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Strategic growth decisions in helper cichlids

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Recently, it has been shown that group-living subordinate clownfish *Amphiprion percula* increase their growth rate after acquiring the dominant breeder male position in the group. Evidence was found for strategic growth adjustments of subordinate fishes depending on the threat of eviction, i.e. subordinates adjust their growth rates so they remain smaller than the dominant fish and thereby limit the threat of being expelled from the territory. However, it is impossible to exclude several alternative factors that potentially could have influenced the observed changes in growth, owing to the nature of that experiment (removing the second-ranking fish – the breeder male – caused the third-ranking fish to change sex to become breeder male and change rank). We studied strategic growth decisions in the group-living Lake Tanganyika cichlid *Neolamprologus pulcher* under controlled laboratory conditions with *ad libitum* food availability. First, we show that male breeders grow faster than subordinate male helpers of the same initial size and confirm that *N. pulcher* shows status-dependent growth. Second, we improved on the experimental design by not removing the dominant breeder male in the group; instead we replaced the breeder male with a new breeder male in a full factorial design and measured growth of the subordinate male helpers is a function of the size difference with the old and the new breeder male. As predicted, male helpers showed strategic growth adjustments, i.e. growing faster when the size difference with the breeder male is large. Strategic growth adjustments were less pronounced than status-dependent growth adjustments.

Keywords: growth rate; cooperative breeding; dominance; eviction; Cichlidae

1. INTRODUCTION

In fishes, social status, such as territory ownership, position in a dominance hierarchy or the relative size difference between ranks, may have a profound influence on growth rate (e.g. Taborsky 1984; Metcalfe *et al.* 1989, 1992; Huntingford & de Leaniz 1997; Hofmann *et al.* 1999; MacLean & Metcalfe 2001; Buston 2003). Status-dependent growth, i.e. the effect of a change in dominance rank or status on growth rate, might arise by any of, or a combination of, at least four factors: (i) breeding status, as formerly non-breeding individuals increase in size to become more attractive mates or prepare for gonadal development (or decrease their growth rate as resources are shifted to reproduction); (ii) priority of access to resources (e.g. the effects of monopolization on food intake, access to shelters, etc.); (iii) group size (which again may influence food intake, perceived risk of predation, etc.); and (iv) conflict with other group members.

Recently, Buston (2003) has shown that group-living subordinate clownfish *Amphiprion percula* increase their growth rate after acquiring the dominant breeder male position in the group. He also found evidence for strategic growth adjustments of subordinate fishes depending on the threat of eviction, i.e. subordinates adjust their growth rates so they remain smaller than the dominant fish and thereby decrease the threat of eviction (factor (iv) above). This is a novel finding, which is of particular interest because it entails either subordinate restraint or dominant manipulation of growth and therefore bears some conceptual similarities to other strategic explanations for social behaviour, such as concession- and restraint-based models of reproductive skew (see review by Johnstone 2000), self-inhibition of reproduction (Hamilton 2004) and pay-to-stay arguments for helping behaviour (Kokko *et al.* 2002).

In the experiment of Buston (2003), the second-ranked fish (the breeder male) was removed and the third-ranked fish responded by increasing its growth rate. The third-ranked fish probably experienced a reduction in conflict, as the size gap between it and the fish immediately above it increased, but it also changed sex to become a breeder male and increased in rank. Therefore, it is possible that several of the aforementioned alternative mechanisms for status-dependent growth may have influenced Buston's experimental results. Strong support for the hypothesis that growth is adjusted to avoid conflict and eviction (which we call the 'strategic growth hypothesis') is generated if it can be shown that subordinates adjust their growth rate solely owing to factor (iv). Note that strategic growth is one component of status-dependent growth, not an alternative mechanism.

Under the strategic growth hypothesis, fishes should reduce their growth rates when the threat of conflict with other group members depends on size differences between group members and when those differences are small. We tested this hypothesis in a laboratory experiment, where we would be able to distinguish this novel effect convincingly from other social factors affecting growth by keeping factors (i)–(iii) constant and manipulating only factor (iv). Our study species, the group-living Lake Tanganyika cichlid *Neolamprologus pulcher*, shows status-dependent growth (Taborsky 1984). In this species, subordinates help dominants raising offspring by active territory maintenance and defence and through brood care behaviour (Taborsky 1984, 1985). Experiments have shown that subordinates (i) positively influence the clutch size produced by the breeding female in the group (Taborsky 1984) and (ii) increase reproductive output (L. Brouwer, D. Heg and M. Taborsky, unpublished data), i.e. they are 'true' helpers. Helpers are evicted from the group when their body size is similar to that of the dominant same-sex breeder (Balshine-Earn *et al.* 1998); hence it might advantage helpers to adjust their growth strategically to prevent expulsion from the group. In the first part of our experiment we show

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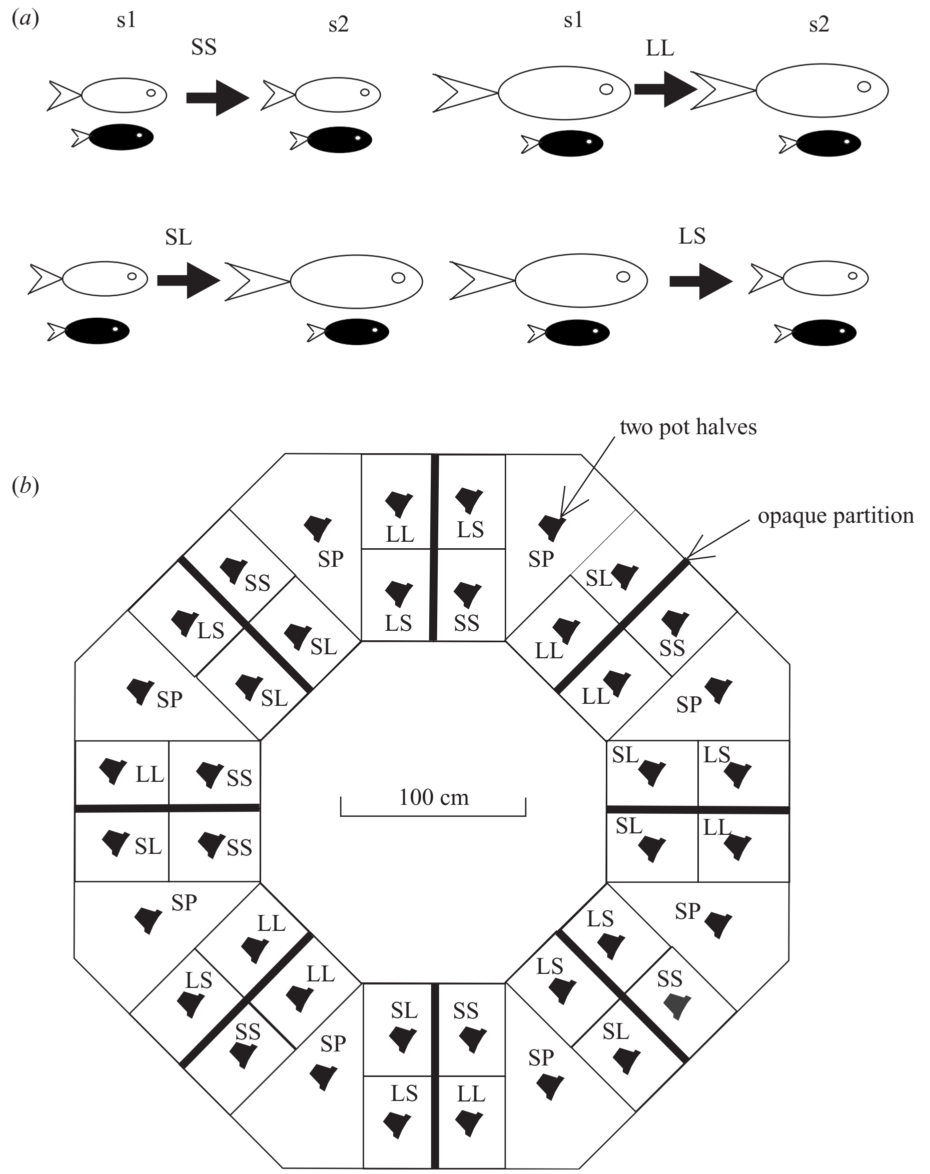

Figure 1. (*a*) Design of the strategic growth experiment. Focal large helper males (black) were helping either a small or a large breeder male (both white) in the first sequence (s1). After 30 days all breeder males were changed, whereas the focal helper males, breeding females and small helper males remained (breeding females and small helper males not depicted for clarity). Again, focal large helper males were helping either small or large breeder males in the second sequence (s2). (*b*) Experimental set-up of the ring tank. All partitions were clear, except the opaque partitions between the eight sections. In each section, all five treatments were established: SP: single breeding pair both sequences; SS: small breeder male in sequence 1 and sequence 2; SL: small breeder male in sequence 1 and large breeder male in sequence 2; LL: large breeder male in sequence 1 and sequence 2; LS: large breeder male in sequence 1 and small breeder male in sequence 2.

status-dependent growth, i.e. breeder males grow faster than subordinate males. In the second part we vary only factor (iv) and also show strategic growth, i.e. helper males grow faster when living in groups with a large breeder male than when living in groups with a small breeder male.

2. METHODS

We used one large 7200 l ring tank divided into eight sections, each with five group compartments (figure 1), in a climate-controlled room at the Ethologische Station Hasli, University of Bern. The height of the tank is 60 cm, with a 50 cm water column. The floor of the tank was covered with a 30 mm layer of sand (1 mm grain size). Two pot halves were introduced per compartment as breeding substrate. Eggs were counted daily and immediately removed to avoid changes in group behaviour and helper expulsion. Each compartment received *ad libitum* food (two feedings per day; 5 days TetraMin, 2 days fresh food with *Artemia* spp., *Daphnia* spp. and mosquito larvae each week), and excess food was removed the next morning. Water temperature was held constant at 28.0 ± 0.4 °C (mean ± s.d.); water biochemical parameters were kept similar to those of Lake Tanganyika. The illumination cycle was kept constant at 13 L : 11 D (lights on from 8.00 to 21.00).

To test the status-dependent growth hypothesis, eight single breeding pairs were created in the edge compartments of the large ring tank (focal male and female breeder of standard length (SL) = 40–45 mm) and growth was determined on days 30 and 60 (sequences 1 and 2) to compare with the growth of focal helpers of the same size from the second part of the experiment (figure 1). In the second part of the experiment, we tested the strategic growth hypothesis by creating 32 artificial (see Taborsky 1984, 1985) breeding groups of four fishes each in the remaining compartments of the ring tank. Artificial families were created as follows. First, a focal large helper male (SL = 40–45 mm) and a small helper male (SL = 30–35 mm) were introduced into each compartment. Second, 2 days later, a breeding female (SL = 55–65 mm) was added, and in half of the cases a large, and the other half a small, breeder male (SL = 70–75 mm or 46–51 mm; figure 1) was added. All individuals were marked, SL and body mass were determined, and all compartments received *ad libitum* food. All compartments received pot halves as breeding substrate. Helpers and breeders showed digging behaviour in the two pot halves, egg cleaning (both mainly by small helpers and breeder females) and territory defence along the clear partitions against members of other groups.

SL and body mass were again measured after 30 days of growth (sequence 1). The breeder males were then changed from large to large, large to small, small to small or small to large by introducing new breeder males (sequence 2; figure 1). New breeder males were all accepted into their groups and gained the dominant position, as also regularly occurs in nature after breeder replacements (Taborsky & Limberger 1981; Balshine-Earn *et al.* 1998). At the end of sequence 2 on day 60, SL and body mass were measured again to determine growth. Our prediction under the strategic growth hypothesis is that large helpers should grow faster with the large breeder male. Alternatively, if food monopolization plays a role despite *ad libitum* feeding, assuming small breeder males need less food than large breeder males, large helpers should grow faster with a small breeder male.

3. RESULTS

The first part of the experiment confirmed status-dependent growth in *N. pulcher*: male breeders grew faster than similar-sized large helper males (figure 2*a*,*b*; SPSS repeated-measures generalized linear model (GLM) on growth in SL: status $F_{1,36} = 9.08$, $p = 0.005$; growth in mass: status $F_{1,36} = 17.92$, $p < 0.001$, see electronic Appendix A for full statistical table).

To assess the strategic growth hypothesis, focal large helper males breeding with differently sized breeding males were compared, controlling for individual (random), sequence (fixed) and helper size (ln(SL)) effects in an SPSS mixed GLM (see electronic Appendix A). We used ln(growth) as the dependent variable, to account for exponential diminishing growth in fishes. We detected a highly significant positive effect of the difference in size, ln(SL breeder male − helper male), on the helper growth rate in body length ($F_{1,63} = 8.11$, $p = 0.008$), indicating reduced helper growth in groups with small breeder males (figure 2*c*), but this effect was absent in mass (figure 2*d*; ln(mass breeder male − helper male): $F_{1,63} = 0.22$, $p = 0.64$).

The same analyses were carried out for the smallest group members, the small helper males. Since small helpers might adjust their growth rates, not to the difference in initial size with the large helper or the breeding male, but rather to the growth rate of the large helper or the breeder male, we also constructed a model incorporating these two factors. No such adjustments in 30 days' growth were detected in the small male helpers (identical GLM method to above, ln-transformed, SL/mass: ln(large helper − small helper) $F_{1,63} = 0.50/0.03$, $p = 0.48/0.87$; ln(breeder male − small helper) $F_{1,63} = 0.02/1.23$, $p = 0.90/0.28$).

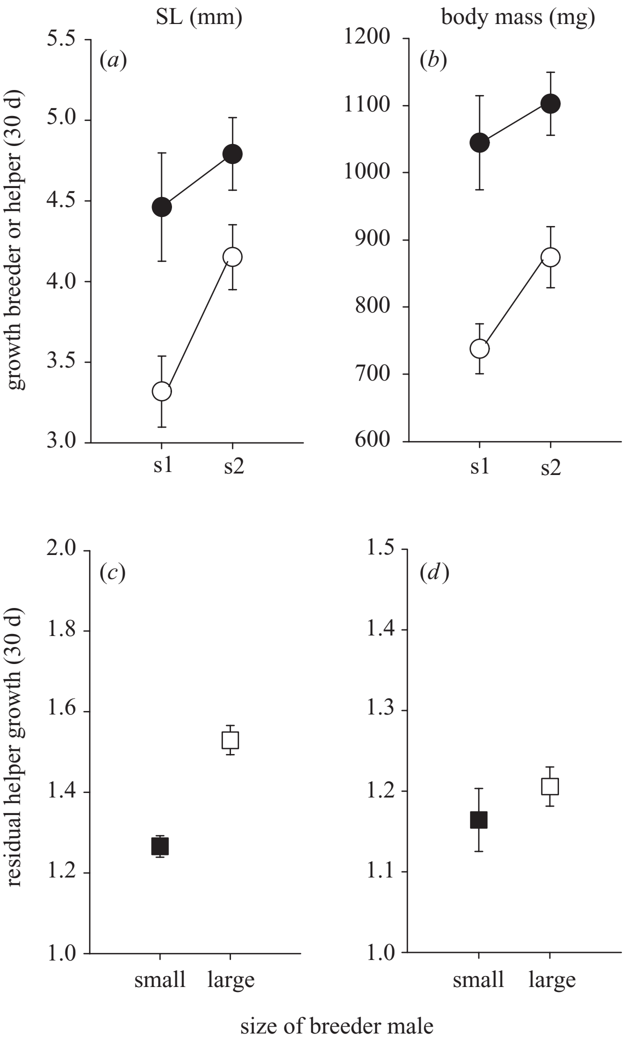

Figure 2. Growth adjustments in the cichlid *Neolamprologus pulcher*. (*a*,*b*) Males show status-dependent growth in (*a*) standard length (SL) and (*b*) body mass: breeders (filled circles, $n = 8$) grow faster than helpers (open circles, $n = 30$) in both sequences. (*c*,*d*) Helper males show strategic reduced growth in (*c*) size, but not (*d*) mass, when breeding with small breeder males (filled squares, $n = 32$) compared with when breeding with large breeder males (open squares, $n = 31$). Note the differences in scales in the four panels; s1: sequence 1; s2: sequence 2.

4. DISCUSSION

We were able to confirm status-dependent growth (Taborsky 1984; Buston 2003) and show strategic growth adjustments in *N. pulcher*. This reduced growth rate is not confounded by changes in helper status, helper rank, group size or food availability, as might have occurred in the experiment of Buston (2003). Interestingly, helper males showed reduced growth only in body length, not in mass, depending on the size of the breeder male. Similarly, Taborsky (1984) found that helpers had reduced growth in length, but accumulated more mass, than non-group-living fishes of the same size. Taken together, these results show that helpers are not food limited. Helpers strategically invest less in growing to a large size and instead store resources. It is possible that these stored resources allow helpers to grow quickly in length as soon as they have gained a breeding position.

In our first experiment, we demonstrate a large change in growth rate associated with a change in status, which may include all four mechanisms leading to changes in growth mentioned in § 1, and other mechanisms, and is similar to the 'removal effect' in Buston (2003). This is what we call status-dependent growth. When we control for the effects of dominance rank, group size and breeding status by switching breeders in the second part of the experiment (so that helpers do not rise in rank), we still find an effect, but it is relatively small. This shows that helper *N. pulcher* also adjust their growth rate solely according to factor (iv) and supports the strategic growth hypothesis. It is an experimental verification of the 'residual SL effect' in Buston (2003). It also suggests that, at least in *N. pulcher*, (i) the dramatic change in growth upon reaching the head of the queue probably results from more than a release from potential conflict with more dominant fishes (any or all of factors (i)–(iii), or other changes we have not mentioned, also play a role) and/or (ii) it makes a profound difference is merely reduced (as in our experiment) or is completely absent or removed by removing the nearest higher-ranking competitor (as in the first part of our experiment and in Buston (2003)). We note that status-dependent growth is substantial (15–34% increase in SL), whereas, in comparison, the effect of strategic growth is smaller (23–41% of the effect of status-dependent growth), even though we created a very large difference in body size between the large breeder male and the focal helper (compare with Balshine *et al.* 2001).

We found no adjustment in growth rate of the small helpers in relation to the growth rate of the large helpers. We expect that growth adjustments in the small helpers might have been detected if we had created a large difference in size between the small helper and the large helper, but this was not the prime purpose of our experiment. Alternatively, between-helper conflict over the 'queuing rank' in the group for breeding positions might be less pronounced than conflict between the largest helper and the same-sexed breeder in the group for the reproductive position. For instance, breeders might be better able to evict helpers than larger helpers are able to evict smaller helpers. Alternatively, conflicts between helpers (Werner *et al.* 2003) might, on average, be less pronounced owing to some helpers being related or owing to the difference between ranks in the expected future fitness benefits from queuing being less for lower ranks (see Shreeves & Field 2002). Additionally, breeders might also be interested in 'controlling' the size of the largest same-sexed helpers in the group to reduce the likelihood of these helpers engaging in parasitic spawning (males) or polygynous breeding (females) (Limberger 1983).

It is unclear whether the strategic growth adjustments observed in our study result from subordinate restraint or whether subordinates' growth rate might be directly, or indirectly, affected by the behaviour of the dominant breeders. Dominants in *A. percula* do not aggressively interfere with the smaller subdominants, but when they are similar in size, subordinates are aggressively evicted from the territory (P. Buston, personal communication). By contrast, dominants in *N. pulcher* do aggressively challenge helpers without evicting them and hence might influence helper spacing, activity, food intake, costly behaviours, hormone levels (Oliveira *et al.* 2002) and ultimately growth (Taborsky 1984; Metcalfe *et al.* 1989, 1992; Huntingford & de Leaniz 1997; Hofmann *et al.* 1999; MacLean & Metcalfe 2001), ideas that we are currently investigating.

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