evidence and ideas. *Evolution*, *61*, 838–849. https://doi.org/10.1111/j.1558-5646.2007.00081.x

Bonduriansky, R., & Day, T. (2003). The evolution of static allometry in sexually selected traits. *Evolution*, *57*, 2450–2458. https://doi.org/10.1111/j.0014-3820.2003.tb01490.x

Borazjani, I. (2013). The functional role of caudal and anal/dorsal fins during the C-start of a bluegill sunfish. *Journal of Experimental Biology*, *216*, 1658–1669. https://doi.org/10.1242/jeb.079434

Cheverud, J. M. (1982). Relationships among ontogenetic, static, and evolutionary allometry. *American Journal of Physical Anthropology*, *59*, 139–149. https://doi.org/10.1002/ajpa.1330590204

Clutton-Brock, T. H., Albon, S. D., & Harvey, P. H. (1980). Antlers, body size and breeding group size in the Cervidae. *Nature*, *285*, 565–567. https://doi.org/10.1038/285565a0

Cock, A. G. (1966). Genetical aspects of metrical growth and form in animals. *The Quarterly Review of Biology*, *41*, 131–190. https://doi.org/10.1086/404940

Drucker, E. G., & Lauder, G. V. (2001). Locomotor function of the dorsal fin in teleost fishes: Experimental analysis of wake forces in sunfish. *The Journal of Experimental Biology*, *204*, 2943–2958. https://doi.org/10.1242/jeb.204.17.2943

Eberhard, W. G., Rodriguez, R. L., Huber, B. A., Speck, B., Miller, H., Buzatto, B. A., & Machado, G. (2018). Sexual selection and static allometry: The importance of function. *Quarterly Review of Biology*, *93*, 207–250. https://doi.org/10.1086/699410

Egset, C. K., Bolstad, G. H., Rosenqvist, G., Endler, J. A., & Pelabon, C. (2011). Geographical variation in allometry in the guppy (*Poecilia reticulata*). *Journal of Evolutionary Biology*, *24*, 2631–2638. https://doi.org/10.1111/j.1420-9101.2011.02387.x

Egset, C. K., Hansen, T. F., Le Rouzic, A., Bolstad, G. H., Rosenqvist, G., & Pelabon, C. (2012). Artificial selection on allometry: Change in elevation but not slope. *Journal of Evolutionary Biology*, *25*, 938–948. https://doi.org/10.1111/j.1420-9101.2012.02487.x

Gould, S. J. (1966). Allometry and size in ontogeny and phylogeny. *Biological Reviews of the Cambridge Philosophical Society*, *41*, 587–638. https://doi.org/10.1111/j.1469-185X.1966.tb01624.x

Grafen, A. (1990). Biological signals as handicaps. *Journal of Theoretical Biology*, *144*, 517–546. https://doi.org/10.1016/S0022-5193(05)80088-8

Green, A. J. (1992). Positive allometry is likely with mate choice, competitive display and other functions. *Animal Behaviour*, *43*, 170–172. https://doi.org/10.1016/S0003-3472(05)80086-7

Green, A. J. (2000). The scaling and selection of sexually dimorphic characters: An example using the marbled teal. *Journal of Avian Biology*, *31*, 345–350. https://doi.org/10.1034/j.1600-048X.2000.310310.x

Harrell, F. E. (2017). *rms: Regression modelling strategies*. R package version 5.1-0. Retrieved from https://CRAN.R-project.org/package=rms

Hosken, D. J., Minder, A. M., & Ward, P. I. (2005). Male genital allometry in Scathophagidae (Diptera). *Evolutionary Ecology*, *19*, 501–515. https://doi.org/10.1007/s10682-005-1023-z

Hsieh, S. T. (2010). A locomotor innovation enables water-land transition in a marine fish. *PLoS ONE*, *5*, e11197. https://doi.org/10.1371/journal.pone.0011197

Huxley, J. S. (1924). Constant differential growth-ratios and their significance. *Nature*, *114*, 895–896. https://doi.org/10.1038/114895a0

Huxley, J. S. (1932). *Problems of relative growth*. L. MacVeagh.

Karino, K., Ishiwatari, T., Kudo, H., & Sato, A. (2011). Female mate preference for a costly ornament in male guppies. *Behavioral Ecology and Sociobiology*, *65*, 1305–1315. https://doi.org/10.1007/s00265-011-1144-z

Kawano, K. (2000). Genera and allometry in the stag beetle family Lucanidae, Coleoptera. *Annals of the Entomological Society of America*, *93*, 198–207. https://doi.org/10.1603/0013-8746(2000)093[0198:GAAITS]2.0.CO;2

Klomp, D. A., Ord, T. J., Das, I., Diesmos, A., Ahmad, N., & Stuart-Fox, D. (2016). Ornament size and colour as alternative strategies for effective communication in gliding lizards. *Journal of Evolutionary Biology*, *29*, 1689–1700. https://doi.org/10.1111/jeb.12908

Kodric-Brown, A., Sibly, R. M., & Brown, J. H. (2006). The allometry of ornaments and weapons. *Proceedings of the National Academy of Sciences of the United States of America*, *103*, 8733–8738. https://doi.org/10.1073/pnas.0602994103

Kojima, W., Sugiura, S., Makihara, H., Ishikawa, Y., & Takanashi, T. (2014). Rhinoceros beetles suffer male-biased predation by mammalian and avian predators. *Zoological Society*, *31*, 109–115. https://doi.org/10.2108/zsj.31.109

Kotiaho, J. S. (2001). Costs of sexual traits: A mismatch between theoretical considerations and empirical evidence. *Biological Reviews*, *76*, 365–376. https://doi.org/10.1017/S1464793101005711

Kotiaho, J. S., Alatalo, R. V., Mappes, J., Nielsen, M. G., Parri, S., & Rivero, A. (1998). Energetic costs of size and sexual signalling in a wolf spider. *Proceedings of the Royal Society of London B: Biological Sciences*, *265*, 2203–2209. https://doi.org/10.1098/rspb.1998.0560

Lande, R. (1979). Quantitative genetic analysis of multivariate evolution, applied to brain: Body size allometry. *Evolution*, *33*, 402–416. https://doi.org/10.1111/j.1558-5646.1979.tb04694.x

Laporte, M., Claude, J., Berrebi, P., Perret, P., & Magnan, P. (2016). Shape plasticity in response to water velocity in the freshwater blenny *Salaria fluviatilis*. *Journal of Fish Biology*, *88*, 1191–1203.

Lemaitre, J. F., Vanpe, C., Plard, F., & Gaillard, J. M. (2014). The allometry between secondary sexual traits and body size is nonlinear among cervids. *Biology Letters*, *10*, 20130869. https://doi.org/10.1098/rsbl.2013.0869

Martin, K. L. M. (1995). Time and tide wait for no fish: Intertidal fishes out of water. *Environmental Biology of Fishes*, *44*, 165–181. https://doi.org/10.1007/BF00005914

Martin, K. L. M., & Lighton, J. R. B. (1989). Aerial CO_2 and O_2 exchange during terrestrial activity in an amphibious fish, *Alticus kirki* (Blenniidae). *Copeia*, *1989*, 723–727. https://doi.org/10.2307/1445501

McCullough, E. L., Ledger, K. J., O'Brian, D. M., & Emlen, D. J. (2015). Variation in the allometry of exaggerated rhinoceros beetle horns. *Animal Behaviour*, *109*, 133–140. https://doi.org/10.1016/j.anbehav.2015.08.013

Moller, A. P. (1996). The cost of secondary sexual characters and the evolution of cost-reducing traits. *Ibis*, *138*, 112–119. https://doi.org/10.1111/j.1474-919X.1996.tb04317.x

Morgans, C. L., Cooke, G. M., & Ord, T. J. (2014). How populations differentiate despite gene flow: Sexual and natural selection drive phenotypic divergence within a land fish, the Pacific leaping blenny. *BMC Evolutionary Biology*, *14*, 97. https://doi.org/10.1186/1471-2148-14-97

Ord, T. J., & Cooke, G. M. (2016). Repeated evolution of amphibious behaviour in fish and its implications for the colonization of novel environments. *Evolution*, *70*, 1747–1759.

Ord, T. J., & Hsieh, S. T. (2011). A highly social, land-dwelling fish defends territories in a constantly fluctuating environment. *Ethology*, *117*, 918–927. https://doi.org/10.1111/j.1439-0310.2011.01949.x

Ord, T. J., Summers, T. C., Noble, M. N., & Fulton, C. J. (2017). Ecological release from aquatic predation is associated with the emergence of marine blenny fishes onto land. *The American Naturalist*, *189*, 570–579. https://doi.org/10.1086/691155

Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, *401*, 877–884. https://doi.org/10.1038/44766

Paradis, E., Claude, J., & Strimmer, K. (2004). APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, *20*, 289–290. https://doi.org/10.1093/bioinformatics/btg412

Pelabon, C., Bolstad, G. H., Egset, C. K., Cheverud, J. M., Pavlicev, M., & Rosenqvist, G. (2013). On the relationship between ontogenetic and static allometry. *The American Naturalist*, *181*, 195–212. https://doi.org/10.1086/668820

Petrie, M. (1988). Intraspecific variation in structures that display competitive ability: Large animals invest relatively more. *Animal Behaviour*, *36*, 1174–1179.

Plard, F., Bonenfant, C., & Gaillard, J. M. (2011). Revisiting the allometry of antlers among deer species: Male–male sexual competition as a driver. *Oikos*, *120*, 601–606. https://doi.org/10.1111/j.1600-0706.2010.18934.x

Rasband, W. S. (1997–2016). *ImageJ*. U. S. National Institutes of Health. Retrieved from https://imagej.nih.gov/ij/

Robitzch, V., Schröder, M., & Ahnelt, H. (2021). Morphometrics reveal inter- and intraspecific sexual dimorphisms in two Hawaiian *Schindleria*, the long dorsal finned *S. praematura* and the short dorsal finned *S. pietschmanni*. *Zoologischer Anzeiger*, *292*, 197–206. https://doi.org/10.1016/j.jcz.2021.04.002

Shimizu, N., Sakai, Y., Hashimoto, H., & Gushima, K. (2006). Terrestrial reproduction by the air-breathing fish *Andamia tetradactyla* (Pisces; Blenniidae) on supralittoral reefs. *Journal of Zoology*, *269*, 357–364. https://doi.org/10.1111/j.1469-7998.2006.00113.x

Simmons, L. W., & Tomkins, J. L. (1996). Sexual selection and the allometry of earwig forceps. *Evolutionary Ecology*, *10*, 97–104. https://doi.org/10.1007/BF01239350

Standen, E. M., & Lauder, G. V. (2007). Hydrodynamic function of dorsal and anal fins in brook trout (*Salvelinus fontinalis*). *Journal of Experimental Biology*, *210*, 325–339.

Summers, T. C., & Ord, T. J. (2021). Data from: The stabilising impact of natural selection on the allometry of sexual ornaments: Fish that escape locomotor constraints exhibit extravagant ornamentation. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.70rxwdbzp

Swallow, J. G., Wilkinson, G. S., & Marden, J. H. (2000). Aerial performance of stalk-eyed flies that differ in eye span. *Journal of Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology*, *170*, 481–487. https://doi.org/10.1007/s003600000124

Tidiere, M., Lemaitre, J. F., Pelabon, C., Gimenez, O., & Gaillard, J. M. (2017). Evolutionary allometry reveals a shift in selection pressure on male horn size. *Journal of Evolutionary Biology*, *30*, 1826–1835. https://doi.org/10.1111/jeb.13142

Tobler, A., & Nijhout, H. F. (2010). Developmental constraints on the evolution of wing-body allometry in *Manduca sexta*. *Evolution and Development*, *12*, 592–600. https://doi.org/10.1111/j.1525-142X.2010.00444.x

Tomkins, J. L., LeBas, N. R., Witton, M. P., Martill, D. M., & Humphries, S. (2010). Positive allometry and the prehistory of sexual selection. *The American Naturalist*, *176*, 141–148. https://doi.org/10.1086/653001

Tomkins, J. L., & Simmons, L. W. (1996). Dimorphisms and fluctuating asymmetry in the forceps of male earwigs. *Journal of Evolutionary Biology*, *9*, 753–770. https://doi.org/10.1046/j.1420-9101.1996.9060753.x

Tsuboi, M., Kotrschal, A., Hayward, A., Buechel, S. D., Zidar, J., Lovlie, H., & Kolm, N. (2016). Evolution of the brain-body allometry in Lake Tanganyika cichlids. *Evolution*, *70*, 1559–1568.

Voje, K. L. (2016). Scaling of morphological characters across trait type, sex, and environment: A meta-analysis of static allometries. *The American Naturalist*, *187*, 89–98. https://doi.org/10.1086/684159

Voje, K. L., & Hansen, T. F. (2013). Evolution of static allometries: Adaptive change in allometric slopes of eye span in stalk eyed flies. *Evolution*, *67*, 453–467. https://doi.org/10.1111/j.1558-5646.2012.01777.x

Voje, K. L., Hansen, T. F., Egset, C. K., Bolstad, G. H., & Pelabon, C. (2014). Allometric constraints and the evolution of allometry. *Evolution*, *68*, 866–885. https://doi.org/10.1111/evo.12312

Warton, D. I., Duursma, R. A., Falster, D. S., & Taskinen, S. (2012). SMATR 3—An R package for estimation and inference about allometric lines. *Methods in Ecology and Evolution*, *3*, 257–259.

Webb, P. W. (2002). Control of posture, depth, and swimming trajectories of fishes. *Integrative and Comparative Biology*, *42*, 94–101.

Zahavi, A. (1975). Mate selection—A selection for a handicap. *Journal of Theoretical Biology*, *53*, 205–214. https://doi.org/10.1016/0022-5193(75)90111-3

Zahavi, A. (1977). The cost of honesty: Further remarks on the handicap principle. *Journal of Theoretical Biology*, *67*, 603–605. https://doi.org/10.1016/0022-5193(77)90061-3

Zuk, M., & Kolluru, G. R. (1998). Exploitation of sexual signals by predators and parasitoids. *The Quarterly Review of Biology*, *73*, 415–438. https://doi.org/10.1086/420412

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Summers, T. C., & Ord, T. J. (2022). The stabilising impact of natural selection on the allometry of sexual ornaments: Fish that escape locomotor constraints exhibit extravagant ornamentation. *Functional Ecology*, 36, 500–511. https://doi.org/10.1111/1365-2435.13968