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Rank change and growth within social hierarchies of the orange clownfish, *Amphiprion percula*

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Abstract

Social hierarchies within groups define the distribution of resources and provide benefits that support the collective group or favor dominant members. The progression of individuals through social hierarchies is a valuable characteristic for quantifying population dynamics. On coral reefs, some clownfish maintain size-based hierarchical communities where individuals queue through social ranks. The cost of waiting in a lower-ranked position is outweighed by the reduced risk of eviction and mortality. The orange clownfish, *Amphiprion percula*, maintains stable social groups with subordinate individuals queuing to be part of the dominant breeding pair. Strong association with their host anemone, complex social interactions, and relatively low predation rates make them ideal model organisms to assess changes in group dynamics through time in their natural environment. Here, we investigate the rank changes and isometric growth rates of *A. percula* from 247 naturally occurring social groups in Kimbe Island, Papua New Guinea (5° 12' 13.54" S, 150° 22' 32.69" E). We used DNA profiling to assign and track individuals over eight years between 2011 and 2019. Over half of the individuals survived alongside two or three members of their original social group, with twelve breeding pairs persisting over the study period. Half of the surviving individuals increased in rank and experienced double the growth rate of those that maintained their rank. Examining rank change in a wild fish population provides new insights into the complex social hierarchies of reef fishes and their role in social evolution.

Keywords Vertebrate growth · Reef fish · Clownfish · Social hierarchy

Introduction

Social hierarchies help group-living animals distribute resources, including food, shelter, and mating privileges (Koski et al. 2015). Individuals are ranked by their position

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in the hierarchy, which is driven by physical and competitive fitness (e.g., size, strength, coloration), and how they contribute to the functioning of the social group (Koski et al. 2015). Hierarchies are typically structured according to the individuals' size, age, or sex, and moving up in social rank increases an individual's access to food (Forrester 1991), mates (Buston 2003a), and habitat (Thompson et al. 2007). Social rank often corresponds to feeding success rates, which are correlated to growth rates, and allows dominant individuals to remain well-fed where food is limited (Gurney and Nisbet 1979). Reef fish are a popular vertebrate model to study hierarchy and dominance since they have a clear social structure and can be kept easily in laboratory settings; for example, the coral-dwelling goby *Paragobiodon xanthosomus* exhibits a size-based hierarchy in which members form a queue to inherit breeding status from the dominant pair. Cooperation between subordinates regulates growth and maintains a size ratio between ranks to avoid conflict, punishment, or eviction from the social group (Wong et al. 2007). While studies have examined the causes of rank change and dominance in reef fish by analyzing growth rates (Wong et al. 2007, 2016; Reed et al. 2019), they are conducted as short-term experiments (Buston 2003a, 2003b; Buston and Cant 2006; Rueger et al. 2018). No studies have examined rank change and growth rates in fish over one year in a natural setting. Long-term studies aid in the understanding of population dynamics by providing large datasets that are used to predict future population changes, but large datasets can be challenging to obtain in the marine environment (Reinke et al. 2019).

Mating behavior is essential in driving, establishing, enforcing, and maintaining the social hierarchy. Sexual selection within hierarchical societies elucidates patterns of conflict within as opposed to between sexes. Wong and colleagues determined that food limitation and paternal egg care lead to competition among female coral gobies for males meaning they are less likely to mate with subordinate males, leading to monogamy within social groups (Wong et al. 2008). Most clownfish live in groups comprising one dominant breeding pair and several non-breeding subordinates where the female is the dominant individual. The species *Amphiprion bicinctus* and *Amphiprion akallopisos* have been shown to exhibit monogamy based on the individual recognition (Fricke 1973) and pair-bonding (Fricke 1974). Fricke and Fricke also found that several pairs of *A. bicinctus* remained on the same anemone without changing partners for at least three years (Fricke and Fricke 1977), revealing that social structures are relatively stable for females and males.

In this study, we focus on the orange clownfish, *Amphiprion percula* examining its rank change and growth over an eight-year time gap. The orange clownfish, *A. percula* (Lacepède, 1802), is one of 28 species of clownfish

belonging to the subfamily Amphiprioninae within the family Pomacentridae. It is estimated to have a lifespan of 30 years (Buston and Garcia 2007) and is commonly associated with anemone hosts *Heteractis magnifica* and *Stichodactyla gigantea* (Fautin and Allen 1992). Anemone species may play an essential role in the growth and size of *A. percula* individuals. Previous studies found that, on average, females were 10% larger in *H. magnifica* compared to those living on *S. gigantea*, and individuals that settled on *H. magnifica* had a faster growth rate based on otolith increments (Salles et al. 2016). A recent study (Salis et al. 2021) concluded that juvenile *A. percula* delays the development of their white bars during metamorphosis depending on the anemone species they are hosted by, emphasizing the importance of anemone host species on a variety of biological factors. Additionally, anemone surface area significantly impacts the social structure, with larger anemones hosting larger social groups and individuals (Chausson et al. 2018), which may place additional pressure on resource sharing and individual growth.

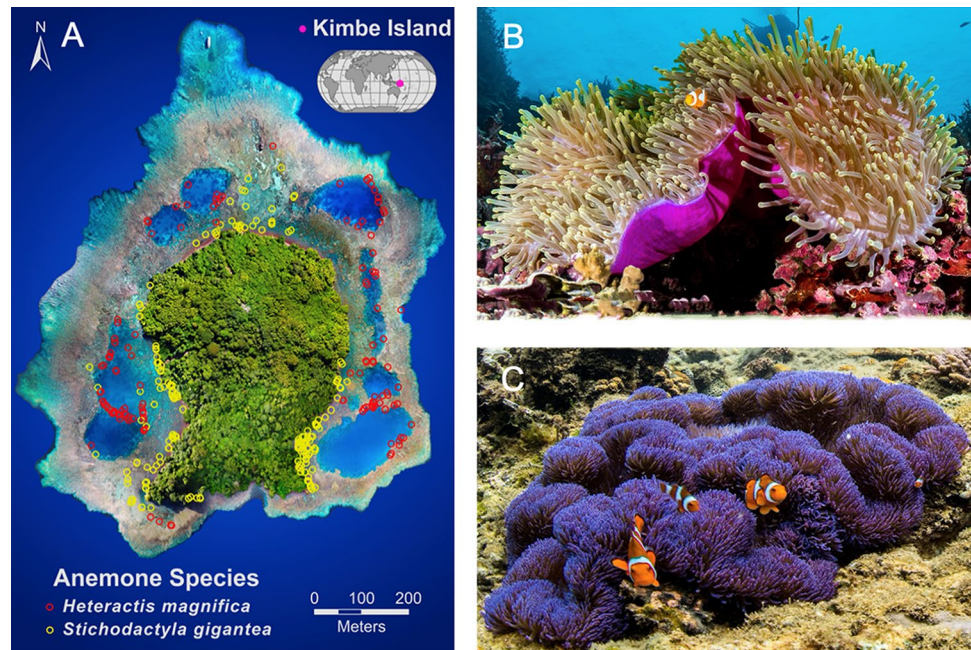
Within social groups of *A. percula*, there is a strict size-based ratio between sequentially ranked individuals in which a dominant individual is approximately 1.26 times the size of its immediate subordinate (Buston 2003b). Similar to gobies, subordinates regulate their growth to maintain this ratio or are otherwise evicted or killed (Buston 2003b; Rueger et al. 2018). In theory, individuals who change rank grow faster due to the increase in the food they consume as they rise in status. This study aimed to examine rank changes and growth in naturally occurring social groups of *A. percula* clownfish over eight years on shallow coral reefs on Kimbe Island, Papua New Guinea. We hypothesize that individuals who change rank will grow faster than those who do not change rank, and those with higher rank will have better survivorship. During this time, individuals were exposed to natural levels of predation risk, food availability, and recruitment.

Materials and methods

Sample collection

The *Amphiprion percula* population on Kimbe Island (5° 12' 13.54" S, 150° 22' 32.69" E), a remote island in Kimbe Bay, was sampled in March 2011 and April 2019. Each time, all individuals sized > 25 mm ($n = 660$ in 2011; $n = 533$ in 2019) were caught with hand nets, occasionally anesthetized with a dilute solution of clove oil (if necessary to facilitate capture), and measured to the nearest mm (total length, TL) (Fig. S1). Their host anemone species (*S. gigantea* and *H. magnifica*) were recorded and tagged with a cattle tag and buoy (Fig. 1). Due to the attrition

Fig. 1 A Visual of the study site, Kimbe Island (Papua New Guinea), and surrounding lagoon and reef habitats with tagged anemone locations (*Heteractis magnifica* in red and *Stichodactyla gigantea* in yellow). Kimbe Island = green, shallow (< 1 m) hard bottom substrate = gray, lagoons = light blue, and deeper ocean outside of the fringing reef habitat = dark blue. Host anemones *Heteractis magnifica* (B) and *Stichodactyla gigantea* (C) on the right. Aerial image credit to H.B.H., map courtesy U. Langner (RSRC), photographs credit to M.B.S



of the tags on anemones, we could not confirm that all individual fish had remained on the exact anemone host between sampling times. For some fish, we can only confirm that they were found on the same species of anemone and general area based on GPS. To genotype all individuals, a tissue sample was taken from the caudal fin before they were released back onto their anemone host. The fin clip is regrown within approximately two weeks and has no adverse long-term effects on the fish. Samples were preserved in 96% ethanol. Rank was assigned based on the relative total lengths of individuals within each social group. Rank 1 was the largest individual and assumed to be the female; rank 2 was the second largest and assumed to be the male. Any additional individuals were classed as sub-adults.

Sample processing and genotyping

Genomic DNA from *A. percula* fin clips $\sim 2 \text{ mm}^2$ was extracted using the Macherey–Nagel 96 tissue kits following the manufacturer's protocols. Next, microsatellite loci were amplified using the QIAGEN Multiplex PCR kit following the protocol in Almany et al. (2017). Forward primers were labeled with fluorescent tags and pooled into four multiplex mixes indicated in Table S1. PCR products were analyzed on an ABI 3730 $\times 1$ genetic analyzer (Applied Biosystems). Allele sizes for 20 microsatellite loci were successfully amplified and were manually scored in the fragment analysis software *GENEMAPPER* v4.0. Characteristics of the 20 microsatellite markers were

analyzed in *GenAlEx* v6.5 (Peakall and Smouse 2012) and are presented in Table S2. Alleles were binned in R (R Core Team 2020) using the package *MsatAllele* (Alberto 2009).

Individuals that survived from 2011 to 2019 were identified in the R package *AlleleMatch* (Galpern et al. 2012). Only individuals classed as females, males, or sub-adults were included in this analysis ($n = 660$ in 2011 and $n = 533$ in 2019). A sensitivity analysis indicated that up to 8 genotypic mismatches could confidently identify identical genotypes within the sample.

Statistical analyses

We measured growth between 2011 and 2019 as the percent increase in body length between the two measurements. Variation in growth between anemone species, rank status, or change was assessed using generalized linear mixed models with a beta error distribution with a logit link in the R package *glmmTMB* (Friedman et al. 2010). The interactions between anemone species and rank were explored and found not to be important. Estimated marginal means and Tukey post hoc pairwise comparisons with 95% confidence intervals were calculated using the package *emmeans* (Lenth 2021) and plotted using the package *ggplot2* (Wickham 2016). Model residuals were inspected in the *DHARMA* package (Hartig 2020) and checked for homogeneity of variance, dispersion, and outliers. Model selection was informed by AIC scores using the *MuMIn* package (Bartoń 2020). All analyses were performed in R version 4.0.2 (R Core Team 2020).

Results

In total, 134 of the 660 individuals (i.e., 20%) sampled in 2011 were recaptured in 2019, including 36 females, 52 males, and 46 sub-adults, and comprised 35 of the original 247 social groups from 2011. Of the 134 survivors, 72 individuals were confirmed to have been collected from the same anemone with other individuals from the same social group. We found no evidence of an individual changing anemone host over the eight years; the other 62 individuals were identified in anemones without a matching anemone ID tag between 2011 and 2019 but on the same species of anemone, at similar depths, in the same general location. We found that 60% of the 134 survivors were from anemone *H. magnifica*, and 40% were from *S. gigantea*.

Of the 134 survivors, 67 individuals (50%) maintained the same rank within their respective social groups, and 67 individuals (50%) changed social rank to become male or female (Fig. 2). Additionally, we identified 12 mating pairs that remained together since 2011, of which three remained with other individuals from their original social group. The host anemone, initial rank, and rank change

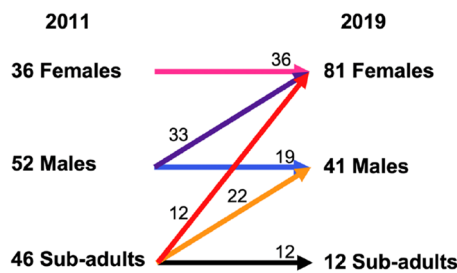


Fig. 2 Rank and rank changes in 134 *Amphiprion percula* individuals collected in 2011 and recaptured in 2019. Their identities were confirmed by their unique DNA profiles

strongly affected individuals’ growth between 2011 and 2019. Changes in rank had the strongest effect on growth resulting in a 26.8% (95% CI [24.5–29.1]) increase in growth for individuals that changed rank compared to 11.7% (95% CI [10.0–13.6]) in individuals that did not change rank, and the difference was significant between the two groups ($p < 0.0001$). The strongest effects were observed in sub-adults that became either male (27.0% growth, 95% CI [23.2–31.2]) or females (31.4% growth, 95% CI [26.4–36.9]) during the eight-year window (Table 1). Males that became females grew by 24.7% (95% CI [21.8–27.8]). Of the individuals that did not change rank, sub-adults grew fastest with 18.9% growth (95% CI [14.4–24.4]), faster than either females (10.8% growth, 95% CI [8.9–13.1]; $p = 0.015$) or males (10.0% growth, 95% CI [7.6–13.0]; $p = 0.012$). Anemone species also had

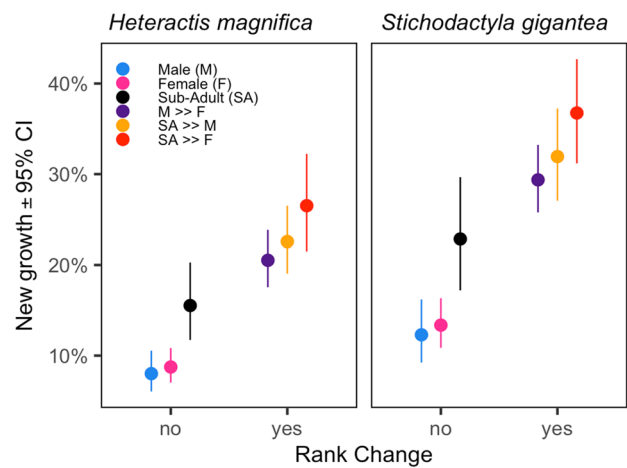


Fig. 3 Growth of *Amphiprion percula* as a percentage of the total body length for females, males, and sub-adults depending on whether individuals changed social rank within different host anemones. Estimated marginal means are shown with 95% confidence intervals around the mean

Table 1 Estimated marginal means and 95% confidence interval of the percent growth in *Amphiprion percula* between 2011 and 2019 for different social ranks and rank changes in *Heteractis magnifica* and *Stichodactyla gigantea*

Anemone sp	Rank	Percent growth	n	SE	df	95% conf. int
<i>H. magnifica</i>	Male (M)	8.0	12	1.1	115	[6.0–10.5]
<i>H. magnifica</i>	Female (F)	8.7	21	1.0	115	[7.0–10.8]
<i>H. magnifica</i>	Sub-adult (SA)	15.5	10	2.2	115	[11.7–20.3]
<i>H. magnifica</i>	M>>F	20.5	17	1.6	115	[17.5–23.8]
<i>H. magnifica</i>	SA>>M	22.6	15	1.9	115	[19.1–26.5]
<i>H. magnifica</i>	SA>>F	26.5	4	2.7	115	[21.5–32.2]
<i>S. gigantea</i>	Male (M)	12.3	7	1.7	115	[9.2–16.2]
<i>S. gigantea</i>	Female (F)	13.4	15	1.4	115	[10.9–16.3]
<i>S. gigantea</i>	Sub-adult (SA)	22.8	2	3.2	115	[17.2–29.7]
<i>S. gigantea</i>	M>>F	29.4	16	1.9	115	[25.8–33.2]
<i>S. gigantea</i>	SA>>M	31.9	7	2.6	115	[27.1–37.2]
<i>S. gigantea</i>	SA>>F	36.7	8	2.9	115	[31.2–42.7]

a strong effect on growth; over eight years, individuals grew 15.7% on *H. magnifica* (95% CI [14.0–17.5]) compared to 23.1% on *S. gigantea* (95% CI [20.6–25.7]), and the difference was significant ($p < 0.0001$) (Fig. 3).

Discussion

Our study examined growth and rank change over eight years in a wild population of *A. percula* clownfish in Kimbe Island, Papua New Guinea. Tracking individuals in the marine environment over long periods can be extremely challenging. The close association of clownfish with their anemones provides a valuable model system to investigate the effects of rank change on growth, providing unique insights on survivorship, growth rates, rank changes, and the persistence of monogamous breeding pairs in coral reef fish. Our findings indicate strong survivorship of individuals over eight years, with 20% of individual resamples in 2019. Related studies of the same population but over ten years found that ~1% of the population had survived from the beginning to the end of the study (Salles et al. 2016). This suggests a complete population turnover after ten years which is short given the potential lifespan of 30 years for *A. percula* females (Buston and Garcia 2007).

Furthermore, we found that individuals that changed rank (i.e., sub-adult to male, sub-adult to female, and male to female) grew faster than those that did not change rank. Half of the surviving individuals changed rank and grew significantly more than those that did not change rank. This is likely not a standard growth, but opportunistic growth that occurs when a female or male is removed from the group since *A. percula* has been known to regulate or suppress their growth to decrease the likelihood of being evicted (Buston 2003b). A recent review by Buston and Clutton-Brock examined strategic growth in social vertebrates and concluded that clownfish species *Amphiprion perideraion* and *Amphiprion frenatus* females acquire dominant positions by increasing in length relative to similarly-sized individuals and that the increase in size is limited by the size of the anemone (Buston and Clutton-Brock 2022).

The 12 male and female pairs that persisted between 2011 and 2019 strongly support that *A. percula* is monogamous. This is consistent with previous studies of mating behavior in reef fish that are site-attached, whereby breeding pairs remain monogamous until one mate is physically removed from the social hierarchy. A review of monogamy in marine fishes included 18 families, and four clownfish species (*A. bicinctus*, *Amphiprion clarkii*, *A. perideraion*, and *A. frenatus*) identified *A. percula* as monogamous from observations only (Whiteman and Cote 2004). We can confirm from genetic analyses that 12 pairs have remained in the same

host anemone over eight years and are likely reproducing. Monogamy and breeding stability are often hard to confirm in the field over long-term studies without the adequate genetic analysis of all individuals present, making this challenging in many other field study systems.

Additionally, we found that species of anemone host significantly affected growth in *A. percula*. All individuals hosted by *H. magnifica* grew slower than those hosted by *S. gigantea*. However, previous research on early settlement in Kimbe Bay (Salles et al. 2016) found that individuals that settled on *H. magnifica* grew faster than those on *S. gigantea*. This may indicate a selective advantage on growth in *H. magnifica* for post-settlement recruits that are lost in subsequent social ranks. Since anemone surface area is positively correlated to the size of the individuals' (Chausson et al. 2018), the faster growth rates are likely explained by the larger surface area provided by *H. magnifica* compared to *S. gigantea* as observed in (Salles et al. 2016). However, this effect may also be confounded by other environmental factors associated with the different habitats occupied by each anemone. *Heteractis magnifica* are found further offshore and in deeper habitats compared to *S. gigantea* anemones found in sheltered shallow habitats close to shore (Fig. 1). Further studies that control variables, such as temperature, flow, turbidity, nutrient/food availability, predation pressure, and intraspecific competition, may provide further insight into the mechanisms that regulate growth in different anemone species. However, the scale at which these variables need to be measured to understand their impacts on the physiology and growth of clownfish would be very difficult to achieve (Burgess et al. 2021).

Conclusion

Together, our findings support the notion that social and environmental characteristics can influence the outcome of group structure and growth (Robbins et al. 2005). This study provides the first long-term evaluation of the social structure and individual growth in a wild population of reef fish, demonstrating that growth in *A. percula* is socially mediated and strongly dependent on the host anemone. Further work should investigate the demographic consequence of faster growth and survivorship in clownfish and whether the loss of dominant and highly reproductive female fish (Saenz-Agudelo et al. 2015) can be mitigated by the rapid progression through social hierarchies and growth of lower-ranked groups.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00227-022-04117-9>.

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Author contributions LMF, HBH, and MLB: contributed to the study conception and design. Data collection was performed by LMF, HBH, PS-A, MS, JEM, LBE, BP, MBS, SRT, SP, GPJ, and MLB. Data analysis was performed by LMF, HBH, DJC, and PS-A. The first draft of the manuscript was written by LMF and all authors commented on previous versions. All authors read and approved the final manuscript.

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Availability of data and material All data generated or analyzed during this study are linked in this published article's supplementary information files.

Declarations

Conflict of interest We declare no conflicts or competing interests.

Ethical approval The authors declare that the sampling of specimens was performed in the respect of the ethical rules and Papua New Guinea laws. All samplings were authorized by King Abdullah University of Science and Technology (KAUST—Field Research Plan 20190227).

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