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Female preference for super-sized male ornaments and its implications for the evolution of ornament allometry

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Abstract

It has been argued that disproportionately larger ornaments in bigger males—positive allometry—is the outcome of sexual selection operating on the size of condition dependent traits. We reviewed the literature and found a general lack of empirical testing of the assumed link between female preferences for large ornaments and a pattern of positive allometry in male ornamentation. We subsequently conducted a manipulative experiment by leveraging the unusual terrestrial fish, *Alticus* sp. cf. *simplicirrus*, on the island of Rarotonga. Males in this species present a prominent head crest to females during courtship, and the size of this head crest in the genus more broadly exhibits the classic pattern of positive allometry. We created realistic male models standardized in body size but differing in head crest size based on the most extreme allometric scaling recorded for the genus. This included a crest size well outside the observed range for the study population (super-sized). The stimuli were presented to free-living females in a manner that mimicked the spatial distribution of courting males. Females directed greater attention to the male stimulus that exhibited the super-sized crest, with little difference in attention direct to other size treatments. These data appear to be the only experimental evidence from the wild of a female preference function that has been implicitly assumed to drive selection that results in the evolution of positive allometry in male ornamentation.

Keywords Blenny · Mate choice · Ornament size · Super-normal stimulus · Visual signal

Introduction

Extravagant morphological features can evolve for a host of reasons, but a particularly powerful force is sexual selection (Andersson 1982; Jennions and Petrie 1997; Andersson and Simmons 2006; Kraaijeveld et al. 2011). For example, some of the most elaborate morphological features are male ornaments that are assessed by females when choosing among prospective mates (e.g., Petrie et al. 1991; Girard et al. 2011; Scholeset al. 2017). Although ornaments come in a variety of forms, the apparent size of the ornament seems to be

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especially useful for evaluating mates, with those males possessing the largest ornaments generally thought to mate with the most females (e.g., Brodsky 1988; Andersson 1992, 1994; Pryke et al. 2001; Giacomello and Rasotto 2005; Kleven et al. 2006). There are also a large proportion of experimental studies reporting female preferences for enlarged male secondary sexual traits (i.e., structures used in reproduction that are not genitalia; reviewed by this study). Males themselves can also assess the size of exaggerated ornamental structures in other males to provide additional cues on a rival's condition and potential fighting ability (e.g., male eye-span in *Diopsidae* flies—Panhuis and Wilkinson 1999; the size of conspicuous dewlaps in male *Anolis* lizards—Vanhooydonck et al. 2005; Lailvaux and Irschick 2007).

The size of secondary sexual traits, such as ornaments (or even weapons), are often (but not always) costly to produce and serve as important indicators of individual 'quality' (Andersson 1982; Grafen 1990; Moller 1996; Kotiaho et al. 1998; Kotiaho 2001; Contreras-Garduno et al. 2008; Polnaszek and Stephens 2014). Furthermore, larger males are often better able to manage the physiological costs associated with developing much larger ornaments than smaller males (e.g., Petrie 1988; Masello and Quillfeldt 2003; Rogers et al. 2008; Somjee et al. 2021; reviewed by Nur and Hasson 1984; Rowe and Houle 1996; Johnstone et al. 2009; Somjee 2021). Based on this phenomenon, it has been argued that the size of ornaments should exhibit a particular scaling relationship with body size when compared across males within the same population (Green 1992; Petrie 1992; Bonduriansky and Day 2003; Somjee 2021). Specifically, this allometric scaling should result in a power function with a positive exponent (i.e., X^b where $b > 1$). That is, as males become larger in a population, there should be a disproportionate increase in the size of the ornaments developed (Kodric-Brown et al. 2006). This has in turn lead to the argument that the extent to which an exponent exceeds 1 (i.e., a linear or proportional increase in ornament size with body size) should reflect the extent to which ornaments are driven by female preferences for increasingly larger ornaments (Green 1992, 2000; Petrie 1992).

As a result, allometric analyses have begun to be used by investigators to indirectly assess the presence or even strength of sexual selection operating on extravagant morphological features (e.g., Tomkins et al. 2010; Ord and Hsieh 2011). For example, ornaments (as well as weapons) have been shown to commonly exhibit exponents greater than 1 (e.g., Echelle et al. 1978; Kawano 2000; Hone et al. 2016), but particularly exponents between 1.5–2.5 (e.g., Petrie 1988; Green 1992; Kodric-Brown et al. 2006; Outomuro and Cordero-Rivera 2012; Voje and Hansen 2013). Indices of the strength of sexual selection have also been found to correlate positively with the allometric exponents of ornaments across populations (eg., Baker and Wilkinson 2001; Voje and Hansen 2013; Morgans et al. 2014). Furthermore, experimental evolution studies have successfully induced positive evolutionary changes in allometric exponents under targeted directional selection (e.g., Tobler and Nijhout 2010; Pavlicev et al. 2011; Bolstad et al. 2015). All of this lends support to the utility of allometry analysis for the study of putative sexually selected structures.

However, despite the renewed interest in the empirical investigation of allometry theory, few studies have investigated how the assessment of sexual morphologies by prospective mates (or rivals) might contribute towards the variation observed in allometric scaling patterns. There are many studies that have sought to experimentally determine how females (and sometimes males) respond to increases or decreases in the size of elaborate morphological structures. Specifically, our review of the literature uncovered 65 experimental studies testing conspecific responses to ornaments of different size (see Results; NB: our search was inclusive of weapons as well, but only one experimental study was found—see Methods). About a quarter of these examined responses over a range of ornament sizes (i.e.,

more than two), but only five studies sought to quantify female responses to structures outside the normal range (i.e., "super-normal" stimuli; NB: we could not find a manipulative study investigating male responses to differing sizes of rival ornaments). This is despite various models of sexual selection explicitly predicting 'hidden' preferences or sensory/cognitive biases for exaggerated sexual structures that do not currently occur in the male population (e.g., runaway sexual selection—Fisher 1958; reviewed by Kokko et al. 2002; Mead and Arnold 2004; pre-existing biases—Basolo 1990; Basolo 1995; see also Rowland 1989; Ryan and Rand 1993; Pryke and Andersson 2002; NB: larger morphological structures presumably make males more conspicuous to distant receivers in general as well: Charles and Ord 2012), and classic ethological experiments that show super-normal stimuli elicit exaggerated responses in the wild (Lorenz and Tinbergen 1938; Tinbergen and Perdeck 1950). More specifically, a study of how females respond to super-sized ornaments should provide the best framework to test the extent to which mate preferences induce disproportionate scaling of ornamental size within species. This is because it allows the assessment of the likely response of females to the evolution of exaggerated ornament sizes yet to evolve in males, and specifically whether disproportionate increases in ornament size would convey disproportionate reproductive advantages to those males.

In this study, we tested the response of conspecifics to altered male ornamental head crest size in an unusual land-dwelling blenny fish, *Alticus* sp. cf. *simplicirrus*, from the island of Rarotonga. Our objective was to provide an experimental manipulative test to uncover whether conspecifics respond proportionally to the size of a large sexual structure (the head crest) in a manner that would be expected to induce the evolution of a positive allometric scaling relationship. The selection of this particular species was deliberate. Previous studies have shown *Alticus* male head crests exhibit positive allometry (and with exponents typically greater than 1.5; Summers and Ord 2022) and that the magnitude of this allometry is positively correlated with indices of sexual selection across populations (Morgans et al. 2014). However, the species on Rarotonga is unusual because male head crests exhibit the lowest exponent so far measured ($b = 1.05$; Summers and Ord 2022), implying that the size of the head crest itself is constrained in some way (e.g., from predator-induced negative selection—Ord et al. 2017), but female preferences for exaggerated crest sizes should nevertheless be apparent. This because every other *Alticus* species so far examined exhibits positive head crest exponents indicative of strong sexual selection ($b = 1.31$–2.05; Summers and Ord, 2022; see also Ord and Hsieh 2011; Morgans et al. 2014), and that the courtship behaviour of males on Rarotonga remains centered on the head crest and its presentation to females through mating display (as with all other *Alticus* species; e.g., Bhikajee and Green 2002; Ord and Hsieh 2011). That is, females were expected to exhibit preferences for larger head crests, and the unusual isometry of this species offered an excellent opportunity to test a biologically realistic, but otherwise super-sized male head crest size. By doing so, we were able to evaluate the extent to which females have 'hidden' preferences for exaggerated head crests in males, which would in turn help explain the origin of positive allometries in other species.

Alticus generally spend their entire adult life living out of the water on rock outcrops in the supralittoral zone (Bhikajee and Green 2002; Ord and Cooke 2016; Ord et al. 2017). The fishes are highly agile on land (Hsieh 2010), but are otherwise restricted to the splash zone in order to remain moist to avoid desiccation and maintain adequate respiration through the gills and skin (Martin and Lighton 1989; Brown et al. 1991; Martin 1995). Behavioral observations of *Alticus* sp. cf. *simplicirrus,* coupled with detail empirical study of closely-related terrestrial blennies on other islands (Bhikajee and Green 2002; Ord and Hsieh 2011; Morgans and Ord 2013; Morgans et al. 2014), provide strong evidence that

males defend rock holes used as nests from rival males, while attempting to entice females to enter those holes to lay eggs (e.g., Bhikajee and Green 2002; Shimizu et al. 2006; Ord and Hsieh 2011).

To perform our experiment, we first used allometric data from a previous study (Summers and Ord 2022) for the same Rarotonga population and a closely related species on another island that exhibits the most extreme allometric scaling known for the male head crest in blenny fishes. This was used to benchmark what would be an average and super-normal (but still biologically realistic) male head crest size (Fig. 1b). We then created models representing these head crest sizes in addition to a control model lacking a head crest altogether. These models were then presented to free-living females and males in a manner that mimicked the natural context in which these fish typically viewed the head crest. Under the allometric model of sexually selected traits (e.g., Kodric-Brown et al. 2006), we predicted that females would attend most to the model with the super-normal sized head crest. More specifically, females should respond at a level that mirrors the extent to which the super-normal crest was disproportionately larger than the average sized head crest (and despite this size being well outside the natural range for this species on Rarotonga). This finding would support the underlying assumption that the positive power function exhibited between ornament size and male body size in most land-dwelling blennies (Summers and Ord 2022) has been driven by female preferences for increasingly larger ornaments.
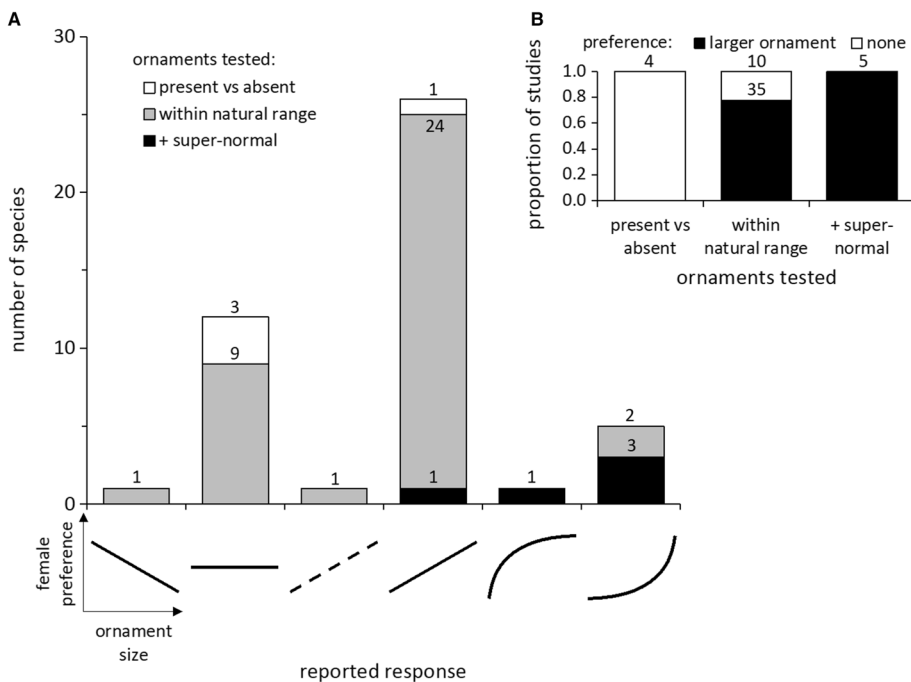

Fig. 1 Past studies investigating female responses to the manipulation of male sexual structures have **A** reported a range of different preferences for ornament size and **B** largely tested ornament sizes within the natural range of populations. Those handful of studies that included a super-sized ornament (i.e., a size outside the natural range) uniformly found female preferences for the super-sized structure, whereas those studies that tested ornament sizes within the natural range tended to report mixed preferences for larger ornaments

In addition, it is possible male blennies themselves use the size of the head crest in rivals to assess rival condition and potential fighting ability before challenging a male over a nest hole (sensu Small et al. 2009; Alonso et al. 2010; Tedore and Johnsen 2012). Past work on male assessment strategies in other animals suggests males increase their engagement with a rival as that rival exhibits increasingly larger condition-dependent traits (displays, weapons or other elaborate physical features) indicating an increased threat (Clutton-Brock et al. 1980; Ord and Evans 2003). However, this will tend to occur up to a point, after which males should start to disengage if a rival exhibits a trait or behavior perceived to reflect a male of likely superior fighting ability (see Clutton-Brock et al. 1980; Ord and Evans 2003). The model with the average sized head crest should therefore receive most of the attention from males, with little attention directed towards the control (no head crest) while the super-normal stimulus should generally be avoided by most males. In this case, the positive power function of the head crest may be generated, in part or entirely, by male-male competition through opponent assessment of rival condition conveyed by the head crest (i.e., males possessing disproportionately larger crest sizes are more intimidating and obtain greater fitness payoffs compared to males with 'average' sized crests).

Materials and methods

Review of past experimental studies

Prior to conducting the experimental manipulation, we first reviewed past experimental investigations of female and male responses to manipulations of ornament size in order to evaluate the context of past experimental study to the allometric theory of sexually selected traits (e.g., Kodric-Brown et al. 2006). Our goal was not to conduct a formal meta-analysis to test the hypothesis of whether or not females (or males) responded positively to increases in sexual structure size. Instead, our objective was to reveal the pattern of conspecific responses, how that might vary among studies, and whether that pattern of response reflected the manner in which studies have manipulated the size of ornaments or weapons. That is, it was the shape of conspecific responses—not their statistical effect size—that was of most interest, given its specific relevance for understanding how conspecific assessments of sexual structures might lead to the evolution of positive allometry. A secondary goal of our review was to highlight how frequently experimental manipulations of ornament or weapon size were conducted with explicit reference to the observed allometry of the structure being manipulated. As we have already revealed in the Introduction, there appears to be a general lack of experimental study of conspecific responses to sexual structures for which the allometric scaling pattern has been quantified. Details on the methods and criteria used to identify studies are provided in the online Supporting Information, as well as a detailed description of each study reviewed (Tables S1 and S2).

Experimental manipulation of ornament size in a land blenny

Our experimental work took place on the South-Pacific island of Rarotonga at Avana Point and the adjacent island of Motutapu (~ 150 m from Avana Point) near the locality of Muri. It was conducted from December 6–18, 2015, a period that was expected to overlap with the peak breeding period for these land blennies (midsummer; e.g., Bhikajee et al. 2006). The experiment involved the presentation of three models varying in head crest size (Fig.

S1) to free-living *Alticus* sp. cf. *simplicirrus* found along a reef wall in the supralittoral splash zone (Fig. S2), where individuals were observed to be active and in high abundance during mid-tide, with males often occupying rock holes as nests. The models were realistic mimics of *Alticus* sp. cf. *simplicirrus* and consisted of two contrasting head crest sizes: (i) a population average or 'normal' sized head crest, which was derived from the allometric curve of this population and was approximately 11 mm^2 (Fig. 2b); and (ii) a 'super-sized' head crest that corresponded to one of the largest head crest sizes recorded for any terrestrial blenny species, which was exhibited by a male *A. monochrus* on the island of Mauritius (Summers and Ord 2022) and was approximately 48 mm^2 (Fig. 2b; NB: the absolute largest head crest that we have ever recorded was 61 mm^2, but creating this on the model that was otherwise life-size for the species on Rarotonga was impossible because it was simply too big to fit on the model's head). This 'super-sized' treatment, while being well outside the bounds for this population on Rarotonga (Fig. 2b), was nevertheless biologically plausible for this genus. We also created a control model that had no head crest and was more typical of a juvenile or female of this species (only mature males possess a
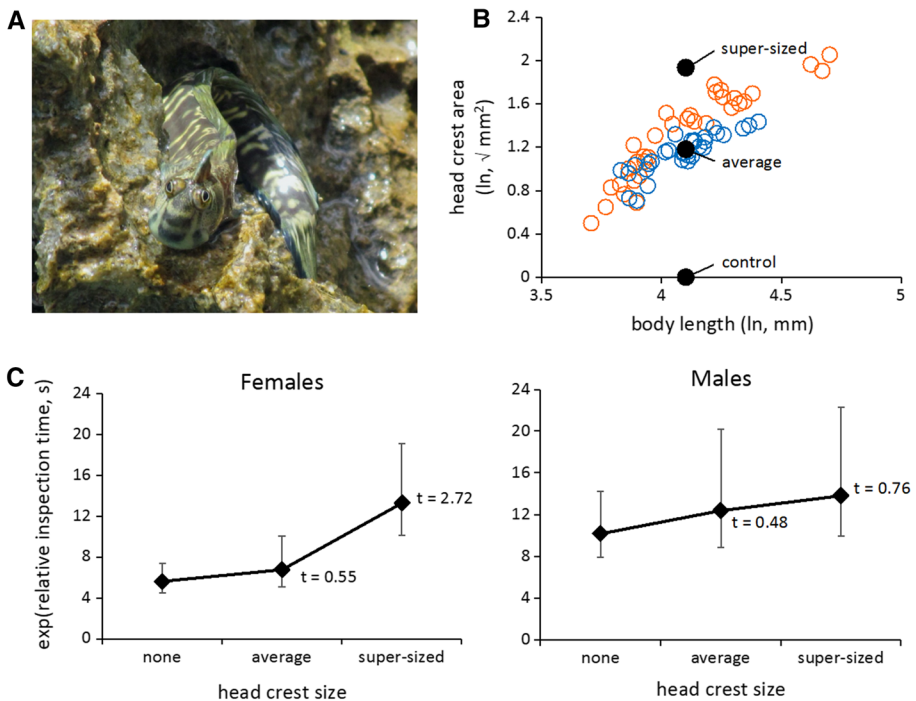

Fig. 2 Head crest size and influence on conspecific behaviour. **A** A male *Alticus* sp. cf. *simplicirrus* exhibiting a prominent head crest (NB: this male is not showing the typical charcoal black courtship colouration; photo courtesy of Georgina Cooke). **B** The allometry of male head crests in *Alticus* sp. cf. *simplicirrus* (blue circles) and *Alticus monochrus* (orange circles; data from Summers and Ord 2022). Shown are the head crest sizes of the models used in presentations (filled circles): control (0mm^2); average (11mm^2); and super-sized (48mm^2). The standard length of models was kept consistent (30 mm), equivalent to the display position of an average male (60 mm). Data are ln-transformed, with head crest area first linearised by a square-root (see Summers and Ord 2022). **C** The time females and males spent inspecting each male model (data are the mean ± SE total time individuals spent within the zone of approach, weighted by the proportion of individuals that approached that model out of all the individuals observed to approach any model during the trial)

head crest). The online Supporting Information provides details on the construction of the models.

Model presentation

The experiment consisted of a simultaneous presentation of all three models to free-living blennies, which approximated the context in which males and females would encounter each other in the wild. Each model was fixed next to each other on the reef wall in a rough line with approximately 30 cm separating each model (e.g., see Fig. S2). The specific position of models was dependent on where they could be attached to the reef wall and this was effectively random across treatments and the control (i.e., there was no statistical bias in model position among treatments; see Table S3). The order in which models were placed relative to each other was changed systematically from one trial to the next. The model blennies were also switched among the three artificial nest holes in a systematic manner every seven trials and the opportunity was taken at this point to also switch out the copy of the model blenny itself.

Trials were recorded using a hand-held video camcorder approximately 5 m from the reef face (Fig. S3). Each trial began with a 2 min acclimation period and was followed by a maximum of 10 min video-recording (mean trial time: 8:55 min, range 1:10 to 10:00; trials were sometimes ended prematurely by wave inundation knocking models off the reef wall). Consecutive trials were conducted in a systematic manner in which the researcher progressively moved along the reef wall in a consistent direction away from the previous trail for several meters before positioning models for the next trial. Based on extensive observations of other species (e.g., Ord and Hsieh 2011) and anecdotal observations of individuals at this location, this distance was anticipated to be far enough between trials to reduce the likelihood of resampling individuals.

Previous studies on closely related amphibious and terrestrial species have indicated social activity on land is generally concentrated during periods of mid-tide, and to a lesser extent during moderate to high air temperatures (Ord and Hsieh 2011; Ord and Cooke 2016). All presentations were consequently made during the approximately two hour mid-tide period. Air temperature ranged from 24.8 to 32.4 °C and was well within the range during which peak social activity has been observed in other species (Ord and Hsieh 2011; Ord and Cooke 2016).

Video and statistical analyses

Videos were scored blind (it was very difficult to discern treatment position in videos) and involved running clips in real-time, repeatedly for each individual fish observed to move into frame during the trial. Each individual was identified as male or female based on the presence/absence of a head crest, gross body size and coloration. In relation to body size, terrestrial blennies (specifically *Alticus*) exhibit age cohorts that allow juveniles to be easily distinguished from adults based on obvious differences in size (e.g., see Bhikajee et al. 2006). Small individuals (approximately < 35 mm standard length) were therefore excluded from observations because they were likely to be juveniles. Individuals were tracked for the entirety of the trial (10 min) or until that individual moved out of frame. Data was collected on which individuals entered a designated 'zone of approach' for each model and total time (in seconds) spent within that zone. This zone was defined as an approach within 10 cm or closer of the circular latex platform, with an orientation of approach being specifically

towards the model blenny. Total time within this zone and orientation towards the model was then recorded using a stopwatch. Timing stopped at any point that an individual oriented away from the model, but otherwise stayed within 10 cm, or left the zone entirely. On occasion individuals re-oriented towards the model or moved back into the zone of approach and timing was recommenced. Our analyses focused specifically on the total time each individual spent oriented towards a given model within that zone. Of 140 trials, observations were made of 84 females and 50 males approaching one or more of the models. Models that were not approached by a given individual were given a time score of zero.

Data were analysed separately for the sexes using R version 3.2.4 (R Development Core Team, The R Foundation for Statistical Computing, Vienna, Austria) and a compound poisson random-effects linear model in the 'cplm' package version 0.7–5 (Zhang 2013) with the 'cpglmm' function. This model is especially suited for our needs because it evaluates the distribution of the data and fits a model with the most appropriate error distribution from the family of tweedie probability distributions. For both sexes, the model identified a poisson-gamma distribution, which accounted for the heavy skew of zero time scores when individuals did not approach a given model and the normal distribution of times when individuals did approach a given model. In this framework, model parameter estimates were effectively the total time individuals spent within the zone of approach for a given blenny mimic, weighted by the proportion of individuals that approached that model out of all the individuals observed to approach any model during the trial.

All models included a random intercept and slope for fish identity and trial number. These random effects accounted for the repeated measures for some individuals (fish approaching two or more models within a single trial) and the possibility that the behavior of other fish observed during a given trial influenced the behavior of the focal fish or that some variable specific to a trial influenced the general behavior of all fish observed (e.g., subtle variation in reef topography). The fixed effect included categories of control (no head crest), normal (population-average sized head crest) and super-normal (a large head crest outside the observed range for this population) and was defined in the model as a factor. The dependent variable was the time (s) individuals spent within the zone of approach, with instances of non-approach scored with a value of 0. By including non-approaches in this way, the tweedie model explicitly considered both the proportion of individuals that did or did not approach a given model and, and for those that did approach, the time individuals subsequently spent inspecting the blenny mimic (see previous paragraph).

Results

Review of past experimental studies

From the 543 articles reviewed, we found 65 articles that met our criteria and covered 38 different species in which the size of sexual structures were manipulated and presented to conspecifics for assessment. The typical method for generating different sized sexual structures was by trimming (N = 42 studies) and artificially extending ornaments in live animals (N = 34 studies), followed by presenting conspecifics with static models (N = 11 studies), still images (N = 3 studies) and video-playback (N = 1 studies). Only three studies were found to manipulate the size of male weapons (see Table S1). A summary of the reported nature of preferences and types of ornaments tested by studies that focused on female responses to male ornaments (i.e., those most

relevant for our empirical study) is provided in Fig. 1. Full details on all studies captured by our review is provided in Table S1 in the online Supporting Information.

Approximately one quarter of studies we reviewed manipulated ornament stimuli across a range of different sizes ($N = 17$ studies), but in only five cases did these include an ornament size outside the natural range for the studied species (i.e., a "super-normal" stimuli; Fig. 1). For these five, all reported a log-linear, positive preference in favor of the super-normal male ornament (Table 1a; e.g., Andersson 1982; Jones and Hunter 1998; Pryke and Andersson 2002). However, the allometric scaling of these ornaments in life remains unknown for these species, so the relevance of these response patterns to the evolution of sexually selected allometry remains unclear. Of those studies testing stimuli in the natural range of sizes seen in nature, nearly a quarter failed to report any preference for larger ornaments (10 of 35 studies). Studies that simply compared the response of females to the presence and absence of male sexual structures all reported a lack of preference for ornamentation in general (Fig. 1b).

Experimental manipulation of ornament size in a land blenny

Only two female land blennies out of the 84 observed approached all three models. One of those females spent the longest time inspecting the super-sized head crest model (12 s; compared to the population-average ("normal") sized head crest and the control (no head crest) models, both 2 s), while the other female spent the longest time inspecting the average-sized head crest model (99 s; compared to the super-sized, 26 s, and the no head crest control, 5 s). Five females approached two of the three models, with two females inspecting the super-sized and average-sized head crest models, a third inspecting the average-sized and control models, and the last two inspecting the super-sized and control models. Three of the five females spent the longer time inspecting the model with the larger head crest (super-sized vs average-sized vs control, female A: 21 s, 7 s, -; female B: 41 s, 8 s, -; female C: -, 54 s, 2 s; female D: 6 s, -, 18 s; female D: 4 s, -, 18 s). The remaining 77 females inspected only one of the three models (super-sized head crest: 32 females; average-sized head crest: 23 females; control: 22 females). Across all individuals, female blennies approached and spent more time attending to the model with the super-sized head crest, and disproportionately so, compared to either the model with the average-sized head crest or the control (no head crest; Table S4 and Fig. 2c). There was little difference between female evaluation times towards the average-sized head crest and the control (Fig. 2c).

No male land blenny of the 50 observed approached all three models. However, seven males inspected two of the three models, with four males shifting between the super-sized and average-sized head crest models, one between the average-sized and control models, and two inspecting the super-sized and control models. Four of the seven males spent the longer time inspecting the model with the larger head crest (super-sized vs average-sized vs control, male A: 32 s, 26 s, - s; male B: 81 s, 9 s, - s; male C: - s, 23 s, 4 s; male D: 4 s, - s, 3 s; male E: 17 s, 22 s, - s; male F: 11 s, 12 s, - s; male G: 18 s, - s, 56 s). The remaining 43 males inspected only one of the three models (super-sized head crest: 13 males; average-sized head crest: 18 males; control: 12 males). Taken together, and in contrast to females, there was no statistical difference in the time males spent evaluating any of our models (Table S4 and Fig. 2c).

Discussion

Experiments that have investigated female or male responses to supernormal sized ornaments or weapons are rare ($< 10\%$ for ornaments; none for weapons; Table S1). The findings of these studies suggest that males capable of exhibiting sexual morphologies greater than the natural size range for a population would likely acquire greater fitness benefits (based on the 5 studies that presented super-normal sized traits; Fig. 1b). The findings of our own experimental study were consistent with this general conclusion as well, but have direct implications for the evolution of sexually selected allometry (see next paragraph). Furthermore, had we not tested an ornament beyond the size range for male *Alticus* sp. cf. *simplicirrus* on Rarotonga, we would likely have failed to detect any difference in female attention towards an average-sized ornament and a male possessing no ornament. Our review revealed this type of null outcome was common. Most experiments examined the consequences of possessing a large or small ornament relative to a standardized control, and this design was the least likely to detect positive preferences for one ornament size over another. At a basic level, this suggests experiments testing a range of ornament sizes, especially those that incorporate supernormal stimuli, are better designed to measure the full extent of female preference behavior.

In our experimental study, we found females likely have a strong positive preference for male head crest size, and that this preference extends beyond the range of male crest sizes actually observed in the population. This result is important because it seems to be the first confirmation of a central assumption underlying the allometry theory of sexually selected characters more broadly (e.g., Kodric-Brown et al. 2006). The size of head crest treatments used in our study corresponded to the positive scaling exponent typically exhibited by members of this genus (Fig. 2b; Summers and Ord 2022). By doing so, our study reveals the probable underlying mechanism that drives positive allometric relationships of a sexually selected ornament in these fishes. That is, the size of the male head crest has likely evolved as an honest indicator of male condition—e.g., his ability to devote resources to growth and development—assessed by females during mate selection. Given the choice, female blennies will more readily associate with a male possessing the largest head crest (Fig. 2c), and such a male will presumably benefit from increased mating opportunities. For example, in several species of *Alticus*, females actively inspect multiple males as they perform courtship displays at the entrance of their rock holes, and central to those displays is the presentation of the head crest (Bhikajee and Green 2002; Ord and Hsieh 2011). Females choosing a male will then enter a male's hole to lay eggs, which he then fertilizes and cares for until hatching (e.g., Bhikajee and Green 2002; Shimizu et al. 2006; Ord and Hsieh 2011). In contrast, the size of the head crest appears not to be used by other males as a cue of the condition of rivals during opponent assessment, despite male land-dwelling blennies aggressively defending rock holes from rival males (Bhikajee and Green 2002; Ord and Hsieh 2011; Fig. 2c; NB: this does not exclude the possibility that males assess other aspects of a rival's morphology such as gross body size).

Positive allometric scaling of sexually selected characters should occur because only larger males can invest in producing disproportionately larger condition-dependent traits (Petrie 1988; Green 1992; Tomkins and Simmons 1996; Emlen and Nijhout 2000; Kodric-Brown et al. 2006). Our experiment provides evidence this investment in exaggerating ornament size should in turn convey advantages in acquiring mates and therefore result in improved fitness for males. Furthermore, disproportionately larger

ornaments receive disproportionately greater attention from females (Fig. 2c), and this includes ornament sizes well beyond the observed range found in a population (Fig. 2b).

Given females seem to exhibit a strong preference for disproportionately exaggerated head crests in this population, it's worth noting again that male *Alticus* sp. cf. *simplicirrus* appear to have an almost isometric head crest exponent (1.05), and one considerably lower than the average *Alticus* head crest exponent within the genus (1.36, CI range = 1.24–1.47; Summers and Ord 2022; see also Fig. 2b). This might reflect either a generally low level of competition among males for females in this population (i.e., relaxed sexual selection despite the presence of strong female preferences for a particular male phenotype) or a constraint on exaggerating ornament size (e.g., natural selection via predation or biomechanical constraints; Summers and Ord 2022). These explanations will need to be confirmed by future study, but this species offers an exciting opportunity to investigate the evolutionary and developmental factors involved in an apparent mismatch between male trait expression and female preference for that trait.

This effectively "hidden" female preference for extravagant ornament sizes in males highlights a challenge for any investigation of mate choice wishing to identify the cues used by females that does not incorporate stimuli outside the observed range in a population. If this phenomenon is frequent in nature (e.g., see also Rosenthal and Evans 1998; Kozak et al. 2008), it could account for instances where preferences for larger ornaments were failed to be detected by many studies (19 overall—see Table S1—14 of which were specific to female preferences—see Fig. 1b). This might reflect a general issue of statistical power. The ability to detect an effect of female preference for larger ornaments will likely be greater in experiments that test ornament sizes outside the normal range simply because the magnitude of difference between treatments is larger, which in turn improves the signal-to-noise ratio in subsequent analyses. All studies we reviewed that tested ornament sizes outside the normal range reported female preferences for larger ornaments. In contrast, as many as a quarter of studies that only tested ornament sizes within the natural range failed to recover any preference for ornament size. Furthermore, documenting that males in a population exhibit an isometric scaling relationship in an ornament does not preclude the possibility that females might otherwise have strong preferences for increasingly larger ornaments. We know the allometry of ornaments can experience complex trade-offs, with opposing selection pressures dampening what would otherwise be positive allometric scaling in ornaments (e.g., predation or biomechanical constraints; see Summers and Ord 2022 for discussion).

Despite several models of sexual selection implicating the potential for animals to harbor hidden preferences for exaggerated sexual characteristics that are otherwise not currently expressed in a population (e.g., sensory bias—e.g., Rosenthal and Evans 1998; Rodd et al. 2002; Smith et al. 2004; Makowicz et al. 2016; see also Basolo 1998; runaway selection—Fisher 1958; Lande 1981; Kirkpatrick 1982; Chandler et al. 2013), there are surprisingly few direct tests of super-size sexual ornaments and apparently none conducted within an explicit allometric context. Yet it is precisely these types of experiments that are vital for improving our understanding of how female preferences contribute to the evolution of complex sexual morphologies. It is especially relevant to allometry theory that implicitly assumes that the development of disproportionately sized sexual structures in males reflects disproportionate increases in fitness as a consequence of elaborating the size of those structures (Kodric-Brown et al. 2006). One of the best ways to investigate this underlying mechanism is to test conspecific responses or fitness outcomes to super-normal characteristics, and those that reflect observed or expected positive exponents of ornament size. This approach has the additional

potential to improve our ability to interpret non-positive allometries of sexually selected characteristics.

Declarations

Conflict of interest None to declare.

Ethical approval The work reported in this study followed protocols submitted to the University of New South Wales Animal Care and Ethics Committee in applications 11/36B and 13/21B and approved on March 10, 2011, and March 4, 2013, respectively.

Consent to participate Not applicable.

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