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Original Article

Phenotypic traits and resource quality as factors affecting male reproductive success in a toadfish

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A male's reproductive success often depends on both his phenotypic quality and the quality of the resources he controls. An important and longstanding challenge for evolutionary biologists has been to disentangle these 2 often-correlated factors. Here, we present a large multiyear, multipopulation field study along with complementary laboratory experiments aimed at disentangling the effects of male quality and nest quality in driving male reproductive success in the plainfin midshipman fish, *Porichthys notatus*. We investigate how these factors are linked to reproductive success using a number of different reproductive success components, including female attraction, cuckolder male attraction, egg acquisition, and rearing success. We show in the field that both male size and nest size are important correlates of reproductive success in this paternal care-giving species, but also that nest size can impose a limit on reproductive success regardless of the quality of the male nest owner. Females in the laboratory prefer large males when nest size is held constant, but females show no detectable preference for larger nests when nest size is varied and male size is held constant. We also explore a suite of additional male and nest traits—including male body condition, sonic organ investment, nest species richness, and nest density. Our results highlight how male and resource quality are multivariate concepts that incorporate information from the male phenotype, the ecological environment, and even the social environment and shape mating systems by influencing an animal's choice of mating partners and nesting sites.

Key words: **alternative reproductive tactics, mate choice, paternal care, plainfin midshipman, resource-holding potential, sexual selection.**

INTRODUCTION

A longstanding challenge for evolutionary ecologists has been to untangle the relative contributions of individual quality and resource quality to reproductive success (Dugatkin and Fitzgerald 1997; Oliveira et al. 2000; Zabala and Zuberogoitia 2014). Determining the relative fitness contributions of individual quality versus resource quality is often complicated by the indirect nature of measuring reproductive success. Strictly, lifetime reproductive success is the number of offspring an individual produces over their lifetime that manage to survive to reproduce themselves (Hamilton 1964; Williams 1966; Grafen 1988). Lifetime reproductive success is notoriously difficult to accurately measure in the wild, especially for long-lived organisms (Newton 1989; Jensen et al. 2004; Rouan et al. 2009). Researchers will therefore measure proxies or "components" of reproductive success that are more easily quantified in the field over realistic time spans (Howard 1979; Clutton-Brock 1988). Such components may include mate attraction (e.g. number of successful courtship attempts), fertilization success (e.g. number of young acquired), and rearing success (e.g. number of young raised to independence) quantified over a single season. However, because selection may act differentially on each component of reproductive

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success and may change across an individual's life span, to gain a more comprehensive understanding of reproductive success in a given species, it is important to study multiple components concurrently (Burger 1982; Clutton-Brock 1988).

When making mating decisions, individuals often integrate information on both the phenotypic quality and the resource quality of their prospective mates (Møller and Jennions 2001; Candolin 2003; Lehtonen et al. 2007). However, the quality of a mate or resource is unlikely to be determined by a single variable (Parker 1974; Johnstone 1996; Candolin 2003; Arnott and Elwood 2009). In a meta-analysis investigating the relative importance of male resource-holding potential and resource value on reproductive success, Kelly (2008) showed that body size is most commonly studied as the primary male quality trait of interest, followed by traits such as song repertoire size or plumage coloration, then male weaponry. These variables that are meant to describe male quality, however, tend to account for little variation in male reproductive success on their own (Kelly 2008).

Here, we investigate the contributions of male quality and nest quality to male reproductive success in the plainfin midshipman fish, *Porichthys notatus*. During late spring and early summer, both sexes of this marine toadfish make an extensive vertical migration from the ocean depths of ~300 m to breed in the shallow rocky intertidal zones of western North America (Arora 1948; Miller and Lea 1972; Warner and Case 1980; Sisneros et al. 2004). Males excavate nesting cavities beneath rocks by removing mouthfuls of sediment and then remain in these nests for months despite the ebbing and flooding of the tides. However, not all intertidal rocks are suitable for nesting beneath and so large rocks are highly sought-after resources, and males compete intensely for nest ownership (Bose et al. 2014). Males are confined to their nests during the breeding season, acoustically courting and luring gravid females, spawning with them in the nesting cavity, and providing sole paternal care for offspring for ~60 days (Arora 1948; Ibara et al. 1983; Brantley and Bass 1994; Cogliati et al. 2013). Male plainfin midshipman fish also express 2 alternative reproductive tactics, a guarder morph and a sneaker morph (Brantley and Bass 1994). While guarder males are large in body size, construct nests beneath rocks, attract females, and care for offspring, sneaker males are on average 8 times smaller in body mass and do not build nests, court females, or provide care, but instead rely on sneak and satellite spawning tactics to steal paternity away from spawning guarder males (Brantley and Bass 1994; Lee and Bass 2004, 2006; Cogliati et al. 2013; Fitzpatrick et al. 2015). It is particularly challenging to tease apart the relative importance of male quality versus nest quality in influencing guarder male reproductive success, because the largest midshipman males often possess the largest nests (Demartini 1988; Bose et al. 2014)—a common phenomenon across many animal taxa (Andersson 1994; Oliveira et al. 2000; Candolin and Voigt 2001; Kelly 2008).

To better understand the mechanisms that underlie variation in reproductive success in the plainfin midshipman, we were guided by Kelly (2008) who recommended that: 1) all 3 pairwise relationships between male quality, resource quality, and reproductive success be assessed; 2) correlational field studies involve large sample sizes and be complemented by controlled manipulative experiments; 3) relevant spatiotemporal variables (i.e. ecological covariates) be accounted for; and 4) accurate measures of reproductive success be obtained. With these recommendations in mind, we conducted 3 studies on the plainfin midshipman fish to assess the relationships between individual quality, resource quality, and reproductive success. In Study 1, we used a large-scale dataset based on multiyear, multisite field sampling to compare the relative importance of male body size (individual quality) and nest size (resource quality) on male reproductive success while accounting for spatiotemporal covariates (e.g. time in the breeding season, site differences, and year effects). In this first study, we quantified reproductive success using 3 components: number of mates attracted, number of eggs acquired, and rearing success. We also quantified the number of sneaker males attracted to each guarder male's nest as a proxy for paternity loss due to cuckoldry. We did this because the presence of sneaker males is known to affect female mate choice decisions (Reichard et al. 2007), and relatedness to offspring is an additional important factor to consider when measuring reproductive success. In Study 2, we conducted a series of complementary controlled laboratory experiments to test female choice for male size while holding nest size constant, and for nest size while holding male size constant. Finally, in Study 3, we explored other traits, beyond male and nest size, that could influence male and resource quality. Specifically, we investigated whether female presence in the nest was linked to the presence of sneaker males, and vice versa, and we also investigated whether reproductive success varied with male body condition, liver, gonad, and sonic muscle investment, as well as with nest density, and the number of other intertidal species sharing the nest space with the males.

METHODS

Study 1: Field studies on male quality and nest quality

Intertidal nest surveys

Between May 4 and July 25 of 2010, 2011, 2013, and 2015, we surveyed a total of 727 plainfin midshipman nests found in the intertidal zones of 9 sites in British Columbia, Canada, Washington State, and California, USA (see Supplementary Table 1 for detailed locations of the sites). We located each nest by gently overturning intertidal rocks to uncover the male and embryos within the nesting cavity beneath. If more than 1 male was present at a nest, we classified the nest owner as the largest and most centrally located male. This classification was based on previous studies that have shown that the largest males secure nests while smaller males resort to cuckoldry tactics (Lee and Bass 2004). For 652 of these 727 nests, we recorded how many females were present in each nest and used these numbers as a measure of mate attraction (range = 0–4 females per nest). We also recorded the number of sneaker male sperm competitors present in these nests (range = 0–3 sneaker males per nest). This method of sampling nests takes a snapshot approach where each nest is visited only once, and we recorded the females and sneaker males present only at the time of observation. We also digitally photographed (Olympus digital cameras TG-820, 12.0 megapixels; TG-850, 16.0 megapixels) each brood and used ImageJ (v1.45, http://rsbweb.nih.gov/ij/) to count the number of embryos in all 727 nests. Plainfin midshipman males often care for broods contributed to by multiple females over the breeding season and hence multiple overlapping age cohorts of offspring (Arora 1948; Demartini 1988; Cogliati et al. 2013). We classified the embryos in each nest into either pre- or post-hatch developmental stages. To quantify the number of eggs acquired by each male, we counted the embryos in nests that contained only pre-hatch offspring (N = 302 nests, range = 4–3425 embryos per nest). To quantify rearing success, we counted the embryos in nests that contained only post-hatch offspring (N = 102 nests, range = 2–1152

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embryos per nest). Post-hatch offspring can be easily counted from nest photographs as they remain adhered to the rock surface via their yolk sac for 3–4 weeks after hatching (Arora 1948; DeMartini 1988; 1991).

We measured the standard length of each male to the nearest 0.1 cm and used this metric as our measure of male quality. We measured the surface area available for egg laying within each nest as our measure of nest quality using one of 2 methods. In 2010 and 2011, we multiplied the length of each nesting cavity's major axis by its perpendicular axis (measured to the nearest cm). In 2013, we digitally photographed the nesting cavity from above, using reference points to delineate the perimeter of the cavity, and later used ImageJ to calculate its area. In 2015, we employed both methods.

We conducted all analyses (including those listed below in Studies 2 and 3) in R (v 3.3.1, R Core Team 2016). We compared the relative influence of male size and nest size on our 3 components of reproductive success, mate attraction, egg acquisition, and rearing success, as well as the number of sneaker males found within each nest. We fit generalized linear mixed effects models assuming a Poisson error distribution (GLMM, lme4 package, Bates et al. 2015) to both the number of females and the number of sneaker males found in the nests. The number of embryos in each nest was fit with a linear mixed effects model (LMM) for pre-hatch and post-hatch offspring separately. In both cases, the number of embryos was cube root transformed to improve normality of the model residuals based on a Box-Cox analysis. We included male standard length and nest surface area in the models as well as their interaction, dropping the interaction whenever it was not significant. We included 3 further fixed effects in each model: Julian date (i.e. the day of sampling between 1– 365), sampling year, and a factor specifying which of the 2 nest size measurement methods was employed for a given nest. We included field site in the models as a random intercept term (Bolker et al. 2009). Male standard length and nest surface area were mean-centered and standardized by dividing by their standard deviation so that we could directly compare their parameter estimates and thus assess their relative importance (Schielzeth 2010; using the glht function from the multcomp package for comparisons, Hothorn et al. 2008). The fish used in this study were sampled from 2 genetically distinct and internally panmictic populations, a northern population comprising field sites from Washington State, USA and British Columbia, Canada, as well as a southern population comprising field sites from Tomales Bay, California, USA (Cogliati et al. 2013, 2014a). Because fish from the northern population study sites are on average larger in body size than fish from the southern population (Cogliati et al. 2014a), we used population-level means and standard deviations for standardizing all numeric predictor variables in our models. When the interaction between male size and nest size was significant, suggesting that the effect of male size on reproductive success changed across the size range of nests, we investigated this interaction more closely. We focused on nests either at the small end or the large end of the spectrum, by centering nest size on a value either −2 or +2 standard deviations from the population mean, and then calculated 95% confidence intervals for the effect of male size and nest size.

Because of the probable correlation between male size and nest size in the models described above, we calculated variance inflation factors (VIFs) for all variables of interest. We merely used the VIFs to assess the extent of any multicollinearity, which was deemed to be minimal (all VIFs ≤ 1.39, Zuur et al. 2010).

Study 2: Laboratory experiments on male quality and nest quality

Do females prefer large males and large nests?

In order to assess the degree of female preference for male size and nest size, we conducted choice experiments in the laboratory. For a more detailed description of the experimental setups, see Supplementary Materials. In brief, we collected adult fish from nests in Ladysmith Inlet, British Columbia, Canada during the summer of 2016. Two males were placed on opposite sides of a glass aquarium, each with his own artificial nest (constructed from bricks and ceramic tiles). Following a 3-day acclimation period, we introduced a gravid female to the center of the aquarium. We then monitored which male the female chose to spawn with. We checked for the presence of eggs every day for 3 days and removed the spent female if a spawning occurred. If no spawning had occurred after 3 days, we removed the still-gravid female and introduced a new gravid female. If after a total of 6 days (and 2 gravid females) no spawning had occurred, we removed both males and the female and started a new trial with entirely new fish. In the first experiment, females (size range = 16.4–21.0 cm in standard length) were provided a choice between 2 males of different sizes (size range = 15.9–30.2 in standard length, mean difference between males in standard length ± SD = 5.6 ± 1.9 cm, and percentage difference in standard length = 22.7 ± 6.3%) each holding an identically sized nest (with 620 cm^2 of roof space for egg laying), representing a nest size commonly found at our study sites (mean ± SD of nest sizes in the field = 587 ± 347 cm^2, $N = 727$). In a second experiment, females (size range = 15.8–20.1 cm in standard length) were provided a choice between 2 size-matched males (size range = 16.9–24.5 cm in standard length, mean difference between males in standard length ± SD = 0.7 ± 0.6 cm, percentage difference in length = 3.0 ± 2.7%), one with a large nest (620 cm^2 of roof space) and one with a small nest (410 cm^2 of roof space). In total, 19 females were offered the differently sized males with identical nests, and 23 females were offered similar sized males with differently sized nests. To see if females preferred one male over the other, we conducted exact binomial tests. To compare the strength of female preference for male size versus nest size, we conducted a chi-square test on the proportions of females that chose to spawn with the large male versus the large nest.

What nest characteristics do males prefer?

To assess male nest preferences, we conducted 2 additional laboratory experiments during the summers of 2014 and 2015 using adult males collected from nests in Ladysmith Inlet, British Columbia. For a more detailed description of the experimental setups, see Supplementary Materials. In brief, we housed each male in a separate experimental tank, each containing 2 artificial nests (constructed from bricks and concrete tiles) placed 30 cm apart. Males were given a 30-min acclimation period before being given 24 h to choose between the nests. We considered the male to have made a choice if he was sitting fully within one of the nests. In the third experiment, we offered the males a choice between 2 nests of differing sizes (one with 360 cm^2 and one with 220 cm^2 of roof space). In the fourth experiment, we offered the males 2 equally sized nests (360 cm^2 of roof space) but one nest had a single, small entrance and was therefore more enclosed (safer) while the other nest had 2 large entrances and was considerably more open (vulnerable). In total, 94 males were offered the differently sized nests,

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and 48 males were offered the nests differing in enclosure. Note that 24 males participated in both experiments, first participating in the third experiment then moving on to the fourth. To see if males preferred one nest type over the other, we fit nest choice with a generalized linear mixed effects model specifying a binomial error distribution (GLMM). Male standard length (mean-centered and standardized) was included as a fixed effect, year as a random effect, and we tested whether the intercepts of these models differed significantly from 0 (a value that would indicate a 50% chance of picking either nest type).

Study 3: Exploration of additional traits influencing male quality and nest quality

During our field surveys described in Study 1, we also measured a suite of phenotypic traits that we considered to be important indicators of individual quality in addition to male size. We measured the body mass of each male nest owner to the nearest 0.1 g and used this to calculate male body condition using the residuals from a regression of ln body mass versus ln standard length (Blackwell et al. 2000). We also dissected a subset of the males (257 out of the original 727) and weighed their livers, testes, and swim bladders (with sonic muscles attached) to the nearest 0.01 g. We could then calculate these males' relative investment into these organ structures, by taking the residuals from a regression of ln organ mass versus ln body mass (Warren and Iglesias 2012). To quantify male energy reserves, we calculated a hepatosomatic index (HSI) using liver mass. To quantify male spawn-readiness, we calculated a gonadosomatic index (GSI) using testes mass. Amorim et al. (2009) suggest that sonic muscle mass may signal male quality in a closely related species, the Lusitanian toadfish, *Halobatrachus didactylus*, and so we calculated a sonic muscle somatic index (SMSI) using the mass of each male's sonic apparatus (swim bladder with attached sonic muscles) as a proxy for male courtship ability.

We explored the effects of these additional male traits by re-fitting the same models described in Study 1, but included male body condition, HSI, GSI, and SMSI as additional fixed effects. Again, we used population-level means and standard deviations to standardize all numeric predictor variables in our models. We assessed both the number of females attracted to each nest and the number of sneaker males attracted using 193 nests for which we had both dissection data and counts of females and sneaker males. We additionally tested for a correlation between the presence of females and sneaker males in the nests. To do this, we included the number of sneaker males in each nest as an additional predictor variable in the female model, and we similarly added the number of females in each nest as a predictor variable to the sneaker male model. As our sample size was restricted to only the nests for which males were dissected, we did not have enough data to independently assess egg acquisition versus rearing success; therefore, we pooled all nests in our analysis whether they included pre-hatch embryos only, post-hatch embryos only, or both. We, therefore, assessed total brood size as a second component of reproductive success using all 257 nests for which we had dissection data as well as embryo counts. We present no *P* values for our exploratory analyses; instead, the model results are illustrated graphically as coefficient plots.

We measured several nest characteristics in addition to nest size that we considered to be important correlates of nest quality. We calculated species richness scores for each nest using the digital images taken of each nest to identify all macro-organisms sharing the nest surface with the embryos. These organisms were identified down to the lowest possible taxonomic grouping and categorized as space competitors or non-space competitors based on whether or not they compete with midshipman embryos for space in the nest (see Demartini 1991). For a subset of nests (339 out of the original 727), we also determined local nest density around each focal nest by measuring the distances to the 3 closest neighboring nests (to the nearest cm, and up to 250cm). We used these distances to calculate a nest density index ranging from 1 to 5, where a score of 1 indicated that the nest was relatively isolated and a score of 5 indicated that the nest was part of a dense cluster of nests (see Supplementary Table 2 for additional details).

We explored the effects of these additional nest traits by re-fitting the same models described in Study 1, but included space competitor richness, non-space competitor richness, and nest density scores as additional fixed effects. We specifically explored the linear and quadratic effects of local nest density (a 5-level ordered factor). While the linear term tests for an increase or decrease in our response variables with local nest density, the quadratic term tests for an optimal density in between both density extremes. We assessed both the number of females attracted to each nest and the number of sneaker males attracted using the 339 nests for which we had additional nest quality data and also counts of females and sneaker males. As described for the above exploratory analyses, we tested for a correlation between female and sneaker male presence here as well. In this reduced dataset, the number of sneaker males observed in nests ranged from 0 to 1 (as opposed to 0 to 3 in the full dataset), and so a Bayesian generalized linear mixed effects model assuming a binomial error distribution was fit here (BGLMM, using the blme package, Chung et al. 2013) instead of the previous model assuming a Poisson error distribution. We used population-level means and standard deviations to standardize all numeric predictor variables in our models. Again, we assessed total brood size using the 339 nests for which we had additional nest quality data as well as embryo counts. Unfortunately, we did not have enough overlap in data to combine both exploratory analyses together (additional male quality and nest quality traits).

Animal ethics

The plainfin midshipman fish is a common intertidal species, not considered threatened or endangered (Collette et al. 2010). Fish were only handled by trained personnel and were kept wet with a moist towel while out of the nest for measurement (no longer than 60 s in duration). Euthanasia prior to dissection was conducted with a bath of benzocaine or MS-222 followed by cervical severance. The procedures used in these studies were approved by the McMaster University Animal Research Ethics Board (AUP number 13-12-52), the Department of Fisheries and Oceans Canada Pacific Region Animal Care Committee (AUP number 13-12-52), the University of Victoria Animal Care Committee (AUP number 2015-009(1)), and are in line with the guidelines set by the Canadian Council on Animal Care (CCAC). All fish sampled for Studies 1 and 3 were also used in numerous additional research projects over the years (e.g. Bose et al. 2014, 2015; Miller 2017; Cogliati et al. 2013; 2014a; b).

RESULTS

The average brood size across the 727 sampled nests was 565 ± 465 embryos (mean ± SD, range 2-3425, including both pre-hatched and post-hatched embryos). Based on an estimated maximum fecundity of 300 eggs per gravid plainfin midshipman female (K.C., personal observations), we conservatively estimate that males

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in our study attracted an average of 2 females to their nests leading up to the time of sampling, and this number ranged from 1 to 12 females per male nest owner.

Study 1: Both larger males and larger nests have higher reproductive success

More females were attracted to larger nests (GLMM, standardized nest surface area, estimate [est.] ± SE = 0.25 ± 0.093, z = 2.72, N = 652, P = 0.006, Figure 1A) but not to larger males (GLMM, standardized male body length, est. ± SE = −0.055 ± 0.084, z = −0.65, N = 652, P = 0.51, Figure 1B). A direct comparison of the model coefficients showed that the relative influence of nest size and male size on mate attraction differed significantly from one another (glht, difference in model coefficients, est. ± SE = −0.31 ± 0.15, z = −2.12, N = 652, P = 0.034). Sneaker males too tended to be attracted to larger nests, though this effect did not quite reach statistical significance (GLMM, standardized nest surface area, est. ± SE = 0.36 ± 0.19, z = 1.93, N = 652, P = 0.054). The number of eggs acquired by a male increased with both nest size (Figure 1C) and body size (Figure 1D), though the effect of body size also interacted with nest size (LMM, interaction term, est. ± SE = 0.31 ± 0.11, t = 2.73, N = 302, P = 0.007). For small nests (i.e. nest size centered on mean – 2 SD), nest size was more strongly correlated with embryo number than was male size (Figure 2A). However, for large nests (i.e. nest size centered on mean + 2 SD), both male size and nest size were similarly positively correlated

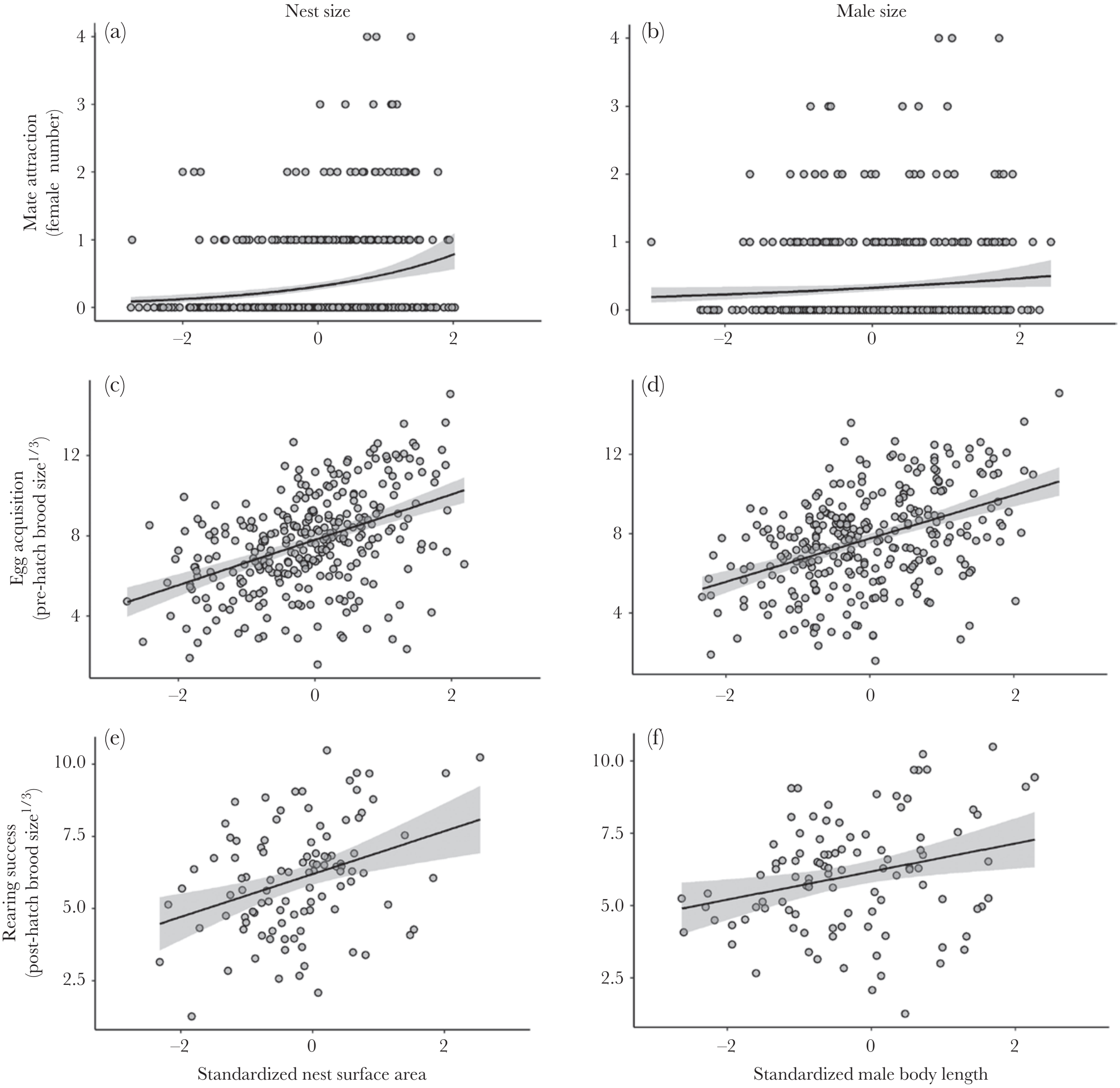

Figure 1

Number of females found in nests plotted against (a) nest surface area and (b) male standard length. Number of eggs acquired plotted against (c) nest surface area and (d) male standard length. Number of embryos successfully reared plotted against (e) nest surface area and (f) male standard length. These plots depict all data pooled across years and sites from Study 1.

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with embryo number (Figure 2A). The number of young successfully reared (post-hatch embryos) also increased with both nest size (Figure 1E) and male size (Figure 1F), but the effect of body size again depended on nest size in a very similar manner (LMM, interaction term, est. ± SE = 0.45 ± 0.19, $t = 2.33$, $\mathcal{N} = 102$, $P = 0.022$; Figure 2A and B). Note that we found the same pattern of results when pooling all nests together ($\mathcal{N} = 727$ nests) and investigating total brood size, as opposed to subsampling and investigating egg acquisition ($\mathcal{N} = 302$ nests with eggs only) separately from rearing success ($\mathcal{N} = 102$ nests with hatched embryos).

Study 2: Females prefer larger males

Ten of the 19 females that were offered 2 differently sized males chose to spawn with one of the males. Of these 10 females, 9 preferred the larger male and one preferred the smaller male (exact binomial test, $P = 0.02$, Figure 3A). Fourteen of the 23 females to which we offered 2 size-matched males with differently sized nests chose to spawn with one of the males. We did not detect a preference for larger nests in these trials (9 females chose the larger nest and 5 chose the smaller nest; exact binomial test, $P = 0.40$, Figure 3B). Female preference for large males (9 out of 10 females) was not significantly different from their preference for large nests (9 out of 14 females; chi-square test, $\chi^2 = 2.06$, $P = 0.33$).

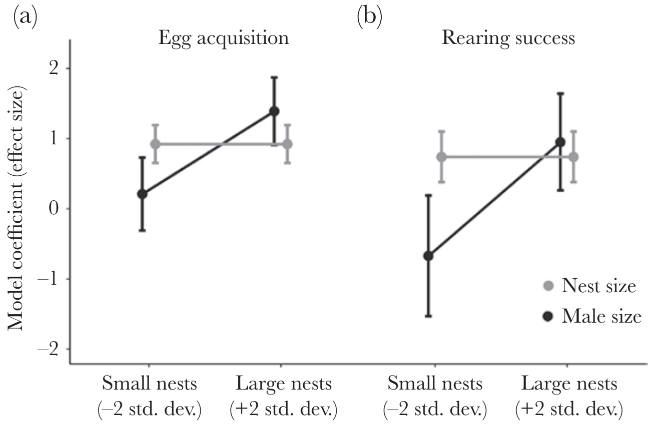

Figure 2
Interaction effects found in Study 1. The effect of male size relative to nest size on 2 components of reproductive success, (a) egg acquisition and (b) rearing success, across a wide range of nest sizes measured in the field. Error bars represent 95% confidence intervals.

Study 2: Males prefer larger and more enclosed nests

Sixty-eight of the 94 males offered a large versus small nest made a choice after 24 h, and 47 (72%) of these males preferred the larger of the 2 nests (GLMb, est. ± SE = 0.81 ± 0.26 log odds, $z = 3.07$, $P = 0.002$, Figure 4A). Male body size had no detectable effect on nest choice (GLMb, est. ± SE = 0.048 ± 0.26 log odds, $z = 0.18$, $P = 0.86$). Thirty-one of the 48 males offered an enclosed versus open nest had made a choice after 24 h, and 29 of these males (94%) preferred the more enclosed of the 2 nests (GLMb, est. ± SE = 3.38 ± 1.30 log odds, $z = 2.60$, $P = 0.009$, Figure 4B).

Study 3: Additional male quality and nest quality traits

Males that had heavier swim bladders for their body size (including attached sonic muscles used for acoustic courtship) tended to attract more females, but not significantly so (SMSI, Figure 5A), though they did attract more sneaker males (Figure 5B). Males with lower GSIs had larger broods in their nests (Figure 5C). The number of females in a nest was also consistently and positively associated with the number of sneaker males observed in the same nest and vice versa (Figure 5A, 5B, 6A, 6B).

Densely clustered nests contained more females than nests that were more isolated (Figure 6A). Furthermore, nests that had more species of space competitors had fewer females (Figure 6A), more sneaker males (Figure 6B), and smaller brood sizes (Figure 6C). At this point, we ran 2 post hoc analyses to test whether the effects of space competitors could be explained by an association between a high richness of space competitors and either small male body size or small nest size. That is, we asked as smaller males or or smaller nests more likely to have more space competitors? We fit 2 linear mixed effects models with male size and nest size as the response variables, and added space competitor richness, non-space competitor richness, and nest density scores as predictors, Julian date and year as covariates, and field site as a random intercept. Neither

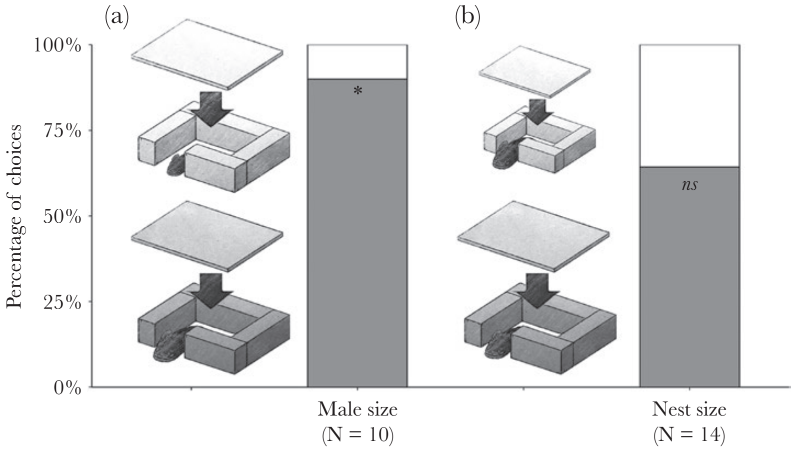

Figure 3
(a) Female choice between a large male (grey) versus a small male (white) in size-matched nests (95% binomial confidence interval = 0.555, 0.997). (b) Female choice between size-matched males in a large nest (grey) versus a small nest (white) (95% binomial confidence interval = 0.351, 0.872). Picture inlays illustrate the nest designs; fish are not drawn to scale.

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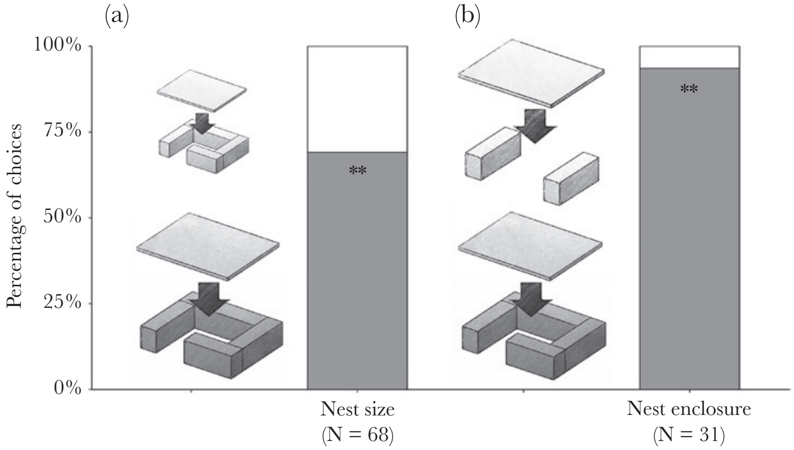

Figure 4

Male choice (a) between a large nest (gray) versus a small nest (white) and (b) between an enclosed nest (grey) versus an open nest (white).

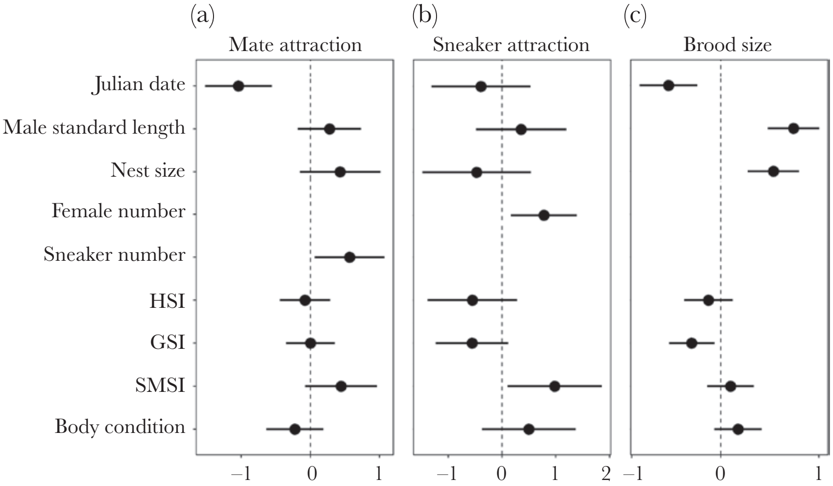

Figure 5

Coefficient plots depicting model estimates (dots) and 95% confidence intervals (solid bars) for additional putative male quality traits.

small males (LMM, est. ± SE = 0.014 ± 0.049, $t = 0.27$, $N = 339$, $P = 0.78$, 95% confidence interval = −0.081, 0.11) nor small nests (LMM, est. ± SE = 0.10 ± 0.055, $t = 1.83$, $N = 339$, $P = 0.068$, 95% confidence interval = −0.010, 0.20) were significantly associated with more space competitors. Common space competitors in our plainfin midshipman nests included colonial tunicates (e.g. *Botrylloides violaceous*, *Didemnum vexillum*), encrusting bryozoans (e.g. *Schizoporella japonica*), encrusting sponges (e.g. *Halichondria panacea*, *Haliclona permollis*, *Clathria pennata*), and egg masses of other organisms including dorids (e.g. *Doris montereyensis*) and snails (e.g. *Nucella lamellosa*).

DISCUSSION

To evaluate the relative impacts of male and nest quality on reproductive success in a wild fish, *P. notatus*, we combined large-scale field-based surveys with laboratory-based controlled experiments. Both male size and nest size positively correlated with male reproductive success in the field. Our laboratory studies provided complementary results indicating that males preferred the larger of 2 nests and that females prefer the larger of 2 males. Expanding the list of traits that may influence male reproductive success beyond male size and nest size, our data suggest that the size of a male's sonic apparatus, the richness of space competitor organisms within a nest, and the local density of nesting males may be important variables of interest for future work. Our results fit in with and extend previous studies, providing a clearer picture of how the ecological and social landscape in which *P. notatus* breeds influences nest-site and mate choices, thereby shaping the mating system in general.

Study 1: Male reproductive success increases with both male size and nest size

In *P. notatus*, intertidal rocks are a critical resource needed for reproduction. Males compete intensely with one another over rock (and nest) ownership, and a positive relationship is commonly documented between male size and nest size (Demartini 1988, 1991; Bose et al. 2014). In many taxa, body size correlates with a male's resource-holding potential permitting the largest males to secure the highest-quality resources or territories (e.g. green frogs, *Rana clamitans*, Wells 1977; damselflies, *Megaloprepus coerulatus*, Fincke 1992; Azorean rock-pool blennies, *Parablennius sanguinolentus parvicornis*, Oliveira et al. 2000). Our results extend previous results by showing that the relationships between body size, nest size, and

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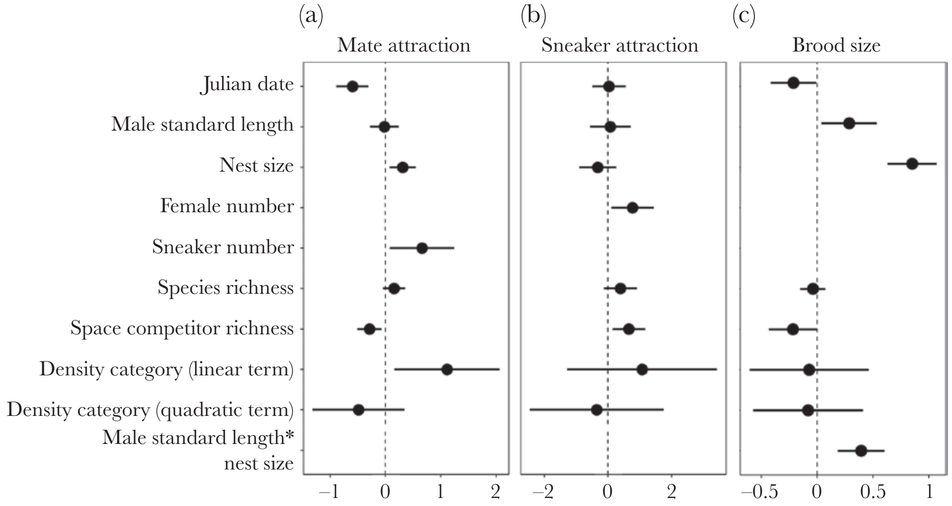

Figure 6
Coefficient plots depicting model estimates (dots) and 95% confidence intervals (solid bars) for additional putative nest quality traits.

reproductive success hold true across numerous breeding populations, and that the relative importance of male size and nest size can depend on their interaction.

More females were found in larger nests in the field. Theory suggests that the relative importance of resource quality versus male quality on mating success depends on whether female choice and offspring fitness are predominantly affected by male traits, nest characteristics, or both (Searcy 1979; Pomiankowski 1988; Møller and Jennions 2001; Candolin 2003). Females may prefer to spawn in large nests if such nests contain larger broods that will subsequently receive more paternal care (Coleman et al. 1985), if nest size correlates with the nest builder's health or phenotype (e.g. blue tits, *Cyanistes caeruleus*, Tomás et al. 2006), or if males increase courtship effort when guarding larger nests (e.g. sand goby, *Pomatoschistus minutus*, Pampoulie et al. 2004; Lindström et al. 2006). Similar to females, sneaker males also tended to be attracted to larger nests. It is likely that sneaker males are attracted to nests that contain gravid females. Indeed, previous work has shown that sneaker male presence in a nest is positively correlated with female presence (Bose et al. 2014). It is important to consider here that *P. notatus* nests are often small, confined spaces excavated by males (Demartini 1991). Adult *P. notatus* take up a considerable amount of space within nesting cavities (see Bass 1996; McIver et al. 2014). Thus, the positive relationships between female and sneaker number with nest size may in part be driven by the small nests not containing enough space to simultaneously hold multiple fish.

The number of embryos a male acquired and the number he successfully reared increased with both male size and nest size. Interestingly, for small nests, nest size was more strongly related to these components of reproductive success than was male size. This may be because the dimensions of small nests impose an upper limit on brood size regardless of the size of male occupying the nest. Other studies have also found that nest size can dictate brood size or maximum reproductive success of the nest owners (e.g. Marsh Tits, *Parus palustris* and Willow Tits, *Parus montanu*, Karlsson and Nilsson 1977; sand gobies, *P. minutus*, Lindström 1992a), and so nest size may be an important ecological constraint in many taxa that breed in small spaces. In large nests, however, both male size and nest size were positively related to embryo number to similar degrees.

It is currently unknown whether female *P. notatus* engage in mate choice copying. Mate choice copying has the potential to dramatically influence mating patterns (Alonzo 2008). For example, female Trinidadian guppies, *Poecilia reticulata*, may even reverse their mating preferences and begin preferring a previously rejected male after observing him being chosen by other females (Dugatkin and Godin 1992). In a similar vein, females may also express a preference for laying eggs with a male who is already caring for offspring if by doing so, for example, increases the survival of her offspring through the dilution of predation (Jamieson 1995; Kraak 1996). The questions remain whether female *P. notatus* exhibit copying behavior and whether copying can lead females to spawn with males or in nests that they would otherwise have rejected.

Study 2: Females prefer larger males and males prefer larger nests

Experimental studies have a marked advantage over correlational studies, because they allow researchers to independently manipulate variables that tend to be highly correlated under natural conditions (Kelly 2008). In our series of 2-choice experiments, females preferred large males, but had no clear preference for large nests. However, given our limited sample size, we could not detect any difference in the strength of female preference for male size versus nest size, and so additional testing with more spawning trials in the laboratory would be valuable. Male body size is a reliable predictor of a male's ability to win contests in a variety of taxa (e.g. sand gobies, *P. minutus*, Lindström 1992b; orb-web spiders, *Metellina mengei*, Bridge et al. 2000; Magellanic penguins, *Spheniscus magellanicus*, Renison et al. 2002; red deer, *Cervus elaphus*, Clutton-Brock et al. 1979) and could therefore be a reliable cue of a male's ability to defend a nest or territory (Lindström and Pampoulie 2005; Schütz and Taborsky 2005). Male body size is also a reliable predictor of nest ownership in *P. notatus* (Lee and Bass 2004). Nest takeovers are a frequent occurrence in the *P. notatus* breeding season, and successful nest takeovers are associated with embryo cannibalism by the usurping male (Bose et al. 2014) and a decline in offspring survival

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(Bose et al. 2016). Thus, large males may represent the safer option for a female to entrust her eggs, especially if small males are less likely to retain resource ownership over the extended (~60 day) parental care period, as similarly found in other species (e.g. sand gobies, *P. minutus*, Lindström and Pampoulie 2005; *Lamprologus callipterus*, Maan and Taborsky 2008).

It is also possible that our results are in part due to the larger male preventing the smaller male from attracting the female. The fish in our choice trials were free to physically interact with one another. Brantley and Bass (1994) documented that guarder males in the lab would sometimes lunge out from their nests at nearby gravid females and drag them into their nest; however, it was exceedingly rare that such behavior resulted in a successful spawning. While, we did not observe any signs on the fish that would indicate aggressive interactions, we suggest that future studies incorporate video recordings and assess all behavioral interactions between the fish, as well as courtship effort made by each of the males, in such mate choice trials leading up to spawning.

Male *P. notatus* preferred larger and more enclosed nests. Preferences for nest size may result from a tradeoff between the benefits of having a nest with space for many offspring with the costs of maintaining and defending a large nest (Kvarnemo 1995; Mainwaring et al. 2014). It has been proposed that male sand gobies, *P. minutus*, choose smaller and easier-to-defend nests when egg-predation risk is high, but prefer larger nests when the risk is low (Björk and Kvarnemo 2012). Interestingly, we did not detect any effect of male size on their choice of nest size suggesting that males pursue large nests regardless of their own body size. Perhaps, the benefits of owning a large nest outweigh the costs associated with defending it because in the wild, small nests constrain the reproduction of all males alike. Future studies could test a greater diversity of nest sizes to more explicitly test size-assortative nest choice in *P. notatus*.

Study 3: Additional male and nest quality traits

Male plainfin midshipman fish generate an advertisement call typically referred to as a "hum" to attract gravid females by rapidly contracting the sonic muscles attached to their swim bladder walls (Cohen and Winn 1967; Ibara et al. 1983; Bass and Marchaterre 1989; Brantley and Bass 1994; McKibben and Bass 1998). Interestingly, males with larger sonic apparatuses, i.e. swim bladders and sonic muscles, for their body size attracted more sneaker males to their nests, and so the overall size of this organ may influence characteristics of the male song. While the fundamental frequency of a male's advertisement hum appears to be unrelated to his body size (McIver et al. 2014), and thus sonic muscle or swim bladder size (Brantley et al. 1993), males inflate their swim bladder during advertisement calling (Bass et al. 2015), likely as an adaptation to enhance sound amplitude (Russell et al. 1999). Females will choose the louder of 2 simulated advertisement calls even when both are audible, and sneaker males will also respond to acoustic playbacks of male advertisement calls (McKibben and Bass 1998). Furthermore, call loudness scales with sonic muscle mass in other fish species (e.g. Lusitanian toadfish, *Halobatrachus didactylus*, Vasconcelos and Ladich 2008; weakfish, *Cynoscion regalis*, Connaughton et al. 1997). Therefore, males with large swim bladders may have louder advertisement calls that could, in part, explain the increased attraction of sperm competitors. It still remains to be tested whether spectral or temporal song characteristics, beyond amplitude, correlate with swim bladder size in this species.

Interestingly, large swim bladder and sonic muscle investment did not correlate significantly with larger broods. Perhaps after entering a nest, females use additional information to assess males. In the dark conditions of male's nests, females might use mechanosensory information from their lateral lines to further assess male size and quality as has been shown in Atlantic mollies, *Poecilia mexicana* (Plath et al. 2004) and himé salmon, *Oncorhynchus nerka* (Satou et al. 1994). The mechanosensory lateral line of midshipman is also sensitive to the frequency content of male calls (Weeg and Bass 2002). Hence, the lateral line might play a role in mate assessment based on advertisement calls that the males sometimes continue to produce up to 1 min after female entry into the nest (Brantley and Bass 1994).

Females were found in greater numbers in nests that were densely clustered relative to more isolated nests, yet the densely clustered nests did not have correspondingly larger broods. Breeding under conditions of high nest density may present both costs and benefits. For example, as density increases, females may be more efficient at comparing males and so make better or more efficient mating decisions (e.g. common yellowthroat warblers, *Geothlypis trichas*, (Taff et al. 2013). High density can also reduce a female's search time before she encounters a suitable male mate (e.g. bushcrickets, *Xederra charactus*, (Lehmann 2007). However, if high density provides more opportunity for males to interfere with one another's reproduction, then high density may reduce the overall success of many males in the population and potentially counteract the benefits of nesting in dense areas (Kokko and Rankin 2006). The community of intertidal organisms living in the vicinity also had a large influence on the quality of a nest. Indeed, nests containing many species of space competitor organisms were associated with fewer females, smaller broods, and more sneaker males. Space competitor organisms represent an interesting and novel angle from which to study territory quality because they reduce the effective size, and thus quality, of a nest without changing its physical dimensions (Hastings 1988; Demartini 1991). Nests with more space competitor species may also offer additional positions around the periphery of the nest from which sneaker males may stay concealed from the guarder male. We suggest that a fruitful avenue for future research will be to investigate how species biodiversity at both small and large spatial scales impacts reproductive success and influences mating systems more generally.

Lastly, sneaker male abundance in the nest was significantly and positively correlated with female abundance, consistent with the findings of a previous field study (Bose et al. 2014). Female choice is known to be influenced by the presence of cuckolder males in many fishes with females often preferring to avoid spawning with cuckolder males (Taborsky 2008; but see Reichard et al. 2007). Given that the guarder male tactic is thought to have a higher average fitness than the sneaker tactic in *P. notatus* (Cogliati et al. 2014a) and that a high level of paternal care is crucial for offspring survival (Bose et al. 2014, 2015, 2016), we expect that female midshipman fish will prefer to avoid spawning alongside sneaker males. Unfortunately, our data cannot be used to ascertain whether females prefer or avoid spawning in the presence of sneaker males, and this remains an outstanding question for future work.

In this study, we attempted to disentangle the relative influence of male quality and nest quality on male reproductive success in the plainfin midshipman fish. We did not find that one variable was consistently more important than the other; but rather, we showed that their interactions need to be carefully considered. We also highlight the importance of considering traits beyond male size and

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nest size when studying reproductive success and including multiple components of reproductive success whenever possible. We suggest that future studies focus on whether females only use auditory cues to assess their potential male mates or whether they use any other sensory information while in the presumably dark conditions of the male nest. Furthermore, future studies should also measure paternity more directly while assessing male reproductive success in *P. notatus* as paternity loss in this system can be not only from cuckolding sneaker males, but also from cuckolding guarder males as well as nest takeovers (Brantley and Bass 1994; Lee and Bass 2004, 2006; Cogliati et al. 2013; Bose et al. 2014; Cogliati et al. 2014a,b; Fitzpatrick et al. 2015). Finally, we underscore the utility of combining correlational analyses from the field with controlled laboratory experiments to investigate the typically correlated variables that underlie reproductive success.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Bose et al. (2018).

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