

Figure 2. Mean percent of trials (\pm SEM) in which subjects selected the lower cup as a function of condition.

Only the first 32 trials for each group are included, with the first block containing trial number 1–16 and the second block containing trial number 17–32. Double asterisk: $p < 0.001$.

a given outcome (the effect). We argue that the current study revealed evidence that chimpanzees can engage in the ‘comprehensive’ aspect of causal reasoning with regard to object weight. Further research is needed to clarify whether such basic comprehensive aspect of causal reasoning represents a precursor of more sophisticated forms of physical reasoning found in adults involving abstract concepts such as gravity.

Supplemental data

Supplemental data are available at <http://www.current-biology.com/cgi/content/full/18/9/R370/DC1>

Acknowledgments

We are grateful to L. Ajarova, D. Cox, and the trustees and staff of Ngamba Island Chimpanzee Sanctuary for their enthusiasm, help, and support. In particular, we appreciate the hard work of the animal caregivers: M. Gum, P. Kibirege, I. Mujaasi, L. Mugisha, M. Musumba, G. Musingo, A. Okello, R. Okello, and S. Nyandwi. We also appreciate permission from the Ugandan National Council for Science and Technology and the Uganda Wildlife Authority for

allowing us to conduct our research in Uganda. Finally we thank Raik Pieszek for his technical support and Roger Mundry for his statistical help.

References

- Penn, D.C., and Povinelli, D.J. (2007). Causal cognition in human and nonhuman animals: A comparative, critical review. *Annu. Rev. Psychol.* 58, 97–118.
- Call, J. (2006). Descartes’ two errors: Reason and reflection in the great apes. In *Rational Animals?* S. Hurlley and M. Nudds eds. (New York: Oxford University Press), pp. 219–234.
- Visalberghi, E., and Trinca, L. (1989). Tool use in capuchin monkeys: Distinguishing between performing and understanding. *Primates* 30, 511–521.
- Hauser, M.D., Williams, T., Kralik, J.D., and Moskovitz, D. (2001). What guides a search for food that has disappeared? Experiments on cotton-top tamarins (*Saguinus oedipus*). *J. Comp. Psychol.* 115, 140–151.
- Hood, B.M., Hauser, M.D., Anderson, L., and Santos, L. (1999). Gravity biases in a non-human primate? *Dev. Sci.* 2, 35–41.
- Call, J. (2004). Inferences about the location of food in the great apes (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, and *Pongo pygmaeus*). *J. Comp. Psychol.* 118, 232–241.
- Visalberghi, E., and Tomasello, M. (1998). Primate causal understanding in the physical and psychological domains. *Behav. Process.* 42, 189–203.

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Fasting or feasting in a fish social hierarchy

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Understanding why and how subordinates of many social animals remain consistently smaller than dominants is important for determining the mechanisms underlying the structure and stability of hierarchical societies. Here we show that competition over food and conflict over social rank are ultimately responsible for the regulation of subordinate growth in the group-living reef fish, *Paragobiodon xanthosomus* (Gobiidae). Subordinates benefit from reducing their own food intake, and hence growth, when they approach a size where they risk conflict with dominants. Dieting appears to be a behavioural mechanism ensuring that subordinates remain smaller than dominants within the hierarchy.

P. xanthosomus is a goby that lives in colonies of the coral *Seriatophora hystrix*. Inside colonies, they form groups of up to 20 gobies: a breeding male and female (dominant breeders) plus several smaller non-breeding females (subordinate non-breeders) [1]. Subordinate non-breeders are organised into a size-based hierarchy with each female remaining consistently smaller than the one ranked above it [2]. Hierarchies function as queues for breeding. When a dominant dies, all subordinates below it grow and shift up in rank. Only when they reach the front of the queue can they breed [2].

Traditionally, subordinate growth regulation in size-based hierarchies has been viewed as a non-adaptive consequence of competition over limiting food resources — subordinates are out-competed by dominants, obtain less food and grow more slowly [3]. More recently, an alternative adaptive perspective has emerged — in hierarchies where body size determines dominance rank and rank determines reproductive opportunity, conflict over rank between dominant and subordinates is thought to select for social regulation of subordinate growth [2,4,5]. We tested the relative effects of both processes by training subordinate

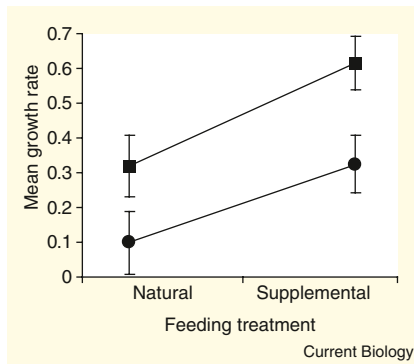


Figure 1. Effect of female removal and feeding on subordinate growth rates. Mean growth rates (% change in SL/day) \pm S.E. of subordinates ranked 3–5 that received either natural (Natural) or supplemental food (Supplemental) in the presence (circles) and absence (squares) of the dominant, breeding female. Standard length is measured from the tip of the head to the base of the tail. Means represented are least square means after controlling for effects of initial size ratio between subordinates and their immediate dominants in the group.

non-breeders (but not dominant breeders) within natural groups to feed from a supplemental food source having removed or not removed the dominant breeding female. Both feeding and breeder removal had equal positive effects on subordinate growth rates (Figure 1), suggesting both food and social processes together ensure consistent size differences are maintained between group members. Stable societies are thus likely to be maintained via adaptive and non-adaptive growth adjustments in subordinates.

The social regulation of subordinate growth in response to conflict within groups has long been thought to be mediated through aggression-induced stress imposed by dominants on subordinates [6]. We tested whether an alternative behavioural mechanism, namely that subordinates restrain their own growth when they become a threat to the rank of their dominants, could also promote the social suppression of subordinate growth [2,4,5]. Rank 4's receiving supplemental food grew significantly faster than their unfed, rank 3 immediate dominants from the same group (Paired T-test: $t_{16} = 4.4$, $p = 0.0005$) and unfed rank 4's from Natural groups (T-test: $t_{15} = 3$, $p = 0.004$). Subsequently, rank 4's in approximately half the groups abruptly ceased feeding despite no

feeding interference from dominants. In the remaining groups, rank 4's continued eating but were evicted from the group by their dominants (Figure 2). Size ratios between rank 4's and rank 3's (SL subordinate/SL immediate dominant) when the former stopped eating or were evicted fell within the range of body-size ratios at which subordinates are known to become a threat to the rank of their immediate dominant (0.9–0.95) (Figure 2) [2]. Rank 3's were not significantly more aggressive to rank 4's in Supplemental (0.12 ± 0.06 displays/minute) versus Natural groups (0.28 ± 0.08 displays/minute) (T-test: $t_8 = 1.5$, $p = 0.16$), indicating that the reduction in food intake in some fed rank 4's was unlikely to be due to increased aggression from their immediate dominants. Power for this analysis was low (Power test with $\alpha = 0.05$, $n_{(natural)} = 5$, $n_{(supplemental)} = 5$: $P = 0.41$); however, the trend is towards higher aggression in Natural than Supplemental groups which is opposite to that expected if dominant aggression caused reduced subordinate food intake. These results support the view that subordinates can reduce their food intake, and hence their growth, when conflict over rank intensifies, and that such self-imposed growth restraint is beneficial as subordinates otherwise suffer high costs from being evicted [7]. Subordinate *P. xanthurus* appear capable of dieting to avoid social conflict. Diet restriction has also been shown to prolong lifespan in many species [8], so diet restriction in *P. xanthurus* may also enhance a subordinate's chances of outliving its dominants and inheriting breeding status. As yet, we lack a complete understanding of how widespread the self-imposed reduction of food intake is in nature, and how it benefits individuals. Data on human dieting suggests that, while humans generally diet to improve health or increase attractiveness, rarely does it improve long-term health and males regularly prefer females that are fatter than the female's own ideal [9]. Further research into the occurrences, variation in and pay-offs of food-intake restraint would be enlightening for our understanding of the adaptiveness of dieting in animal societies.

Supplemental data

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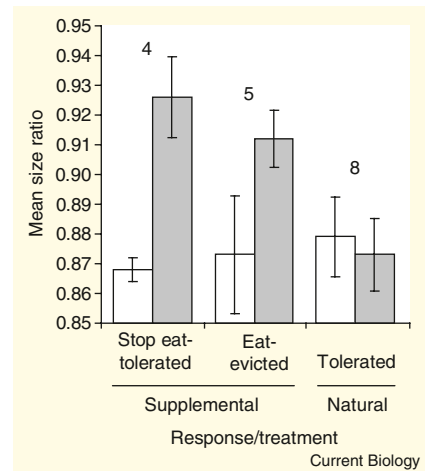


Figure 2. Behavioural responses to feeding. Mean body size ratios \pm S.E. between ranks 3 and 4 at the start (white) and end (grey) of the supplemental feeding period. Supplemental refers to the treatment in which the rank 4 received supplemental food throughout the experimental period, and Natural refers to the treatment in which the rank 4 obtained only natural food. Stop eat-tolerated, Eat-evicted and Tolerated refer to the responses of rank 4 subordinates to the Supplemental and Natural treatments. Numbers above bars refer to the sample sizes of each response/treatment.

References

- Wong, M.Y.L., Munday, P.L., Buston, P.M., and Jones, G.P. (2008). Monogamy when there is potential for polygyny: tests of multiple hypotheses in a group-living fish. *Behav. Ecol.* doi: 10.1093/beheco/arm141.
- Wong, M.Y.L., Buston, P.M., Munday, P.L., and Jones, G.P. (2007). The threat of punishment enforces peaceful cooperation and stabilizes queues in a coral-reef fish. *Proc. R. Soc. Lond. B* 274, 1093–1099.
- Metcalfe, N.B. (1986). Intraspecific variation in competitive ability and food intake in salmonids: consequences for energy budgets and growth rates. *J. Fish Biol.* 28, 525–529.
- Buston, P.M. (2003). Size and growth modification in clownfish. *Nature* 424, 145–147.
- Heg, D., Bender, N., and Hamilton, I. (2004). Strategic growth decisions in helper cichlids. *Proc. R. Soc. Lond. B* 271, S505–S508.
- Booth, D.J. (1995). Juvenile groups in a coral-reef damselfish: density-dependent effects on individual fitness and population demography. *Ecology* 76, 91–106.
- Lassig, B.R. (1981). The significance of epidermal ichthyotoxic secretion of coral-dwelling gobies. *Toxicon* 19, 729–735.
- Partridge, L., and Brand, M.D. (2005). Special issue on dietary restriction: Dietary restriction, longevity and ageing – the current state of our knowledge and ignorance. *Mech. Ageing Dev.* 126, 911–912.
- Polivy, J., and Herman, C.P. (2006). An evolutionary perspective on dieting. *Appetite* 47, 30–35.

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