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2 The costs and benefits of paternal care in fish: a meta-analysis

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10 selection

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24 **Abstract**

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26 Male-only parental care, while rare in most animals, is a widespread strategy within teleost fish.
27 The costs and benefits to males of acting as sole carer are highly variable between fish species
28 making it challenging to determine the selective pressures driving the evolution of male-only care
29 to such a high prevalence. We conducted a phylogenetic meta-analysis to examine the costs and
30 benefits of paternal care across fish species. We found no evidence that providing care negatively
31 affects male condition. In contrast to other taxa, we also found limited evidence that male care has
32 evolved as a strategy to improve offspring survival. Instead, we found that males already caring
33 for a brood are preferred by females and that this preference is strongest in those species in which
34 males work harder to care for larger broods. Thus, in fish, investment in offspring care does not
35 constrain a male's mating success but rather augments it, suggesting that the relatively high
36 prevalence of male-only care in fish may be in part explained by sexual selection through female
37 preference for caring males.

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39 **Introduction**

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41 Male-only parental care, where the male is the sole carer of his offspring, is a rare strategy in most
42 animals. In birds, for example, most species show biparental care with male-only care present in
43 fewer than 1% of species (1), while in mammals and reptiles male-only care is entirely absent (2).
44 In these taxa, lower investment in parental care by males than females is considered a consequence
45 primarily of sexual selection acting more strongly on males to increase their mating rate, although
46 other factors such as paternity uncertainty and the influence of adult sex ratios on mate availability

likely also play a role (reviewed in 3). In teleost fish, however, male contributions to offspring care are unusually high, with males acting as the sole carer in more than 50% of families with any parental care (4). The only other taxonomic group that shows comparable levels are amphibians, where male-only and female-only care are equally common (2). Why male-only care should be so prevalent fish, including in species where sexual selection is stronger in males than females (5), remains unclear.

Fish possess several traits less commonly found in other taxa that are likely to increase the benefits and reduce the costs of paternal care, potentially explaining its prevalence in this group. First, parental care, which typically consists of defence against predators and fanning the eggs to increase aeration, is shareable among offspring without depreciating, meaning that the costs of care do not increase with offspring number. In contrast, depreciable care such as direct feeding of offspring is very rare - the only known examples are the nourishment of embryos by some syngnathids (pipefish and sea horses) (6) and the provision of epidermal mucus to offspring in some cichlids (7). Second, while brood defence constitutes a critical aspect of parental care in fish, the substantial differences in size between adults and larvae means that brood predators are rarely a threat to adults (8). The non-depreciable nature of care and the low risks associated with brood defence are thus expected to reduce the energetic and survival costs of care in fish compared to other taxa (9). Third, the trade-off between investment in care and investment in mating, which underpins sex differences in care strategies in birds and mammals, could be less important in fish (10). Male-only care occurs exclusively in species with external fertilisation with eggs frequently deposited directly within the male's territory (11,12). Male territoriality predates paternal care, and brood defence may, therefore, be a by-product of territory defence (13), as such imposing no additional

costs on males (14,15). Furthermore, males caring for broods may simultaneously obtain further matings from additional females visiting the territory, thereby avoiding mating costs (16). Combined, these factors can decrease the total costs associated with providing care for males (17). In addition, there is evidence in some species that females prefer to mate with males already caring for eggs (18,19), or with larger broods (20,21). Indeed, it has been suggested that a preference for males with broods may even drive males to raid one another's nests for eggs (22). Female preference for males with broods increases the benefits to males of providing care and indicates a possible role for sexual selection in maintaining male-only care in fish (23).

To determine the selection pressures favouring the evolution of male-only care in fish, studies have examined the relationship between paternal care and fitness parameters including condition, offspring survival and mating success, across a wide range of species. Collectively, the results of these studies paint a complex picture, with species showing diverse and often opposing effects of paternal care on components of reproductive success. For instance, increased paternal care reduces condition in both painted greenling (*Oxylebius pictus*) and pumpkinseed fish (*Lepomis gibbosus*), but in the former species, care increases offspring survival and the presence of broods is attractive to females, while in the latter, care has little effect on offspring survival and females find males with large broods unattractive (24,25). This variation, which in part likely reflects species differences in reproductive biology and life-history, but also differences in methodology among studies, currently makes it challenging to determine what combination of costs and benefits have driven the evolution of male-only care to the relatively high levels observed in fish.

Here, we quantify the costs and benefits of male-only care using phylogenetically-controlled meta-analyses. By synthesising the results from studies of 48 teleost species, our approach enables us to determine whether selection for male-only care in fish is shaped principally by (a) low costs of offspring care, arising from the peculiarities of teleost reproductive biology; (b) benefits to offspring in terms of enhanced survival, or, more intriguingly, (c) benefits to the males themselves from attracting additional mates. We quantified costs of care by determining the effect of paternal effort on male condition, while survival benefits to offspring were quantified by determining the effect of paternal effort on the survival of eggs to hatching. Finally, female preference for caring males was quantified by determining the preference for males with versus without broods, and for males with large versus small broods. Additionally, we determined the effect of brood size on paternal effort to test the hypothesis that variation in female preference for males with broods across species is driven by variation in the amount of care that males provide to larger broods. At the same time, our analyses controlled for other factors potentially contributing to variation in the payoffs of paternal care across species, including shared phylogeny, the brooding environment and methodological differences among studies.

Methods

Data collection and selection criteria:

A literature search was conducted using Web of Science with the search terms ‘Fish AND (care* OR offspring OR egg* OR fry)’ to identify studies reporting the effect of paternal care on male condition and offspring survival, the effect of brood size on male care and the effect of brood size and brood presence on female choice. The search included all relevant papers up until June 2020.

Studies were screened manually for four criteria: 1) The species studied exhibits predominantly male-only parental care; 2) a result was reported for one of the above five relationships; 3) sufficient statistical information was present to calculate an effect size; 4) the direction of any relationship was specified. The selection process is summarised in a PRISMA diagram (Figure S1). This search returned a large number of studies which were outside the field of behavioural ecology and could be easily excluded by title or abstract. For the remaining studies, abstracts were screened for evidence mainly of criterion 2 followed by full-text screening to confirm all criteria and extract data. The full dataset included 253 effect sizes from 97 studies, across 48 species (Tables S1-S5).

We used Fisher's Z -transformation of the correlation coefficient (Z_r) as our effect size (26). Where possible, this was calculated from raw data presented in graphs and tables, otherwise test statistics (t , X^2 , or F) or p -values were converted using the R package 'esc' (27) or published formulae (28). The sampling variance of each effect size was calculated as $1/(n-3)$ where n is the number of individuals studied. Data from graphs were extracted using WebPlotDigitizer v4.1 (29). When studies reported multiple results for the same relationship, we included all results as separate data points. When results involved comparisons among more than two treatment groups we included all pairwise comparisons when these data could be obtained. We quantified the following five relationships:

1) Care and condition ($Z_{r_{condition}}$)

To estimate the costs of care, 43 effect sizes were calculated from 25 studies on 19 species measuring the effect of parental care on male condition. In the absence of studies quantifying long-

term costs of care, this analysis focuses on the short-term energetic costs of care. Positive values of $Zr_{condition}$ indicate that providing parental care increases a male's condition. Our dataset includes studies that measured care effort in the following ways: the frequency, duration or rate of fanning behaviour (using fins to move water around the eggs to increase aeration); the duration of defensive behaviour; the duration of total care; the number of broods in a season; and whether a male was with or without a brood. Measurements of male condition in these studies were: growth rate, weight change, hepatosomatic index, lipid mass, survival, and condition factors based on a relationship between length and weight (Table S1).

2) Care and offspring survival ($Zr_{offspring}$)

To determine the effect of paternal care on offspring survival we calculated 36 effect sizes from 18 studies for 16 species. Positive values of $Zr_{offspring}$ indicate that greater care from males increases offspring survival. Studies estimated offspring survival as the number or proportion of eggs surviving to hatching. Care variables were: the frequency, duration or rate of fanning behaviour; the duration of total care; the duration or probability of defensive behaviour; nest attendance duration; and whether the male parent was present or absent (Table S2). Partial filial cannibalism, whereby males consume a proportion of the brood, is a behaviour that has obvious negative consequences for the survival of some offspring but may increase the survival of the remaining offspring, either through reinvestment of energy into parental care (22) or by reducing disease (30,31) or competition among eggs for oxygen (32,33). The costs and benefits of partial filial cannibalism are thus difficult to determine and we chose not to include it among the paternal behaviours that we analysed.

In species where parental care is considered obligate, such as in the Syngnathidae (pipefish and seahorses) where offspring are cared for in a specialised brood pouch, the effect of care on offspring survival is naturally expected to be large (34). While our analysis of $Zr_{offspring}$ includes one pipefish study reporting the effect of duration of care on offspring survival in the broad-nosed pipefish (*Syngnathus typhle*), there are no published data from any syngnathid on the effect of the presence versus absence of care on offspring survival. This omission could lead us to underestimate the mean effect of paternal care on offspring survival across teleosts. To investigate this, we undertook supplementary analyses in which syngnathids were included, specifying an almost perfect correlation between care and offspring survival to represent the likely obligate nature of care in this group (Supplementary Methods).

3) Brood presence and female preference ($Zr_{preference1}$)

To estimate the effect of the presence of eggs in a male's nest on female mating preference we calculated 57 effect sizes from 34 studies for 23 species. Positive $Zr_{preference1}$ values indicate that females prefer males already caring for a brood over those without a brood. Female preference was measured as spawning choice, nest association preference, or the number of eggs received by the male (Table S3).

4) Brood size and female preference ($Zr_{preference2}$)

In addition to brood presence, the size of a male's brood may provide information to females about the quality of the male or his nesting site. We therefore also investigated the effect of brood size on female mating preference. For this analysis we calculated 30 effect sizes from 16 studies for 11 species. Positive $Zr_{preference2}$ values indicate that females prefer males caring for larger broods.

Female preference was measured as spawning choice, nest association preference, or the number of eggs received by the male (Table S4).

5) Brood size and care ($Zr_{brood\ size}$)

Our analysis of the effect of brood size on male care effort included 87 effect sizes from 50 studies on 25 species. Measurements of care were: the frequency, duration or rate of fanning behaviour; the amount or probability of defensive behaviour; whether the brood was cared for or abandoned; and whether the brood was cared for or fully cannibalised. Measurements of brood size were the number of eggs or clutches (Table S5).

Moderator variables:

1) Study design and measures

To explore effects of study design on effect size estimates we recorded whether studies were conducted in the laboratory or the field and whether they were observational or experimental. For analyses of $Zr_{condition}$ and $Zr_{offspring}$, we recorded whether studies measured differences in care effort between guarding males or differences between guarding and non-guarding males or guarded and unguarded broods respectively. For $Zr_{brood\ size}$ we recorded whether studies quantified the effect of brood size on care effort or on the decision to care for or abandon or cannibalise their broods. For analyses of $Zr_{preference1}$, $Zr_{preference2}$, and $Zr_{brood\ size}$ we recorded whether variation in brood size had been experimentally manipulated and for $Zr_{preference1}$ we recorded whether the “no-brood” treatment had been created by removing broods from males. Finally, we also asked whether the size of the effects depended on how the variables (care effort, male condition, offspring survival, brood size and female preference) were measured.

2) Brooding environment

Although males engage in similar care behaviours across species, there is diversity in the brooding environment that may affect the outcomes of care (Figure 1). Differences in $Zr_{offspring}$ between exposed and covered brooding sites might signal a difference in the importance of care for offspring survival; for instance, open nests may require greater defence while broods in closed nests may be at greater risk of hypoxia and so require more fanning to maintain aeration. Similarly, if males must work harder to ensure the survival of broods in particular nest types, the effect of care on a male's condition ($Zr_{condition}$) may then vary across brooding environments. Finally, differences between nest builders and substrate brooders might exist if environmental modifications by males influence the costs or benefits of subsequent care. For each species we therefore classified their brooding environment as: covered substrate (e.g rock crevices), open substrate, covered nest, open nest, brood pouch or mouth brooder (information from published studies and Fishbase (35)).

Statistical analyses:

We constructed five multi-level meta-analytic models to estimate mean effect sizes across species for the five relationships described above. Each model contained random terms for phylogeny, study and species to account for statistical non-independence due to shared ancestry, repeated measures within studies and repeated measures within species respectively and accounted for sampling error variance. The phylogenetic tree was adapted from the most comprehensive published molecular phylogeny of bony fishes (36) (Figure S2, full details reported in the supplementary methods and R script). To explore how differences in study design, study measurements and brooding environment affected our estimates of each effect size, we added each

moderator to the models described above as a fixed effect. The moderator variables included in each of these models for each effect size are shown in Table S9.

We fitted these models in the MCMCglmm (37) and metafor (38,39) packages. The parameter estimates reported in the results are the mode and credible interval (CI) of posterior distribution of the mean effect size estimate from the MCMCglmm models and p values (pMCMC) are calculated from the Markov Chain as either the proportion of posterior samples greater or less than 0 (for mean effect sizes) or the proportion of samples where one parameter is greater than the other (when comparing parameter estimates between two levels of a fixed effect).

Finally, to test whether the strength of female preference for brood presence is driven by the effort that males make when caring for larger broods, we calculated species-level effect sizes for the 13 species for which we had estimates of both $Zr_{brood\ size}$ and $Zr_{preference1}$. Using these data, we fitted a final $Zr_{preference1}$ model in MCMCglmm including $Zr_{brood\ size}$ as a fixed effect. We included sample size (log transformed) associated with each $Zr_{brood\ size}$ estimate as a covariate in this model to account for differences in sampling effort across studies. As the data used in this analysis were summarised to the species level, phylogeny was the only random term. Further details of statistical models are given in the supplementary methods and R script.

Publication bias:

We tested for publication bias for each of the five effect sizes using trim and fill analysis and Egger's regression test using the 'metafor' R package. We found no evidence of publication bias in any of the effect sizes using Egger's regression (Table S7). For $Zr_{condition}$, $Zr_{offspring}$ and

$Zr_{preference1}$, there was some evidence of funnel plot asymmetry, but not for the other two analyses (Figure S2).

Results

No effect of care on male condition

Providing care negatively impacted male condition in 9/19 of the species in our dataset while in one species condition increased while caring (Figure 2a). When averaged across species, caring did not affect male condition ($Zr_{condition}$ mean effect = -0.28, 95% credible interval (CI) = -0.62 to 0.08, $pMCMC=0.12$; $N_{species} = 19$, $N_{studies} = 25$, $N_{effect\ sizes} = 43$; Table S6). Differences in brooding environment failed to explain variation among species in the effect of care on condition (Figure S4a; Table S10).

No effect of male care on offspring survival

Care increased offspring survival in 8/16 species (Figure 2b). Across species we found no significant effect of male care on offspring survival ($Zr_{offspring}$ mean effect = 0.25, CI = -0.18 to 0.76, $pMCMC = 0.23$; $N_{species} = 16$, $N_{studies} = 18$, $N_{effect\ sizes} = 36$; Table S6). When including syngnathids where paternal care is considered obligate, the mean effect size increased but remained nonsignificant (Table S8). The effect of male care on offspring survival did not differ among brooding environments (Figure S4b; Table S11).

Females prefer caring males but not larger broods

Females preferred males with broods in 14/23 species, while in two species females avoided these males (Figure 3a). Across species, females show a significant preference for males already caring for broods ($Zr_{preference1}$ mean effect = 0.51, CI = 0.04 to 1.38, pMCMC = 0.04; $N_{species} = 23$, $N_{studies} = 34$, $N_{effect\ sizes} = 57$; Table S6). In contrast we found no effect of brood size on female mating preference ($Zr_{preference2}$ mean effect = 0.19, CI = -0.32 to 0.7, pMCMC = 0.42; $N_{species} = 11$, $N_{studies} = 16$, $N_{effect\ sizes} = 30$; Figure 3b, Table S6).

To investigate whether female preference for caring males is driven by the effort males expend when caring for larger broods, we examined how males adjust care in relation to brood size. We found that males significantly increased their care effort when guarding larger broods ($Zr_{brood\ size}$ mean effect = 0.47, CI = 0.19 to 0.86, pMCMC = 0.006; $N_{species} = 25$, $N_{studies} = 50$, $N_{effect\ sizes} = 87$; Figure 4, Table S6). Across 13 species for which we had estimates for both $Zr_{brood\ size}$ and $Zr_{preference1}$, we found that female preferences for males with broods were stronger in those species where males cared more for larger broods (estimate = 1.24, CI = 0.24 to 2.35, pMCMC = 0.028; Figure 5).

No effect of study methodology

Variation in effect sizes was not explained by differences in study design or the way in which the variables were measured. A detailed breakdown of these results is provided in the Supplementary Methods.

Discussion:

Compared to other taxa, paternal care in fish appears to have little impact on offspring survival. Instead, we find that the benefit of providing care comes from increased mating success. Females prefer caring males, particularly when males increase care with more offspring. This supports the hypothesis that caring males do not suffer a mating opportunity cost and indicates that sexual selection through female choice is likely to be an important mechanism maintaining male-only care in fish (40). In addition to making males attractive to females, care has little impact on condition, either because it is not energetically demanding, or because males can obtain sufficient resources to sustain the required investment. In summary, male fish have little to lose by investing in the care of offspring, and much to gain.

Despite our results revealing on average little cost to care, and little benefit in terms of survival of offspring, variation in these effects across species is evident. However, this variation was not explained by methodological differences among studies and therefore the estimation of the costs and benefits of parental care are robust to the specific methodology that a study employs. Variation in the effects of care on male condition and offspring survival was also not explained by differences in the environment in which offspring develop. This may indicate that selection and modification of brooding environments represent important adaptations that successfully mitigate risks to offspring and thus reduce the costs and benefits of active male care. Moreover, this may help to explain why we failed to find any effect of care on offspring survival or male condition across species.

The relationships between care, condition, and offspring survival, may be influenced by factors we were unable to account for. First, a number of species in our dataset exhibit partial brood

cannibalism, which may affect both offspring survival and male condition (e.g. 32,33,41–43). If males regularly compensate for energy lost during care through filial cannibalism, the observable effect of care on male condition would be reduced. Alternatively, if males cannibalise some eggs to improve the survival of their remaining brood, this positive effect of care will not be reflected in measures of hatching success. Second, the lack of studies measuring the effects of care beyond hatching means we were unable to assess the longer-term consequences of care for offspring survival and male condition which may have resulted in underestimates of these effects. Further research into the longer-term effects of care as well as the adaptive function of filial cannibalism will be important for a more complete understanding of the costs and benefits to males of offspring care, as well as the benefits to females of mating with caring males.

We found that female preferences for males with broods were particularly strong in species where males substantially increased their care for large broods. This could indicate that females are selected to choose males already caring for broods when this will result in greater care for their offspring. However, if offspring survival is not enhanced by male care, as our results indicate, females would not benefit from increased care by males. An alternative explanation for this correlation is that the presence of a brood provides an honest signal of male quality. If providing care is costly, only high-quality males will be able to raise a brood. Although we find that care does not reduce condition, this does not necessarily contradict the idea that care is a condition-dependent signal of quality, since observed levels of care may reflect what males can afford to invest without losing condition. Experiments that manipulate the costs of care for males of differing quality will be necessary to determine the extent to which paternal care reliably reflects male quality in fish. In addition to using the presence of broods as a cue to male quality, females

may also benefit from choosing males with broods if this dilutes the risk to their offspring of predation or filial cannibalism by the male (22,44,45), but at present the relative importance of these different factors remains unclear.

Although our results suggest that females prefer males already providing care, this preference was not universal and across species there was no evidence that females preferred males with larger broods. Large broods may be associated with increased egg mortality due to reduced oxygen availability (46), increased disease transmission (47), or filial cannibalism by males (33,48). Larger broods also often contain older clutches which are more valuable to the male leaving younger clutches vulnerable to cannibalism or abandonment (49,50). Such effects may reduce the benefits to females of choosing males with large broods, thus helping to explain why we see a preference for males with broods but not for males with larger versus smaller broods. A clear example of this is seen in the painted greenling, where male care improves offspring survival and where hatching success initially increases with brood size but then declines sharply beyond eight clutches (24).

In general, we expect selection to favour use of the most cost-effective cues that permit accurate assessment of males (51). In this respect, the presence of a brood is simpler information to process than continuous brood size, since the latter requires a mechanism for quantity discrimination (52). By choosing males with any number of eggs, females can quickly identify caring males without incurring high processing costs. It has also been hypothesised that female choice on the basis of brood presence/absence reduces sampling costs by copying the choices of other females (53). Other traits used by female fish to assess males include body size (54,55), colour (56), nest quality

(57) and courtship displays (56,58). In some species, these traits may provide more accurate information about a male's quality; in fifteen-spined sticklebacks (*Spinachia spinachia*), for example, females show no preference based on brood size but instead prefer males that demonstrate better care during courtship (59,60).

Male-only care is more common in fish than in any other taxa, but examples of this strategy are nonetheless widespread. In arthropods, species with male-only care share similar traits with fish including association between the male and the eggs and simultaneous paternal care and mating (61). Female choice for caring males has also been found in some species (62,63). Similarly, in amphibians, external fertilisation combined with male defence of nest sites within territories has been linked to the evolution of male care (64). Simultaneous care and mating also occurs, but is generally limited to species that attend to but do not transport eggs or larvae (65,66). It is possible that similar selective processes are responsible for male-only care in these groups but further studies are needed for both arthropods and amphibians to address this.

In contrast, male-only care in birds appears to result from different processes. Species with male-only care often exhibit classical polyandry, where males do not benefit from additional matings when providing care (67), and are also characterised by lower remating opportunities for both sexes than species with female-only care (68). This suggests that the trade-off between care and mating opportunities is important in determining the costs of paternal care in birds. Similarly, sex-role reversal is common within polyandrous birds, whereby females compete for access to males, in contrast to many fish where males remain the more competitive sex (5). Parental care in birds is considered highly demanding with a greater risk of predation to parents than observed in fish

(69,70). However, male-only care is predominantly found in bird species with precocial young where the demands of care are reduced. Additionally, in some groups, such as the ratites and megapodes, males care for the eggs of multiple females which resembles more closely the situation observed in fish (1).

In summary, this study provides support for the hypothesis that male care in fish has evolved by sexual selection, and not as a strategy to simply increase offspring survival. The simple nature of parental care in fish and a territorial system, whereby males guard territories that attract females, creates an environment in which caring for offspring and continuing to mate can be achieved simultaneously. Although a similar situation is found in some arthropods and amphibians, this contrasts to the majority of taxa where males lose mating opportunities by providing care. In addition, males increase the effort they put into caring for larger broods, which may encourage females to choose males that are already guarding broods. These results suggest that sexual selection does not always act predominantly on the less caring sex, but rather can select for increased care investment in males and lead to largely different parental care patterns in different taxonomic groups.

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Data accessibility statement

The data and R code supporting this article are available from the Dryad Digital Repository: <https://doi.org/10.5061/drad.bg79cnp7s>

Competing interests statement

We declare we have no competing interests

Author contributions

JPG and ASG conceived of the study; RLG JPG and ASG designed the study; RLG collected the data; RLG and PAD analysed the data; all authors wrote the manuscript and gave final approval for publication.

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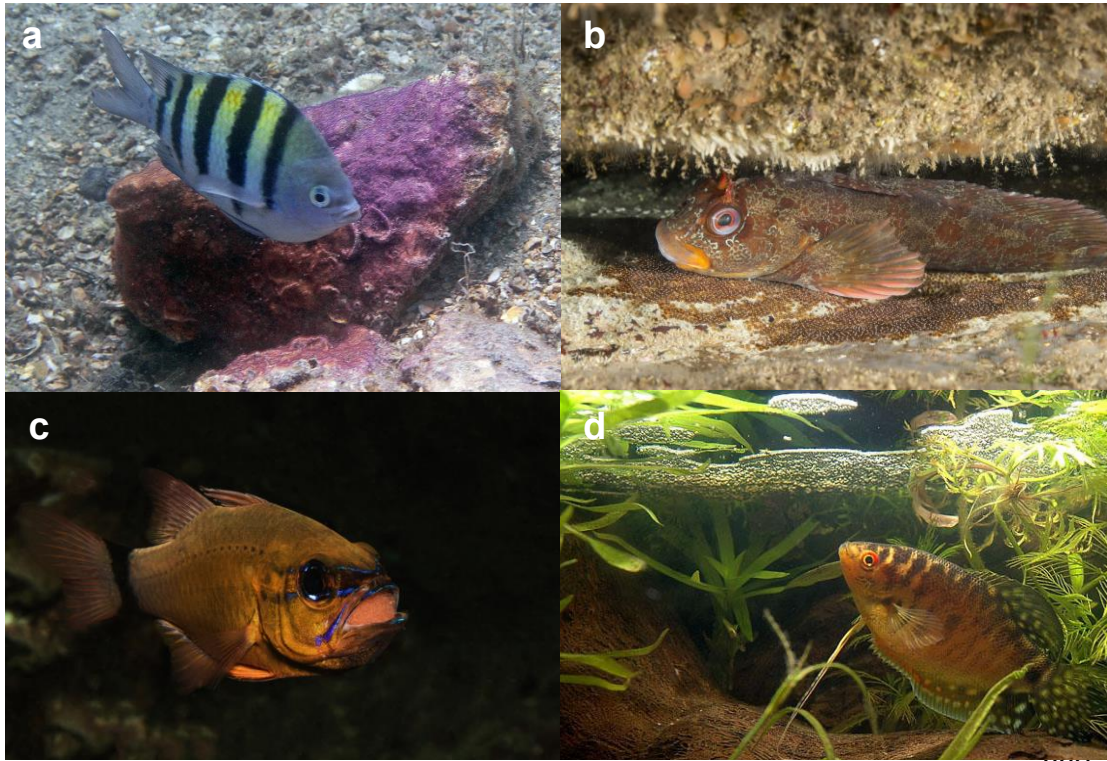
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609

610 **Figure 1. Diversity of paternal care in fish.** Males care for their brood in different brooding
 611 environments. a) Substrate spawners, such as the sergeant major (*Abudefduf saxatilis*), guard their
 612 brood on an unaltered substrate in the open. b) Some males, such as the tompot blenny
 613 (*Parablennius gattorugine*) create simple nests by locating a rock crevice or bivalve shell and may
 614 alter it, for example by covering it in sand or algae. c) Mouth brooders, such as the ring-tailed
 615 cardinalfish (*Ostorhinchus aureus*), carry offspring (eggs and larvae) within their mouths. d)
 616 Gouramis from the family Ophronemidae build a more complex ‘bubble nest’ creating a bubble of
 617 air for each egg. Photo permissions and credits: a) Kevin Bryant b) Paul Naylor marinephoto.co.uk
 618 c) Antje Schultner d) Alberto Garcia. Images a, c and d are under licence CC BY-NC-SA 2.0
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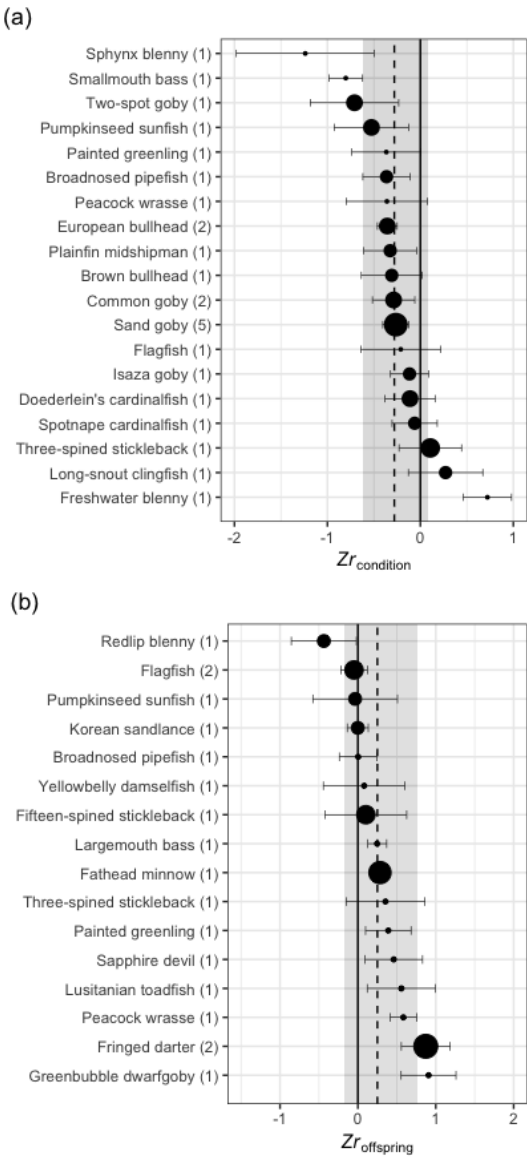


Figure 2. The effect of paternal care on (a) male condition and (b) offspring survival. Points are species-level, weighted mean effect sizes with 95% confidence intervals. The dashed line indicates the mean effect size across species with credible intervals donated by the shaded bar. Point sizes are scaled to the total number of effect sizes while the number of studies is given in brackets beside the species names.

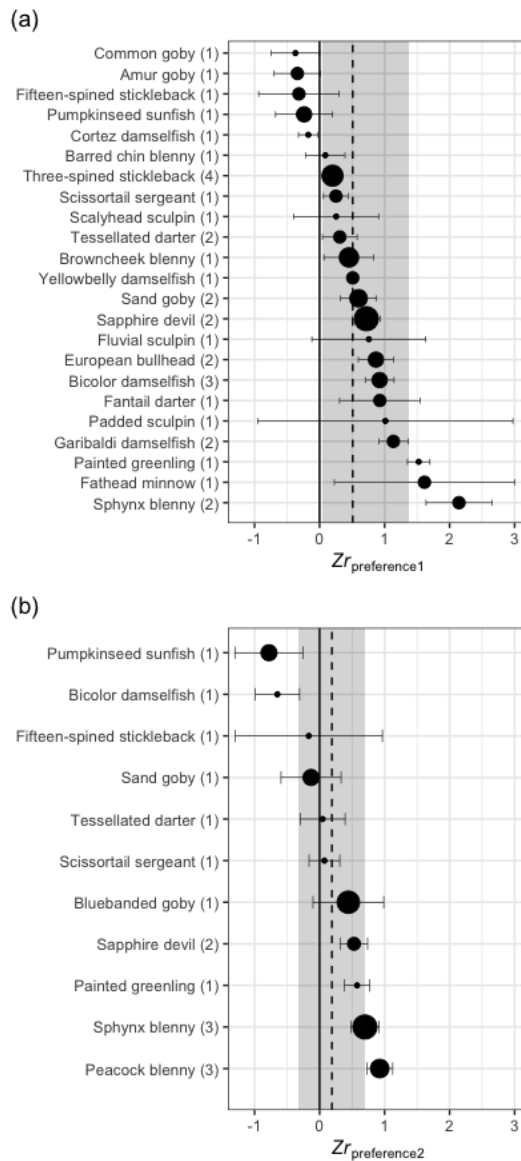


Figure 3. Female preference in relation to (a) brood presence and (b) brood size. Points are species-level, weighted mean effect sizes with 95% confidence intervals. The dashed line indicates the mean effect size across species with credible intervals donated by the shaded bar. Point sizes are scaled to the total number of effect sizes while the number of studies is given in brackets beside the species names.

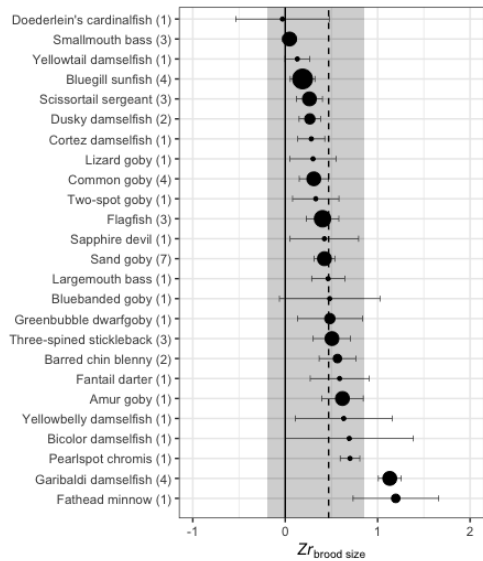


Figure 4. The effect of brood size on male care effort. Points are species-level, weighted mean effect sizes with 95% confidence intervals. The dashed line indicates the mean effect size across species with credible intervals donated by the shaded bar. Point sizes are scaled to the total number of effect sizes while the number of studies is given in brackets beside the species names.

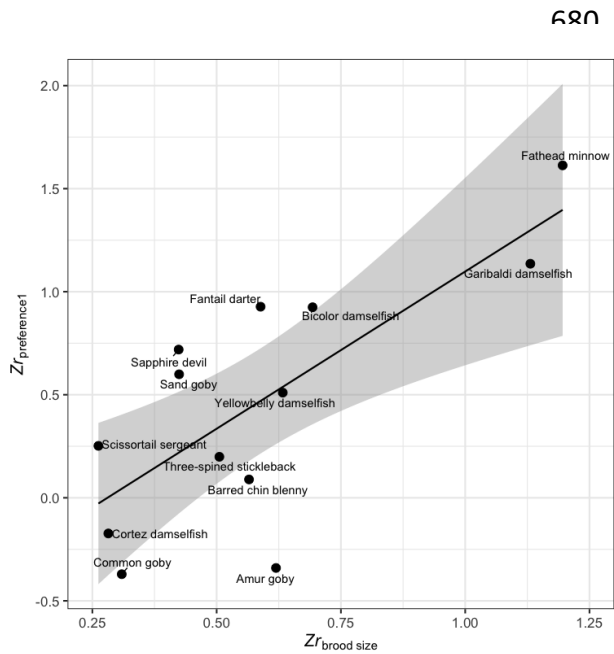


Figure 5. Correlation between female preferences for brood presence and male care adjustment with brood size.