BIOLOGY
LETTERS

royalsocietypublishing.org/journal/rsbl

Research

Cite this article: Reed C, Branconi R, Majoris J, Johnson C, Buston P. 2019 Competitive growth in a social fish. *Biol. Lett.* **15**: 20180737.
http://dx.doi.org/10.1098/rsbl.2018.0737

Received: 20 October 2018
Accepted: 14 January 2019

Subject Areas:
behaviour, ecology, evolution

Keywords:
vertebrate growth, competitive growth, phenotypic plasticity, social evolution, *Amphiprion percula*, *Suricata suricatta*

Author for correspondence:
Peter Buston
e-mail: buston@bu.edu

Electronic supplementary material is available online at https://dx.doi.org/10.6084/m9.figshare.c.4381718.

THE ROYAL SOCIETY
PUBLISHING

Animal behaviour

Competitive growth in a social fish

Cymone Reed, Rebecca Branconi, John Majoris, Cara Johnson and Peter Buston

Department of Biology, Boston University, 5 Cummington Mall, Boston, MA 02215, USA

PB, 0000-0001-5513-8259

Many animal societies have dominance hierarchies in which social rank is correlated with size. In such societies, the growth and size of individuals can be a strategic response to their social environment: in fishes, individuals may decrease their growth rate to remain small and retain a subordinate position; in mammals, individuals may increase their growth rate to become large and attain a dominant position—a strategy called competitive growth. Here, we investigate whether the clown anemonefish, *Amphiprion percula*, exhibits competitive growth also. We show that juvenile clownfish paired with a size-matched reproductive rival increase their growth rate and size relative to solitary controls. Remarkably, paired individuals achieved this, despite being provided with the same amount of food as solitary controls. Our results demonstrate that clownfish are able to increase their growth rate in response to social competition. This study adds to the growing body of evidence that the growth of social vertebrates can be a fine-tuned plastic response to their social environment.

1. Introduction

In many animal societies, there are dominance hierarchies within which an individual's social rank determines its access to reproduction [1–3]. Often, the social rank of individuals is dependent, either partially or completely, on their size [4–6]. In these societies, where size and rank influence reproductive success, there should be strong selection for growth strategies that maximize an individual's chances of retaining its current rank or attaining higher rank. In the tomato anemonefish, *Amphiprion frenatus* [7], Kalahari meerkats, *Suricata suricatta* [8], and the mole-rats *Heterocephalus glaber* and *Fukomys damarensis* [9,10], when females acquire the dominant rank, they may increase their growth rate to increase their reproductive output and/or reinforce their position (see also [11,12] for evidence of a similar phenomenon in male fishes). By contrast, in the clown anemonefish, *Amphiprion percula* [13], the cooperatively breeding cichlid *Neolamprologus pulcher* [14] and the emerald goby, *Paragobiodon xanthosomus* [15], within established dominance hierarchies, subordinate individuals decrease their growth rate to remain small and retain their current rank. Most recently, it has been shown that, in Kalahari meerkats, *S. suricatta*, at the formation of dominance hierarchies, size-matched individuals increase their growth rate to become large, outcompete their rivals and attain dominance—a strategy known as competitive growth [16]. Outstanding questions are, how flexible are these strategies and can individuals of the same species adopt different strategies in different contexts?

Here, we investigate whether clownfish *A. percula* are capable of competitive growth also. Groups of clownfish inhabit sea anemones which afford protection from predators [17–22]. Each group is composed of a breeding pair and 0–4 non-breeders [23,24]. Within each group, there is a size-based dominance hierarchy: the female is largest, the male is second largest, and the non-breeders get progressively smaller [13,25]. Clownfish are protandrous hermaphrodites [4,26]: if the female of the group dies, then the male changes sex and assumes the position vacated by the female, and the largest non-breeder from the anemone inherits

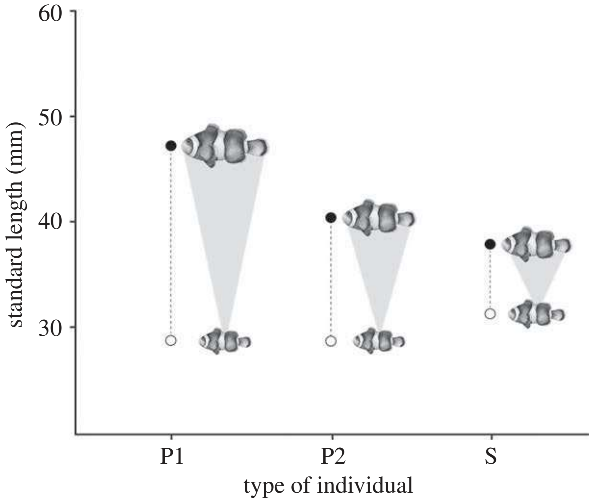

Figure 1. Initial standard length and final standard length of clownfish in the wild ($n = 1$ replicate, $n = 3$ individuals). Three individuals are shown: one that became rank 1 in the pair (P1), one that became rank 2 in the pair (P2) and one that lived solitarily (S). Open circles represent initial lengths and closed circles represent final lengths. (Illustrations by R.B.)

the position vacated by the sex-changing male [23,24]. The size hierarchy represents a queue to attain dominance: individuals only ascend in rank when a higher rank individual disappears, and the smallest fish in the group is always the most recent recruit [13,23]. A single anecdotal observation suggests that, on the rare occasions that anemones are vacant, they may be colonized by size-matched recruits [27]. Under these conditions, the individuals seem to engage in a growing race, the outcome of which determines which individual becomes dominant (figure 1). Here, we experimentally test the hypothesis that *A. percula* individuals paired with size-matched rivals exhibit competitive growth.

2. Material and methods

(a) Study population

We conducted these experiments at Boston University (Boston, MA, USA) in November–December 2016 and 2017. All fish used in these experiments were reared from broodstock wild-caught as non-breeders (less than 30 mm in standard length) in Papua New Guinea and supplied by Quality Marine and Sea Dwelling Creatures. The removal of non-breeders is considered a sustainable practice. A detailed description of broodstock housing conditions and larval rearing conditions can be found elsewhere [28,29].

(b) Housing conditions

Experimental fish, reared in the laboratory, were housed in 1 l tanks which were part of a re-circulating saltwater aquarium system. Flow through each tank was approximately $9\ \mathrm{l\ h^{-1}} \pm 0.5\ \mathrm{l}$. Abiotic conditions were monitored regularly and maintained as constant as possible: $\mathrm{pH} = 8.1 \pm 0.1$, temperature $= 26.1 \pm 0.6°\mathrm{C}$ and salinity $= 32 \pm 0.5$ ppt were monitored daily; ammonia (0 ppm), nitrite (0 ppm) and nitrate (0 ppm) were monitored weekly (API test kits, Mars Fishcare, North America). Lighting was provided by ambient fluorescent lighting and the room was maintained on a 12 h L : 12 h D light cycle. The life support system consisted of a biomedia bed for biological filtration and a UV sterilizer for disinfection.

(c) Experimental set-up

To test the hypothesis that juvenile clownfish will exhibit competitive growth, we conducted two experiments: the first in 2016; the second in 2017 to demonstrate the repeatability of the results. We measured the initial standard length (ISL) of 27 juvenile clownfish to within 0.1 mm using a microscope and ImageJ [30]. We then formed nine trios (nine replicates), within which the fish were length-matched. For each replicate, two fish were housed as a pair in one tank and the third fish was housed solitarily in another tank. The fish could not see individuals in other tanks. All 27 individuals were fed the same ration of fish pellets: six C1 pellets (840–1410 µm) in 2016; 0.1 g of B1 pellets (250–360 µm) in 2017; TDO Chroma Boost, APBreed, Reed Mariculture Inc., CA, USA, in both years. The pair was divided by a partition during feeding; a partition was also placed in the singleton tank during feeding as a sham control. After feeding, the partitions were removed. When aggression was observed between individuals, the experiment was stopped (after two weeks in 2016; after three weeks in 2017). The final standard length (FSL) of all surviving individuals ($n = 6$ replicates and $n = 18$ individuals in 2016; $n = 7$ replicates and $n = 21$ individuals in 2017) was measured to within 0.1 mm using a microscope and ImageJ. Within pairs, we assigned each individual to a type (pair-rank-1, P1; or, pair-rank-2, P2) on the basis of their FSL, with the larger being P1.

(d) Statistical analyses

To test the hypothesis that juvenile clownfish will exhibit competitive growth, we used a mixed-effects ANOVA with FSL as the dependent variable and type of individual (pair-rank-1, P1; pair-rank-2, P2; or solitary, S) as the independent variable (R version 3.3.1). To account for the lack of independence among individuals from the same replicate, we entered replicate ID as a random effect using the R package lme4 [31,32]. The data from the two experiments (two years) were analysed separately because pooling the data from the two years would have resulted in a non-normal (bi-modal) distribution.

3. Results

(a) Experiment 1: 2016

The type of individual was a significant predictor of FSL (mixed-effects ANOVA: type of individual, $F_{2,10} = 6.918$, $p = 0.0130$). The parameter estimates indicated that while P1 tended to be larger than P2 (Tukey's HSD (honestly significant difference): $p > 0.05$) and P2 tended to be larger than S (Tukey's HSD: $p > 0.05$), P1 was significantly larger than S (Tukey's HSD: $p = 0.0106$; figure 2*a*). The whole model explained an estimated 94.7% of the variation in FSL; a reduced model including only the random effect explained 89.4% of the variation; a reduced model including only the fixed effect explained 4.3% of the variation.

(b) Experiment 2: 2017

The type of individual was a significant predictor of FSL (mixed-effects ANOVA: type of individual, $F_{2,12} = 26.1925$, $p < 0.00001$). The parameter estimates indicated that P1 was significantly larger than P2 (Tukey's HSD: $p = 0.0021$), P2 was significantly larger than S (Tukey's HSD: $p = 0.0452$) and P1 was significantly larger than S (Tukey's HSD: $p < 0.0001$; figure 2*b*). The whole model explained an estimated 73.7% of the variation in FSL; a reduced model including only the random effect explained 0% of the variation; a reduced model including only the fixed effect explained 67% of the variation.

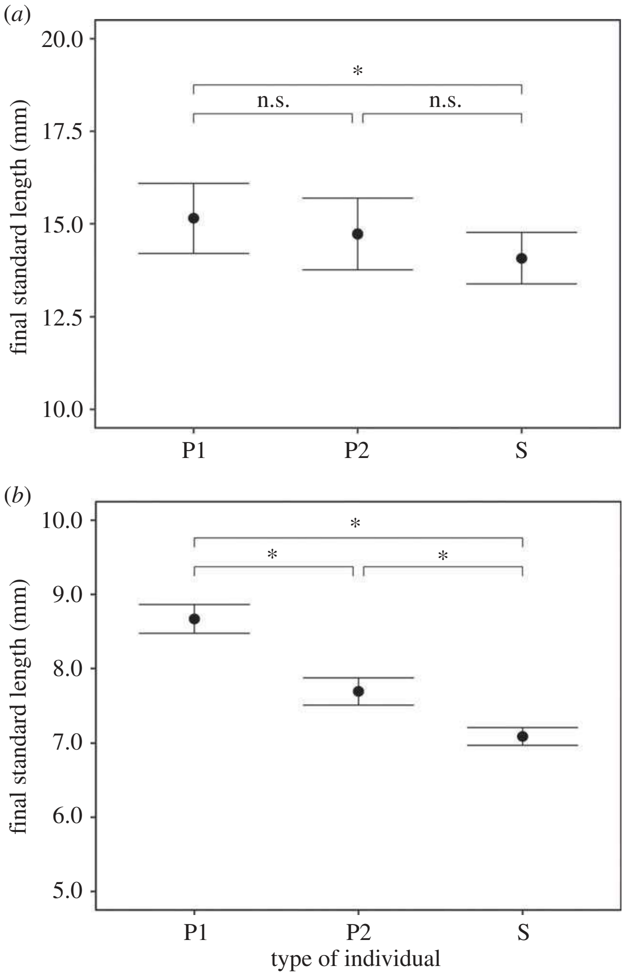

Figure 2. (*a*) Final standard length of clownfish in experiment 1 ($n = 6$ replicates, $n = 18$ individuals); (*b*) Final standard length of clownfish in experiment 2 ($n = 7$ replicates, $n = 21$ individuals). Three types of individuals are shown: those that became rank 1 in the pair (P1), those that became rank 2 in the pair (P2) and those that lived solitarily (S). Circles represent observed means and bars represent associated standard errors. '*' The pairwise comparison is statistically significant (Tukey's HSD: $p < 0.05$); 'n.s.' indicates that it is not significant (Tukey's HSD: $p > 0.05$).

4. Discussion

In animal societies where size and rank influence an individual's reproductive success, there should be strong selection for growth strategies that maximize an individual's chances of either retaining its current rank or attaining a higher rank—assuming that such growth plasticity is mechanistically possible. It is becoming increasingly apparent that labile growth strategies exist in a variety of social vertebrates [7–16], raising the question: what are the limits on vertebrate growth plasticity? The limits appear to be few. Wikelski & Thom [33] showed that marine iguanas, *Amblyrhynchus cristatus*, can shrink during times of low food availability associated with El Niño events. Buston [13] showed that subordinate clownfish can reduce their growth rate to remain small, thereby avoiding conflict with their immediate dominants and retaining current status. Here, we demonstrate that juvenile clownfish can also increase their growth rate to become large, thereby outgrowing a size-matched competitor and attaining dominant status.

We found that clownfish individuals living in pairs grew faster than singletons, and one individual of the pair grew faster than the other. While these results were consistent across the two experiments, there was a difference in the proportion of the variation in FSL explained by the fixed effects: in 2016, the majority of the variation in FSL is due to the random effect, because individuals within replicates were size-matched, but replicates were not size-matched; in 2017, the majority of the variation in FSL is due to the fixed effect, because individuals within replicates were size-matched and replicates were also size-matched. This subtle difference in experimental design between years explains the difference in the significance of pairwise comparisons and error bars between figure 2*a*,*b* also. Taken together, our results demonstrate that clownfish can exhibit competitive growth and that this can explain a lot of the variation in the growth and size of individuals.

Given that we focused on testing one hypothesis, it is important to consider alternative explanations for, and interpretations of, our data. One possibility is that the lower growth rate of the singleton relative to the pair could be due to stress of being held in isolation in captivity. We consider this unlikely, given that the same pattern was observed in the field (figure 1), though perhaps the best way to rigorously test this hypothesis would be to look at endocrine and/or gene expression profiles of all fish to determine which are the most stressed. A second possibility is that the higher growth rate of one individual in the pair relative to the other could be due to a dominance hierarchy being established almost immediately after the fish were confined together [34]. Quite possibly this occurred, but this hypothesis cannot explain why both individuals in the pair grow faster than the singleton and this is key evidence for competitive growth (figure 2*b*).

Our results are consistent with those of Huchard *et al.* [16], who demonstrated competitive growth in response to same-sex rivals in meerkats. While the phenotypic response to being paired with a size-matched competitor is the same in clownfish and meerkats, the proximate mechanism must be different. In the meerkat study, one individual was given an egg each day and grew more, and in response, the other individual increased its foraging rate and growth rate to keep up [16]. In the clownfish study, all individuals were given the same food ration, but the pair outgrew the singleton and one individual of the pair outgrew the other. The fish must be allocating more resources to skeletal growth, which suggests that there must be a life-history trade-off. Whatever the trade-off, the long-term benefits of attaining dominant status must outweigh the short-term costs of accelerated growth.

Our results suggest that individuals may employ a variety of growth strategies in response to social competition, increasing their growth rate in some contexts while decreasing it in others. These strategies have been detected multiple times and might be common in social fishes and cooperative mammals [7–16]. In these societies, especially societies with high reproductive skew, size and rank strongly influence reproductive success and there will be strong selection for growth strategies that maximize an individual's chances of retaining its current rank or attaining a higher rank. Such strategies might be less common in cooperative birds, owing to constraints imposed by flight. The key to detecting these strategies in any system is to track changes in the size of individuals in response to changes in social rank and group composition. This study adds to the growing body of evidence that the growth of social vertebrates can be a fine-tuned plastic response to their social environment.

Ethics. All work was approved by Boston University's Institutional Animal Care and Use Committee (protocol number 17-001).

Data accessibility. All data have been uploaded with this manuscript and are available as electronic supplementary material. All data are also available in the Dryad Digital Repository (doi:10.5061/dryad.h550gp2) [35].

Authors' contributions. C.R. participated in research design, data collection, data analysis and writing of the manuscript. R.B. participated in research design, data analysis and writing of the manuscript. J.M. participated in research design, data analysis and writing of the manuscript. C.J. participated in research design, data collection and writing of the manuscript. P.B. participated in research design, data collection, data analysis and writing of the manuscript. All authors approved the final version of the manuscript, and agree to be held accountable for the content therein.

Competing interests. We have no competing interests.

Funding. C.R. was supported by the Summer Undergraduate Research Fellowship Program at Boston University. R.B., J.M., C.J. and P.B. were supported by the Trustees of Boston University.

Acknowledgements. We would like to thank Alex Ascher, Tina Barbasch, Daniel Chavez, Alex Maytin, Jeremiah Seymour and Sadie Thompson for their help in the lab. We would also like to thank three anonymous reviewers whose comments greatly improved the manuscript.

References

1. McDonald DB. 1993 Delayed plumage maturation and orderly queues for status: a manakin mannequin experiment. *Ethology* **94**, 31–45. (doi:10.1111/j.1439-0310.1993.tb00545.x)
2. Field J, Shreeves G, Sumner S. 1999 Group size, queuing and helping decisions in facultatively eusocial hover wasps. *Behav. Ecol. Sociobiol.* **45**, 378–385. (doi:10.1007/s002650050574)
3. East ML. 2001 Male spotted hyenas (*Crocuta crocuta*) queue for status in social groups dominated by females. *Behav. Ecol.* **12**, 558–568. (doi:10.1093/beheco/12.5.558)
4. Fricke H, Fricke S. 1977 Monogamy and sex change by aggressive dominance in coral reef fish. *Nature* **266**, 830–832. (doi:10.1038/266830a0)
5. Reeve HK, Peters JM, Nonacs P, Starks PT. 1998 Dispersal of first 'workers' in social wasps: causes and implications of an alternative reproductive strategy. *Proc. Natl Acad. Sci. USA* **95**, 13 737–13 742. (doi:10.1073/pnas.95.23.13737)
6. Clutton-Brock TH, Hodge SJ, Spong G, Russell AF, Jordan NR, Bennett NC, Sharp LL, Manser MB. 2006 Intrasexual competition and sexual selection in cooperative mammals. *Nature* **444**, 1065–1068. (doi:10.1038/nature05386)
7. Hattori A. 1991 Socially controlled growth and size-dependent sex change in the anemonefish *Amphiprion frenatus* in Okinawa, Japan. *Jpn J. Ichthyol.* **38**, 165–177.
8. Russell AF, Carlson AA, McIlrath GM, Jordan NR, Clutton-Brock T. 2004 Adaptive size modification by dominant female meerkats. *Evolution* **58**, 1600–1607. (doi:10.1111/j.0014-3820.2004.tb01739.x)
9. Dengler-Crish CM, Catania KC. 2007 Phenotypic plasticity in female naked mole-rats after removal from reproductive suppression. *J. Exp. Biol.* **210**, 4351–4358. (doi:10.1242/jeb.009399)
10. Young AJ, Bennett NC. 2010 Morphological divergence of breeders and helpers in wild Damaraland mole-rat societies. *Evolution* **64**, 3190–3197. (doi:10.1111/j.1558-5646.2010.01066.x)
11. Ross RM. 1987 Sex-change linked growth acceleration in a coral reef fish *Thalassoma duperrey*. *J. Exp. Zool.* **244**, 455–461. (doi:10.1002/jez.1402440311)
12. Hamilton IM, Heg D. 2008 Sex differences in the effect of social status on the growth of subordinates in a cooperatively breeding cichlid. *J. Fish Biol.* **72**, 1079–1088. (doi:10.1111/j.1095-8649.2007.01787.x)
13. Buston PM. 2003 Size and growth modification in clownfish. *Nature* **424**, 145–146. (doi:10.1038/424145a)
14. Heg D, Bender N, Hamilton I. 2004 Strategic growth decisions in helper cichlids. *Proc. R. Soc. Lond. B* **271**, S505–S508. (doi:10.1098/rsbl.2004.0232)
15. Wong MY, Buston PM, Munday PL, Jones GP. 2007 The threat of punishment enforces peaceful cooperation and stabilizes queues in a coral-reef fish. *Proc. R. Soc. B* **274**, 1093–1099 (doi:10.1098/rspb.2006.0284)
16. Huchard E, English S, Bell MBV, Thavarajah N, Clutton-Brock T. 2016 Competitive growth in a cooperative mammal. *Nature* **533**, 532–534. (doi:10.1038/nature17986)
17. Fautin DG. 1992 Anemonefish recruitment: the roles of order and chance. *Symbiosis* **14**, 143–160.
18. Elliott JK, Elliott JM, Mariscal RN. 1995 Host selection, location, and association behaviors of anemonefishes in field settlement experiments. *Mar. Biol.* **122**, 377–389. (doi:10.1007/BF00350870)
19. Elliott JK, Mariscal RN. 2001 Coexistence of nine anemonefish species: differential host and habitat utilization, size and recruitment. *Mar. Biol.* **138**, 23–36. (doi:10.1007/s002270000441)
20. Buston PM. 2003 Forcible eviction and prevention of recruitment in the clown anemonefish. *Behav. Ecol.* **14**, 576–582. (doi:10.1093/beheco/arg036)
21. Buston PM. 2003 Mortality is associated with social rank in the clown anemonefish (*Amphiprion percula*). *Mar. Biol.* **143**, 811–815. (doi:10.1007/s00227-003-1106-8)
22. Buston PM, García MB. 2007 An extraordinary life span estimate for the clown anemonefish *Amphiprion percula*. *J. Fish Biol.* **70**, 1710–1719. (doi:10.1111/j.1095-8649.2007.01445.x)
23. Buston PM. 2004 Territory inheritance in clownfish. *Proc. R. Soc. Lond. B* **271**, S252–S254. (doi:10.1098/rsbl.2003.0156)
24. Buston PM. 2004 Does the presence of non-breeders enhance the fitness of breeders? An experimental analysis in the clown anemonefish *Amphiprion percula*. *Behav. Ecol. Sociobiol.* **57**, 23–31. (doi:10.1007/s00265-004-0833-2)
25. Buston PM, Cant MA. 2006 A new perspective on size hierarchies in nature: patterns, causes, and consequences. *Oecologia* **149**, 362–372. (doi:10.1007/s00442-006-0442-z)
26. Moyer JT, Nakazono A. 1978 Protandrous hermaphroditism in six species of the anemonefish genus *Amphiprion* in Japan. *Jpn J. Ichthyol.* **25**, 101–106.
27. Buston PM. 2002 Group structure of the clown anemonefish *Amphiprion percula*. PhD dissertation. Cornell University, Ithaca, NY.
28. Schmiege P, D'Aloia C, Buston PM. 2017 Anemonefish personalities influence the strength of mutualistic interactions with host sea anemones. *Mar. Biol.* **164**, 24. (doi:10.1007/s00227-016-3053-1)
29. Barbasch TA, Buston PM. 2018 Plasticity and personality of parental care in the clown anemonefish. *Anim. Behav.* **136**, 65–73 (doi:10.1016/j.anbehav.2017.12.002)
30. Schneider CA, Rasband WS, Eliceiri KW. 2012 NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods* **9**, 671–675. (doi:10.1038/nmeth.2089)
31. R Core Team. 2014 *R: a language and environmental for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See http://www.R-project.org/.
32. Bates D, Machler M, Bolker B, Walker S. 2015 Fitting linear mixed-effects using lme4. *J. Stat. Softw.* **67**, 1–48. (doi:10.18637/jss.v067.i01)
33. Wikelski M, Thom C. 2000 Marine iguanas shrink to survive El Niño. *Nature* **403**, 37–38 (doi:10.1038/47396)
34. Abbott JC, Dill LM. 1989 The relative growth of dominant and subordinate juvenile steelhead trout (*Salmo gairdneri*) fed equal rations. *Behaviour* **108**, 104–113. (doi:10.1163/156853989X00079)
35. Reed C, Branconi R, Majoris J, Johnson C, Buston P. 2018 Data from: Competitive growth in a social fish. Dryad Digital Repository (doi:10.561/dryad.h550gp2)