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Cooperative growth regulation in coral-dwelling fishes

Philip L. Munday*, Adrian M. Cardoni and Craig Syms

ARC Centre of Excellence for Coral Reef Studies, School of Marine Biology and Aquaculture, James Cook University, Townsville, Queensland 4811, Australia
**Author for correspondence* (*philip.munday@jcu.edu.au*).

Dominant individuals often grow faster than subordinates because they gain a greater share of important resources. However, dominants should also strategically adjust their growth rates, relative to the size of subordinates, if this improves their reproductive success. Here, we show that individuals in breeding pairs of the coral-dwelling fish *Gobiodon histrio* regulate their growth to reduce the size difference between partners. In pairs where one individual was larger than the other, the smaller individual increased its growth rate and the larger individual decreased its growth rate, compared to individuals in size-matched pairs. The reproductive success of breeding pairs is limited by the size of the smallest individual in the pair. Therefore, it appears that the larger individual trades-off its own growth against that of the smaller individual, thereby improving the reproductive success of both individuals in the pair. This demonstrates a remarkable ability of individuals to strategically adjust their body size to suit the local social environment, and reveals a novel mechanism for size-assortative mating.

Keywords: growth rate; strategic growth; size-assortative mating; cooperation

1. INTRODUCTION

Dominant individuals in social groups often have higher growth rates than subordinates, either because they secure a greater share of the available food, or because they suppress the growth of subordinates through agonistic interactions that affect the energy budget and stress levels of subordinates (Jones & McCormick 2002; Krause & Ruxton 2002). However, in a new perspective on social control of growth, several recent studies suggest that subordinates might regulate their own growth depending on the size of dominants within the group (strategic growth regulation). In social groups of the anemonefish *Amphiprion percula*, subordinates appear to regulate their growth to maintain a minimum size difference between themselves and their immediate dominant (Buston 2003). Similarly, helper males of the cichlid *Neolamprologus pulcher* adjust their growth according to the size of the breeder male, increasing their growth rate when paired with a larger breeder (Heg *et al.* 2004). In both these examples, non-breeding subordinates appear to regulate their growth to maximize their chance of attaining a breeding position, while at the same time avoiding conflict with dominants. We predict that dominant breeders will also strategically adjust their growth, relative to the size of others in the social group, if it increases their reproductive success.

Strategic growth adjustment may be particularly beneficial in species where reproductive success is strongly size-dependent. For example, in monogamous coral-dwelling gobies (fishes of the genera *Paragobiodon* and *Gobiodon*), the number of offspring hatched by a breeding pair is dependent on the size of both the male and the female (Kuwamura *et al.* 1993). This pattern appears to occur because fecundity increases with size for females and egg care ability increases with size for males. A consequence of this positive relationship between size and reproductive success for both sexes is that reproductive success of each breeding pair is constrained by the size of the smallest individual in the pair (Kuwamura *et al.* 1993). Therefore, strategic growth adjustment would be beneficial in circumstances where one individual in a pair is larger than the other, as might happen when a new breeding pair forms.

We tested for strategic growth regulation in pairs of the coral-dwelling goby, *Gobiodon histrio*. Individuals in breeding pairs of *G. histrio* are usually approximately size-matched (Munday *et al.* 1998). We experimentally manipulated the size of partners by creating new pairs where the male was larger than the female or vice versa. If individuals regulate their growth to maximize the reproductive success of the pair, we predicted that the smaller individual in the pair would accelerate its growth when there was a large size difference between itself and the larger individual. We also hypothesized that the larger individual might strategically reduce its own growth to enable the smaller individual to grow as rapidly as possible.

2. MATERIAL AND METHODS

(a) *Study species and location*

Gobiodon histrio is a small (less than 60 mm total length) obligate coral-dwelling fish that preferentially inhabits colonies of *Acropora nasuta*. Breeding pairs occupy coral colonies greater than 150 mm diameter and there is usually only one pair per coral (Munday *et al.* 1998). Juveniles occupy smaller coral colonies not used by adults (Hobbs & Munday 2004). Adults rarely move between corals and pairs may remain together for most of their adult life (Munday, unpublished work). Our experiment was conducted between March and May 2005 on the fringing reef at Orpheus Island (18°37′ S; 146°29′ E) on the Great Barrier Reef, Australia.

(b) *Strategic and sex-dependent growth*

To test for strategic growth regulation we used a manipulative field experiment in which adult gobies were placed in new pairs in one of three combinations: (i) male larger than the female, (ii) female larger than the male, or (iii) male and female approximately the same size. This arrangement enabled us to compare the growth rate of individuals of either sex in both the smaller and larger role in a pair.

Adult pairs of *G. histrio* inhabiting colonies of *A. nasuta* were anaesthetized with clove oil solution, collected, and transported to the laboratory. Each fish was measured (standard length (SL) to the nearest 0.1 mm), sexed according to the shape of the genital papilla (Munday 2002) and uniquely marked with subcutaneous elastomer microtags (Northwest Technologies). Elastomer tags have a high retention rate and do not affect the growth or survival of gobies (Malone *et al.* 1999).

Fishes were sorted into: (i) 21 pairs where the male was longer than the female (mean difference 5.1 mm SL), (ii) 23 pairs where

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Table 1. Linear mixed effects analysis of goby growth rates. (The model was fitted by restricted maximum likelihood (REML). The test of coral colony (treatment) was based on the difference of the −2 REML log likelihoods of the model with and without the random term. This difference was tested against the χ^2 distribution with 1 degree of freedom.)

fixed effects

source	d.f.	*F*	*p*
treatment	2,50	1.34	0.2711
sex	1,49	12.80	0.0008
treatment × sex	2,49	77.16	<0.0001
male versus female equal size	1,49	4.75	0.0341
male smaller versus female smaller	1,49	7.05	0.0106
initial size	1,49	10.72	0.0019

random effects

source	estimate	95% confidence interval	likelihood ratio	*p*
coral colony (treatment)	0.2563	0.1303, 0.7170	6.9	0.0086
residual	0.4527	0.3159, 0.7031		

the male was shorter than the female (mean difference 5.2 mm SL), and (iii) 21 pairs where the male was approximately the same length as the female (mean difference 0.1 mm SL). Original partners were never paired together. Each new pair was returned to the reef and placed on a coral colony that had previously been occupied by a pair of *G. histrio*. Neither individual in the new pair was a prior resident of the coral. Pairs were recollected after approximately 60 days. Individuals were identified by their elastomer tags, measured, and sexed by the shape of the genital papilla.

(c) *Analysis*

Growth rate, measured as the difference in SL over the duration of the experiment, was analysed using a linear mixed effects model. Experimental treatment, sex, and their interaction were the key fixed-factor tests of experimental effect. As growth rate often decreases with fish size, we removed this effect using a covariate approach. We could not include initial size as a simple covariate because initial size formed a component of the experimental manipulation. Consequently, we treated size as a partial covariate. We did this by detrending initial size by treatment, sex, their interaction, and coral colony (treatment), and then using the residuals of this model in place of initial size in a standard covariate model. This removed any confounding between the initial-size covariate and the size treatment in the standard covariate model. Because each male–female manipulation occurred within a single coral colony, a random effect of coral colony (treatment) was included in the model to ensure that the fixed effects were tested with the correct degrees of freedom. Two contrasts of the treatment × sex term were constructed to test whether: (i) growth rates of females in the larger role differed from males in the larger role, and (ii) growth rates of males and females differed in equal-sized pairs.

3. RESULTS

Fifty-three of the 65 pairs were intact at the end of the experiment and were included in the analysis. There was a strong interaction between experimental treatment and sex (table 1 and figure 1*a*). When males were initially larger, their growth rate was very low (0.12 ± 0.22 mm) compared to female growth rates (2.60 ± 0.22 mm). In contrast, when females were initially larger their growth rates were very low (0.28 ± 0.19 mm) compared to male growth rates (1.83 ± 0.19 mm). Growth rates of males and females in equal-sized pairs were intermediate between males and females in unequal-sized pairs (male 1.15 ± 0.20 mm, female 1.64 ± 0.20 mm). This indicates that: (i) smaller partners of either sex increased their growth rate when there was a large size difference between themselves and their partner, and (ii) larger partners of either sex decreased their growth rate when there was a large size difference between themselves and their partner.

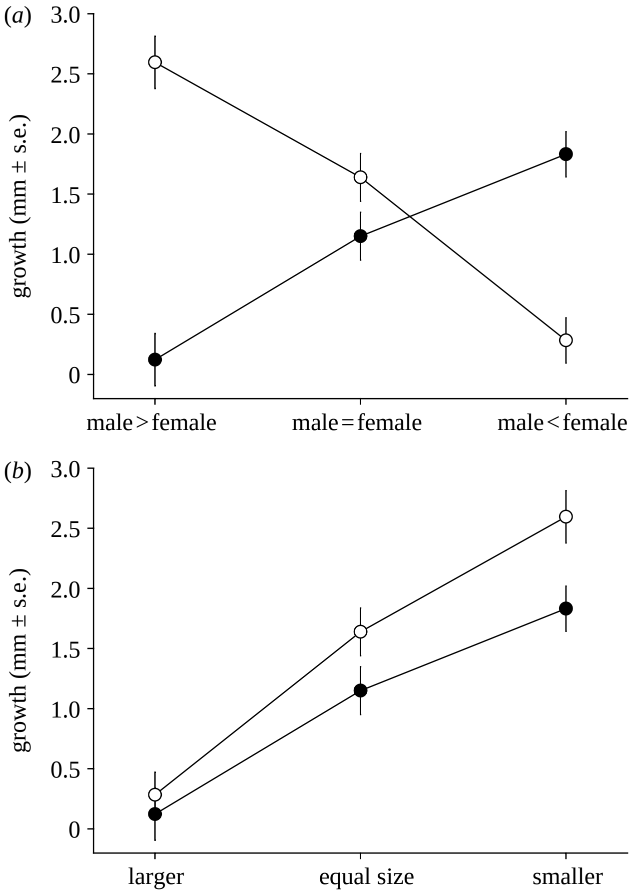

Figure 1. Growth rates of female (open circles) and male (filled circles) in pairs of *Gobiodon histrio*. (*a*) Mean growth over 60 days ordered by experimental treatment to display interaction between treatment and sex. (*b*) Mean growth over 60 days ordered by relative size in pair to display differences between sexes. Means and standard errors are derived from linear mixed effects model estimates.

There was a strong effect of the initial-size covariate (table 1) due to a linear growth decrease with increasing fish size. Examination of model residuals indicated that this relationship was effectively removed from the model, and that the lower observed growth rate of the larger individual in the pair was independent of the growth decrease expected simply due to greater initial size. Similarly, the higher observed growth rate of the smaller individual in the pair was independent of the higher growth rate expected simply due to smaller initial size.

Interestingly, females that were smaller than their partner grew faster than males that were smaller than their partner (table 1 and figure 1*b*). In equal-sized pairs, females also grew faster than males (table 1), although the difference was less than that observed between small males and females (figure 1*b*). There was no difference in the growth rate of males and females when they were larger than their partner. *Gobiodon histrio* has the capacity to change sex in each direction (Munday 2002), but no individuals changed sex during the experiment.

4. DISCUSSION

Social conditions influence growth in many species of fish (Hofmann *et al.* 1999; Jones & McCormick 2002). In particular, large dominant individuals often appear to suppress the growth of smaller subordinates (e.g. Koebele 1985; Forrester 1991; Booth 1995, but see Booth 2004). We show that social control of growth can be more complex than predicted by a simple model of dominant suppression. Both individuals in pairs of *G. histrio* adjusted their growth rate when there was a relatively large size difference between them, and they did so in a way that caused their sizes to converge. This indicates that individuals can strategically modify their growth and may do so in a cooperative manner if it increases their reproductive success.

Cooperative interactions result in a net gain to the participants, but may involve expenditure that would incur a fitness cost if considered outside the partnership (Noë 2006). Larger individuals in pairs of *G. histrio* reduced their growth rate in the same circumstances that smaller individuals increased their growth rate. This suggests that the large partner trades-off its own growth with that of the smaller partner. This should increase the reproductive success of both individuals, because the number of offspring hatched by a pair of coral gobies is limited by the size of the smaller individual (Kuwamura *et al.* 1993). A growth trade-off could occur if reduced feeding by the larger individual provided additional food resources for the smaller one. Thus, a simple behavioural response to differences in body size by the larger individual could produce a cooperative reallocation of resources that benefits both individuals.

An alternative explanation is that the larger individual diverts energy to activities other than growth when paired with a smaller partner, because further growth would not improve its current reproductive success. In this scenario, reduction in growth by the larger individual does not release additional food that is used by the smaller individual. Nevertheless, the smaller individual still opts to increase its growth rate, because a larger body size will improve its own reproductive success (i.e. because it has a large partner). Increased growth by the smaller individual could be achieved by using energy stores, or by spending more time feeding. It is also possible that the larger individual allocates additional energy towards activities that the smaller individual might normally conduct, such as territory defence, thus freeing-up more energy for growth by the smaller partner. Whether individuals in pairs of *G. histrio* share resources or not, it is clear that they regulate their growth to convergence on approximately the same body size.

Strategic growth adjustments can arise from individual restraint, or through the direct effect of dominants on subordinate growth (Buston 2003; Heg *et al.* 2004). Previous examples of strategic growth regulation have not been able to distinguish between these alternatives. For example, the reduced growth of subordinate anemonefish as they approach the size of their immediate dominant (Buston 2003) could arise through individual decisions about growth, or because dominants become more aggressive to subordinates as they get closer in size. Our results are consistent with individual restraint as a mechanism of strategic growth regulation, because the reduction in growth rate of the larger individual in a pair was not affected by dominant suppression. This lends support to several recent theoretical models (reviewed by Johnstone 2000) in which individual restraint is regarded as an important factor in the organization of animal societies.

Females often have lower growth rates than males, presumably because eggs are more expensive to produce than sperm. Contrary to this expectation, we found that female coral gobies had higher growth rates than males in situations where they were smaller or equal in size to their partner. In keeping with these differences in growth, we also found that females were slightly larger than males in a large proportion of natural pairs at Orpheus Island (see electronic supplementary material). This suggests that the relationship between size and reproductive success might not be identical for male and female *G. histrio* at this location, and therefore, females keep growing until they are slightly larger than their partner.

Mechanisms known to generate size-assortative mating include: (i) temporal or spatial synchronicity of similar sized mates (mate availability), (ii) physical limitations to reproduction between different sized partners (mating constraints), and (iii) preference for large mates combined with size-based competition for mates (mate choice) (Crespi 1989; Harari *et al.* 1999). Strategic growth regulation can now be added to this list. Individuals in *G. histrio* pairs that were initially mismatched in size adjusted their growth so that they converged on approximately the same size, and it appears that they did so because it increases their reproductive success.

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