2022-08-01

Strategic growth in social vertebrates

Strategic growth in social vertebrates

Peter Buston[1*], Tim Clutton-Brock[2]

1. Department of Biology, Boston University; Boston, MA 02215, USA.

   E-mail: buston@bu.edu

   ORCID iD: https://orcid.org/0000-0001-5513-8259

   Twitter: @BustonLab

   * Corresponding author.

2. Department of Zoology, University of Cambridge; Cambridge CB3 9EJ, UK.

   E-mail: thcb@cam.ac.uk

   ORCID iD: https://orcid.org/0000-0001-8110-8969

18 **Individual differences in growth and size of vertebrates often represent**

19 **adaptive, plastic responses to contrasts in ecological conditions. Recent**

20 **studies show that vertebrates can also modify their growth and size in an**

21 **adaptive fashion in response to fine-grain changes in social conditions**

22 **(which we refer to as strategic growth). Here, we review experimental**

23 **evidence for strategic growth in social vertebrates. We describe a set of**

24 **conditions under which strategic growth commonly occurs, and highlight**

25 **potential examples of convergent evolution of strategic growth across the**

26 **tree of life. This synthesis has implications for the way we think about**

27 **organismal growth and size, because it underscores that the size of**

28 **individuals can often be fine-tuned to their social environment.**

29

Plasticity of vertebrate body size

31 Phenotypic plasticity is the ability of a genotype to express different phenotypes

32 in response to variation in environmental conditions [1, 2]. Individuals can alter

33 their gene expression, physiology, neurobiology, behaviour, and morphology in

34 response to changing environmental cues. Phenotypic plasticity will evolve by

35 natural selection when i) individuals experience environmental variation, ii)

36 relative fitness of alternative phenotypes varies with environmental conditions,

37 iii) individuals can reliably assess current conditions or predict future ones, iv)

38 benefits of switching phenotypes outweigh the costs, and v) ability to switch

39 phenotypes is heritable [3-6]. While phenotypic plasticity is not always adaptive,

40 e.g., it can be a simple, non-adaptive effect of variation in temperature or

41 resource availability, it can be adaptive under many circumstances [7-9].

42

43   There are a number of well-known examples of adaptive plasticity of vertebrate

44   growth and size in response to varying ecological conditions. For example, crucian

45   carp (*Carassius carassius*) increase their body depth in response to presence of

46   predatory pike in ponds where they develop, thereby reducing their vulnerability

47   to predation [10, 11]. Galapagos marine iguanas (*Amblyrhynchus cristatus*) reduce

48   their body length in response to low food availability associated with El Niño years,

49   thereby reducing their likelihood of starvation [12, 13]. Common shrews (*Sorex*

50   *araneus*) reduce the size of their skull and other parts of skeleton from summer to

51   winter, presumably reducing their likelihood of starvation too [14, 15]. Together,

52   these examples provide compelling evidence of adaptive plasticity in vertebrate

53   body size in response to ecological conditions.

54

55   Examples of adaptive plasticity of vertebrate growth and size in response to

56   variation in social conditions are less well-known. Here, we are not referring to

57   plasticity of growth and size in response to coarse-grain variation in social

58   conditions, such as population density, that affect many individuals. Rather, we

59   are focusing on adaptive plasticity of growth and size in response to fine-grain

60   variation in social conditions [16], such as the opening up of a breeding

61   opportunity or the size of a rival, that affect specific individuals. This fine-grained

62   plasticity has been recognized for at least 50 years, and has been referred to as

63   'social control of size and/or growth' [17, 18], but its adaptive significance and has

64   only become clear in the last 20 years, since when it has been referred to as

65   'adaptive size and/or growth modification' or 'strategic growth' [19-22].

66

67 Here, we review the evidence for strategic growth in social vertebrates, describing

68 four social contexts in which it has been experimentally demonstrated. We

69 describe the general conditions under which strategic growth evolves, and

70 highlight potential cases of convergent evolution of strategic growth across the

71 tree of life.

72

73 **Strategic increase of growth and size in males**

74 In species with polygynous mating systems, where reproductive skew among

75 males is high and breeding competition is intense, strategic increases of growth

76 and size are observed in males. For example, in protogynous sex changing fishes

77 with polygynous mating systems, individuals initially develop as females and only

78 change sex to become male if a local breeding male dies and they acquire the

79 dominant position [23, 24]. In some of these species, such as saddleback wrasse

80 (*Thalassoma duperrey*), acquisition of the male position is associated with rapid

81 increases in growth and length that increase the competitive ability of individuals

82 [25]. The change in size and change in sex can be considered independently of each

83 other for individuals can change size without changing sex and vice versa [17, 26].

84

85 In one of the best documented examples, the increase in growth and size of the

86 ascending male varies with the benefits involved. The cylindrical sandperch

87 (*Parapercis cylindrica*) is a protogynous hermaphrodite, which forms groups

88 consisting of a single breeding male and one-to-ten breeding females [27]. The

89 male is the largest individual in each group and females are smaller; if the male

90 dies, the largest female changes sex and replaces him. The sex-changing individual

91 increases in length more than non-sex-changing females and increases in length

4

92   more when there are more females in the group and the potential for polygyny is

93   higher (Figure 1). The same patterns are found in the lab when all individuals are

94   fed ad-lib, ruling out the possibility that differences in growth in field are solely

95   due to differences in food acquisition [27]. The fact that the growth response is

96   fine-tuned to the polygyny potential, and that some individuals do not engage in

97   the growth spurt, rules out the possibility that this is a predetermined growth

98   trajectory. The magnitude of growth spurt and resulting sexual size dimorphism

99   are likely to be adaptive because the number of females in the group reflects both

100 benefits of becoming dominant and costs of maintaining dominance — individuals

101 that did not engage in the growth spurt would have forfeited the fitness gains that

102 came with being the dominant male in these groups [27].

103

104   INSERT FIGURE 1 HERE

105

106 Similar strategic increases in growth and size of males in response to the opening

107 up of breeding opportunities may occur in some great apes with polygynous

108 mating systems. For example, in orangutans (*Pongo sp.*), large-bodied males, with

109 prominent secondary sexual characteristics (fleshy protruding cheek flanges), call

110 to attract females passing through their territories [28, 29]. Meanwhile, smaller

111 ‘satellite’ males, who may be as old or older than territorial males, live within these

112 territories but neither show pronounced development of secondary sexual

113 characters nor display to attract females (though they attempt to mate

114 surreptitiously with receptive females). If dominant males die and are replaced

115 by satellite males, the latter shows a rapid increase in size and development of

116 secondary sexual characters and display behaviour [28-30].

5

117

Comparable changes in growth may also occur in some territorial ungulates [31, 32]. For example, in puku (*Kobus vardoni*) — a riverine antelope where males defend resource-based territories that attract females — males that acquire territories show increases in size, weight and conformation [31, 32]. In Iberian red deer (*Cervus elaphus hispanicus*), males have larger antlers in populations with relatively equal sex ratios, where reproductive competition is intense, than in populations that are biased towards females, where competition is reduced [33, 34]. Experiments with captive deer, where males were housed either with males or with females, demonstrated that males grew larger antlers when housed with reproductive rivals [33]. This latter case is analogous to that of the cylindrical sandperch revealing that changes in male size and secondary sexual characters can both be fine-tuned to the degree of reproductive competition.

Strategic increase of growth and size in females

In species with cooperative breeding systems, where reproductive skew among females is unusually high and breeding competition is intense, strategic increases in growth and size are also observed in females. In many singular cooperative breeders, like meerkats and mole-rats [35, 36] only a small proportion of females breed. Females that acquire a breeding position show rapid increases in body size that enhance their fecundity and competitive ability. For example, in naked mole-rats (*Heterocephalus glaber*) and Damaraland mole-rats (*Fukomys damarensis*), females that acquire dominant breeding positions increase in length and weight over the next 3-4 months (Figure 2) [36-41] as a result of growth of individual vertebrae and lengthening of spinal column [37, 38, 42]. Experiments with age,

142   size, and litter matched controls rule out the possibility that this growth spurt

143   represents a pre-determined trajectory. Across breeding females, increases in

144   body length are associated with increases in litter size and pup mass, indicating

145   that the change in size is adaptive — individuals that did not increase their length

146   in this context would have lower relative fitness [40].

147

148   INSERT FIGURE 2 HERE

149

150   Similar increases in body weight and size after the acquisition of dominant

151   breeding positions also occur in female Kalahari meerkats (*Suricata suricatta*)

152   which also live in groups where a single dominant female virtually monopolises

153   reproduction [21, 22, 43]. Here, too, these increases in body size are associated

154   with increases in litter size and pup weight [22]. Furthermore, in meerkats, the

155   magnitude of increases in weight rises if the individual that has acquired dominant

156   status is close in weight to the heaviest resident subordinate female in her group,

157   who is consequently a potential competitor, suggesting that increases in weight

158   may also serve to help dominant females to retain their position [21].

159

160   Strategic increases of growth and size in females in response to breeding

161   opportunities also occur in some fishes. For example, in protandrous sex changing

162   fishes with cooperative breeding systems, such as anemonefishes, individuals

163   initially develop as non-breeders, then become males, and only change sex to

164   become female if a breeding female dies and they acquire the dominant position

165   in the group [44-49]. There is evidence from pink anemonefish (*Amphiprion*

166   *perideraion*) [50], tomato clownfish (*Amphiprion frenatus*) [51], and clown

167 anemonefish (*Amphiprion percula*) (PMB personal observation) that individuals

168 acquiring dominant female positions increase in length relative to size-matched

169 individuals that either remain male or have been female for some time. Further,

170 the increase in size is fine-tuned to anemone size [50, 52, 53] which is an indicator

171 of resource availability and females' potential reproductive output [54]. In

172 anemonefishes, as in mole-rats and meerkats, increases in female size are

173 associated with increases in clutch size [55-57]. Whether female mole-rats also

174 fine-tune their size to their potential reproductive output is an outstanding

175 question but, if they do, this might help to explain the more extreme morphological

176 divergence between breeders and non-breeders in naked mole-rats, which live in

177 larger colonies and produce larger litters than other mole-rats [40].

178

179 **Strategic increase of growth and size in non-breeders**

180 In the cooperative breeding systems described above there are pronounced

181 dominance hierarchies and access to breeding opportunities is determined by

182 social rank, which is dependent on size and age of individuals. In these systems,

183 there is likely to be selection on non-breeders for growth strategies that maximize

184 their chances of retaining or increasing their rank. For example, in Kalahari

185 meerkats, which queue for breeding opportunities that follow the death of

186 breeders [43], non-breeders of both sexes respond to experimentally induced

187 increases in the growth of younger individuals who are potential rivals for

188 breeding positions by raising their own growth rates (Figure 3) [21]. Non-

189 breeding females also respond to new breeding opportunities presented by the

190 immigration of unrelated males by increasing their growth rates [58]. Here, too,

191 comparisons with appropriate experimental controls reveal these changes in

192 growth are not a consequence of pre-determined growth trajectories, rather they

193 are the response of specific individuals to aspects of their own, very specific, social

194 environment. These growth strategies are likely adaptive, because they will

195 maximize individuals' chances of retaining their social rank which confers access

196 to breeding positions — individuals that did not increase their growth in response

197 to the growth of their rivals would have lost out in the race for dominance.

198

199   INSERT FIGURE 3 HERE

200

201 Similar strategic increase of growth and size in non-breeders in response to size-

202 matched rivals occurs in some anemonefishes, which also form queues for

203 breeding positions [44, 47, 48]. In clown anemonefish, in the field and the lab, non-

204 breeders paired with size-matched rivals increase their growth and size relative

205 to solitary controls [59, 60]. Remarkably, paired individuals do this despite being

206 provided with the same food ration as solitary controls. As for the meerkats

207 described above, the increase in growth and size is likely adaptive because it will

208 maximize the chances of an individual retaining or increasing its social rank,

209 thereby maximizing the probability of acquiring breeding positions [48].

210

211 **Strategic decrease of growth and size in non-breeders**

212 In many social vertebrates, conflict is most intense between individuals that are

213 most similar in size or competitive ability, with dominants targeting the

214 subordinates that are their closest competitors for aggression or eviction from the

215 group [45, 61]. Given this, selection may favour individuals that remain small to

216 minimize the risks associated with aggression or eviction [19]. For example, in

217 clown anemonefish, which live in groups composed of a breeding pair and a small

218 number of non-breeders, there are well-defined size differences between

219 individuals adjacent in rank [19, 62]. The size differences are maintained because

220 subordinate individuals reduce their growth as they approach 80% of the size of

221 their immediate dominant (Figure 4) [19, 62]. The non-random nature of the size

222 differences and precision with which they are maintained suggests that they are

223 adaptive. Indeed, experimental manipulations of the size of individuals reveals

224 that subordinates whose size approaches that of their immediate dominant are

225 evicted from groups with severe consequences for their fitness in the field [63, 64].

226

227   INSERT FIGURE 4 HERE

228

229 Similar modifications of growth and size in response to the threat of eviction are

230 seen in other social fishes that queue for breeding positions. In the emerald coral

231 goby (*Paragobiodon xanthosomus*) there is also a non-random distribution of size

232 ratios between individuals adjacent in rank [65]. The non-random pattern

233 indicates that size differences are not simply a product of asymmetric competition

234 for food, and this is confirmed by an experiment in which subordinates were fed

235 ad-lib but stopped eating and growing when they reached a certain size [66]. Here,

236 too, these size ratios are maintained by reductions in growth of individuals as their

237 length approaches that of individuals immediately above them in the hierarchy

238 [19, 62, 65]. Staged contests revealed that subordinates are more likely to be

239 evicted from the group when they are more similar in size to their dominants [65].

240 Similar patterns, with some nuances, are found in Lake Tanganyika cichlids

241 (*Neolamprologus pulcher*) [20, 67, 68].

242

While examples of decreased growth and size modification in response to threats have been most extensively explored in social fishes, the phenomenon may also be occurring in social mammals. Whenever there is a relative increase in growth by one individual on the acquisition of a breeding position, as in mole-rats and meerkats, there is a relative decrease in growth exhibited by others who do not acquire the breeding position. That is, those individuals that do not acquire the breeding position remain relatively small. The adaptive significance of remaining relatively small in mammalian systems remains elusive, because most studies have focused on the benefits of becoming large [22, 40], but the benefits may lie in the social costs of becoming large and challenging the breeder as in fishes [64, 65]. Selection can favour remaining small and waiting to inherit a breeding position following the dominant's death rather than trying to grow large and contest for the territory, if the former conveys a higher probability of success than the latter [48, 69]. The latter may confer a low probability of success due to hidden threats — the invisible scaffold of animal societies — that are only revealed when the system is manipulated [70-73]. Testing this idea requires phenotypic manipulation of the small individuals, either by switching in other individuals of slightly different sizes (e.g., [64]) or by altering their phenotype by manipulating diet (e.g., [21]), manipulating hormones (e.g., [74, 75]) or by gene knockout, and observing resulting aggression and evictions.

Strategic changes of growth and size in amphibians and reptiles?

We could find no experimental evidence of strategic growth in amphibians and reptiles, despite adaptive growth plasticity in response to changes in ecological

267   conditions being well-documented in these groups [12, 13, 76, 77]. This might be

268   because there are relatively few long-term studies of marked individuals in these

269   taxa or because the formation of cohesive social groups is relatively rare. However,

270   there are some contexts where selection might be expected to favour strategic

271   growth.

272

273   The males of many species of frogs with prolonged breeding seasons form

274   choruses where breeding competition is intense [78]. At choruses, males hold

275   territories and call to attract females, and large-bodied males have higher mating

276   success than small-bodied males. Here, selection might be expected to favour

277   small-bodied males that call less and grow more, increasing their size to compete

278   more effectively. Indeed, in carpenter frogs (*Rana virgatipes*), small males tend to

279   have low calling effort and high growth rate [79]. Even among small males, those

280   that called less grew more [79], indicating this is not a pre-determined growth

281   trajectory.

282

283   Several skink species belonging to the genera *Egernia* and *Liopholis* form social

284   groups composed of kin with overlapping generations [80-82]. Groups may

285   occupy rock crevices or, uniquely among lizards, construct and maintain tunnels

286   [83]. Given the obvious similarities between these skinks and mole-rats [84], this

287   seems like a group in which strategic growth might be favoured by selection. In at

288   least one species, juveniles take several years to reach adult size and individuals

289   have variable growth rates [83], which is the kind of observational evidence that

290   preceded the discovery of strategic growth in fish and mammals..

291

Strategic changes of growth and size in birds?

We could find no experimental evidence of strategic growth in birds, despite many long-term studies of marked individuals in species with cooperative breeding systems and polygynous mating systems. We suggest that strategic growth may be less likely to occur (or be lower in magnitude and so harder to detect) in species where the size of individuals is tightly constrained by their ecological niche or their life history: for example, in birds, the constraints imposed by flight may make the costs of growth and size plasticity too high. If this is correct, then it suggests that it might be worth exploring whether there is any evidence of strategic growth among nestlings and or in flightless species.

Across bird species, nestling growth rates are positively correlated with rates of multiple paternity [85] and brood parasitism [86], which has been interpreted as nestling growth rates responding rapidly to social competition over evolutionary time. It is interesting to consider that nestling growth might, instead, be a plastic response to current social competition. This is a plausible hypothesis: in parasitic brown-headed cowbirds (*Molothrus ater*), growth is accelerated in hosts with shorter nesting periods [87, 88]; in spotless starlings (*Sturnus unicolor*) the gape is increased relative to the body in nests with intense sibling competition [89, 90].

Considering ground birds, great bustards (*Otis tarda*) form leks on which male weight and age are related to social rank and mating success [91]. Unlike most birds, great bustards continue to grow for several years after maturity — a pattern also seen in Australian bustards *Ardeotis australis* and kori bustards *Ardeotis kori* [92]. This creates an opportunity for bustards to strategically modify their growth

317 and size as they progress through the lek hierarchy. While the critical experiments

318 have not been done in birds, the hypothesis that some birds will engage in

319 strategic growth in some contexts is plausible and worth testing.

320

321 **Strategic changes of growth and size in humans?**

322 Evidence of strategic growth in non-human social vertebrates suggests that

323 similar processes may also occur in humans (*Homo sapiens*). Effects of adverse

324 physical or social environments on growth before birth and during early

325 development occur in many human populations [93, 94]. As in other vertebrates,

326 there are often direct consequences of nutritional constraints and other stressors

327 on individual growth. However, not all differences in growth or size appear to be

328 caused by restricted nutrition or poor health: children and adolescents commonly

329 show periods of rapid growth that are often associated with changes in social

330 conditions [95, 96]. Currently, we have limited understanding of the ultimate

331 causes of such growth spurts or their effects on individual fitness, but it would be

332 sensible to consider the possibility that they might represent adaptive responses

333 to fine-grain changes in social conditions [95-98]. Longitudinal studies following

334 individuals and changes in their fine-grain social context in traditional societies

335 are a promising way to test this idea.

336

337 **General conditions for the evolution of strategic growth**

338 In this paper, we have synthesized experimental evidence for strategic changes in

339 growth and size in response to fine-grain changes in social context in vertebrates

340 (Table S1). This reveals that strategic growth occurs when ideal conditions for the

341 evolution of phenotypic plasticity via natural selection are met [5, 6]. First,

342 individuals experience environmental variation in the form of variation in social

343 rank, which confers access to reproduction. Second, the relative fitness of

344 alternative growth and size tactics varies strongly with social rank and differences

345 can be extreme. Third, individuals can reliably assess their current social position

346 and predict their future one: in many cases, individuals are long-lived and group

347 membership is stable, allowing information on rivals to be acquired, growth and

348 size to be adjusted, and the outcome to be predicted with a degree of certainty.

349 Fourth, the benefits of adjusting growth and size outweigh the costs: adjusting

350 growth does not require extensive reorganisation of structures and, as such, costs

351 of strategic growth will be low relative to benefits of retaining or increasing social

352 position. By bringing all of these examples of strategic growth together in one

353 place, this synthesis reveals a set of socio-ecological conditions under which

354 strategic growth will be favoured by selection (Figure 5).

355

356   INSERT FIGURE 5 HERE

357

358 **Convergent evolution of strategic growth beyond vertebrates**

359 Convergent evolution of strategic growth in response to similar socio-ecological

360 conditions occurs across social vertebrates. Likely, there has been convergent

361 evolution of strategic growth in response to these same conditions in social

362 invertebrates, e.g., ants [199, 100] cnidarians [101, 102] shrimp [103, 104], and

363 termites [105, 106]. It is also plausible that there has been convergent evolution

364 of strategic growth in some plants [107, 108]: saplings of some forest trees, e.g.,

365 sugar maple (*Acer saccharum*) and beech (*Fagus grandifolia*), increase growth and

366 get taller in response to the opening up of canopy gaps, but decrease growth and

15

367   remain smaller in the presence of closed canopies [109, 110]. This can lead to the

368   formation of size hierarchies, analogous to those observed in clown anemonefish

369   [62], with individuals going through multiple periods of fast growth and slow

370   growth as they progress through the understory before obtaining a dominant

371   canopy position [111, 112]. In light of this synthesis, this convergence makes

372   sense, because these trees share similar socio-ecological conditions to social

373   vertebrates: high reproductive skew among individuals within a neighbourhood;

374   long-lived individuals and stable neighbourhood membership, with little (no)

375   movement between neighbourhoods (Figure 5).

376

377   **Concluding Remarks**

378   Social vertebrates exhibit adaptive modifications of growth and size in response

379   to fine-grain changes in social conditions. In social groups with high reproductive

380   skew and stable group membership, individuals modify their growth and size in

381   accordance with their social position. There seems to have been convergent

382   evolution on strategic growth across the tree of life, from social vertebrates, to

383   social invertebrates, and social plants. There is still much to be learned about the

384   mechanisms by which individuals assess their social position and modify their

385   growth and size accordingly [60, 113] (see Outstanding Questions). This view of

386   growth has implications for the way we think about organismal growth and size,

387   because it means that we must consider the possibility that the growth and size of

388   our study organisms is a fine-tuned response to their social environment.

389

390

391

References

1. Pigliucci, M. (2001) Phenotypic Plasticity, John Hopkins University Press.

2. West-Eberhard, M.J. (2003) Developmental Plasticity and Evolution, Oxford University Press.

3. Via, S. and Lande, R. (1985) Genotype environment interaction and the evolution of phenotypic plasticity. *Evolution* 39, 505-522.

4. Dudley, S.A. and Schmitt, J. (1996) Testing the adaptive plasticity hypothesis: density-dependent selection on stem length in Impatiens. *Amer. Nat.* 147, 445-465.

5. Berrigan, D. and Scheiner, S.M. (2004) Modeling the evolution of phenotypic plasticity. In Phenotypic plasticity: functional and conceptual approaches (Scheiner, S.M. and DeWitt, T. eds), pp. 82-97, Oxford University Press.

6. Scheiner, S.M. (2020) The theory of the evolution of plasticity. In The Theory of Evolution (Scheiner, S.M. and Mindell, D.P. eds), pp. 254-272, University of Chicago Press.

7. Gotthard, K. and Nylin, S. (1995) Adaptive plasticity and plasticity as an adaptation: a selective review of plasticity in animal morphology and life history. *Oikos* 74, 3-17.

8. Travis, J. (1994) Evaluating the adaptive role of morphological plasticity. In Ecological Morphology, pp. 99-122, University of Chicago Press.

9. Agrawal, A.A. (2001) Phenotypic plasticity in the interactions and evolution of species. *Science* 294, 321-326.

10. Bronmark, C. and Miner, J.G. (1992) Predator-induced phenotypical change in body morphology in crucian carp. *Science* 258, 1348-1350.

11. Domenici, D. *et al.* (2008) Predator-induced morphology enhances escape locomotion in crucian carp. *Proc. R. Soc. B* 275, 195-201.

12. Wikelski, M. (2005) Evolution of body size in Galapagos marine iguanas. *Proc. R. Soc. B* 272, 1985-1993.

13. Wikelski, M. and Thom, C. (2000) Marine iguanas shrink to survive El Nino. *Nature* 403, 37-38.

14. Lazaro, J. *et al.* (2017) Profound reversible seasonal changes of individual skull size in a mammal. *Curr. Biol.* 27, R1106-R1107.

15. Lazaro, J. and Dechmann, D.K. (2021) Dehnel's phenomenon. *Curr. Biol.* 31, R463-R465.

16. Sinervo, B. (2001) Selection in local neighborhoods, graininess of social environments, and the ecology of alternative strategies. . In Model Systems in Behavioral Ecology (Dugatkin, L.A. ed), pp. 191-226, Princeton University Press.

17. Borowsky, R.L. (1973) Social control of adult size in males of *Xiphophorus variatus*. *Nature* 245, 332-335.

18. Volpato, G.L. and Fernandes, M.O. (1994) Social control of growth in fish. Braz. *J. Med. Biol. Res.* 27, 797-810.

19. Buston, P. (2003a) Social hierarchies: size and growth modification in clownfish. *Nature* 424, 145-146.

20. Heg, D. *et al.* (2004) Strategic growth decisions in helper cichlids *Proc. R. Soc. B* 271, 5505-5508.

21. Huchard, E. *et al.* (2016) Competitive growth in a cooperative mammal. *Nature* 533, 532-534.

22. Russell, A.F. *et al.* (2004) Adaptive size modification by dominant female meerkats. *Evolution* 58, 1600-1607.

452 23. Warner, R.R. (1984) Mating behavior and hermaphroditism in coral reef fishes.
453 *Amer. Sci.* 72, 128-136.
454 24. Munday, P.L. et al. (2006) Diversity and flexibility of sex change strategies in
455 animals. *Trends Ecol. Evol.* 21, 89-95.
456 25. Ross, R.M. (1987) Sex-change linked growth acceleration in a coral-reef fish,
457 *Thalassoma duperrey. J. Exper. Zool.* 244, 455-461.
458 26. Hofmann, H.A. *et al.* (1999) Social status regulates growth rate: Consequences
459 for life-history strategies. *Proc. Nat. Acad. Sci. USA* 96, 14171-14176.
460 27. Walker, S.P.W. and McCormick, M.I. (2009) Sexual selection explains sex-
461 specific growth plasticity and posiitve allometry for sexual size dimorphism in a
462 reef fish. *Proc. R. Soc. B* 276, 3335-3343.
463 28. van Schaik, C.P. and van Hooff, R.A.M. (1996) Toward an understanding of the
464 orangutan's social system. In Great Ape Societies (McGrew, W.C. et al. eds), pp. 3-
465 15, Cambridge University Press.
466 29. van Hooff, J.A.R.A.M. (2000) Relationships among non-human primate males:
467 a deductive framework. In Primate Males: Cause and Consequences of Variation in
468 Group Composition (Kappeler, P.M. ed), pp. 183-191, Cambridge University Press.
469 30. Knott, C.D. and Kahlenberg, S.M. (2007) Orangutans in perspective: forced
470 copulations and female mating resistance. In Primates in Perspective (Campbell,
471 C. et al. eds), pp. 290-304, Oxford University Press.
472 31. Clutton-Brock, T.H. *et al.* (1982) Red Deer: The behavior and ecology of two
473 sexes, University of Chicago Press.
474 32. Rosser, A.M. (1990) A glandular neckpatch secretion and vocalizations act as
475 signals of territorial status in male puku (*Kobus vardoni*). *African J.Ecol.* 28, 314-
476 321.
477 33. Carranza, J. *et al.* (2020) Social environment modulates investment in sex trait
478 versus lifespan: red deer produce bigger antlers when facing more rivalry. *Nature*
479 *Sci. Rep.* 10, 9234.
480 34. Carranza, J. *et al.* (2020) The dark ventral patch: A bimodal flexible trait related
481 to male competition in red deer. *PLoS ONE* 15, e0241374.
482 35. Clutton-Brock, T. (2016) Mammal Societies, Wiley Blackwell.
483 36. Bennett, N.C. and Faulkes, C.G. (2000) African mole-rats: Ecology and
484 eusociality, Cambridge University Press.
485 37. Young, A.J. and Bennett, N.C. (2010) Morphological divergence of breeders and
486 helpers in wild Damaraland mole-rat societies. *Evolution* 64, 3190-3197.
487 38. Dengler-Crish, C.M. and Catania, K.C. (2007) Phenotypic plasticity in female
488 naked mole-rats after removal from reproductive suppression. *J. Exper. Zool.* 210,
489 4351-4358.
490 39. Henry, E.C. *et al.* (2007) Growing out of a caste – reproduction and the making
491 of the queen mole-rat. *J. Exper. Zool.* 210, 261-268.
492 40. Thorley, J. *et al.* (2018) Reproduction triggers adaptive increases in body size
493 in female mole-rats. *Proc. R. Soc. B* 285, 20180897.
494 41. O'Riain, M.J. *et al.* (2000) Morphological castes in a vertebrate. *Proc. Nat. Acad.*
495 *Sci. USA* 97, 13194-13197.
496 42. Thorley, J. (2018) The life history of Damaraland mole-rats *Fukomys*
497 *damarensis*: Growth, ageing and behaviour. PhD thesis, Cambridge, UK
498 43. Clutton-Brock, T. and Manser, M. (2016) Meerkats: cooperative breeding in the
499 Kalahari. In Cooperative Breeding in Vertebrates (Koenig, W.D. and Dickinson, J.L.
500 eds), pp. 294-317, Cambridge University Press.

501   44. Fricke, H.W. (1979) Mating system, resource defense and sex change in the
502   anemonefish *Amphiprion akallopisos*. *Z. Tierpsychol.* 50, 313-326.
503   45. Fricke, H.W. and Fricke, S. (1977) Monogamy and sex change by aggressive
504   dominance in coral fish. *Nature* 266, 830-832.
505   46. Mitchell, J.S. (2003) Social correlates of reproductive success in false clown
506   anemonefish: subordinate group members do not pay-to-stay. *Evol. Ecol. Res.* 5,
507   89-104.
508   47. Mitchell, J.S. (2005) Queue selection and switching by false clown anemonefish,
509   *Amphiprion ocellaris. Anim. Behav*. 69, 643-652.
510   48. Buston, P.M. (2004a) Territory inheritance in the clown anemonefish. *Proc. R.*
511   *Soc. B* 271, S252-S254.
512   49. Buston, P. (2004b) Does the presence of non-breeders enhance the fitness of
513   breeders? An experimental analysis in the clown anemone fish *Amphiprion*
514   *percula. Behav. Ecol. Sociobiol.* 57, 23-31.
515   50. Allen, G.R. (1972) The Anemonefishes: Their classification and biology, 2nd
516   edn., TFH Publications.
517   51. Hattori, A. (1991) Socially controlled growth and size-dependent sex change
518   in the anemonefish *Amphiprion frenatus* in Okinawa, Japan. *Japan J. Ichthyol*. 38,
519   165-177.
520   52. Fautin, D.G. (1992) Anemonefish recruitment: the roles of order and chance.
521   *Symbiosis* 14, 143-160.
522   53. Rueger, T. *et al.* (In review) Vertebrate growth plasticity in response to
523   variation in a mutualistic interaction. *Sci. Rep.*
524   54. Barbasch, T. *et al.* (2020) Substantial plasticity of reproduction and parental
525   care in response to local resource variability in a wild population of clownfish.
526   *Oikos* 129, 1844-1855.
527   55. Buston, P.M. and Elith, J. (2011) Determinants of reproductive success in
528   dominant pairs of clownfish: a boosted regression tree analysis. *J. Anim. Ecol.* 80,
529   528-538.
530   56. Saenz-Agudelo, P. *et al.* (2015) Mothers matter: contribution to local
531   replenishment is linked to female size, mate replacement and fecundity in a fish
532   metapopulation. *Mar. Biol.* 162, 3-14.
533   57. Promislow, D.E.L. *et al.* (1992) Life history allometry in mammals and
534   squamate reptiles: taxon level effects. *Oikos* 65, 285-294.
535   58. Dubuc, C. and Clutton-Brock, T. (2019) Male immigration triggers increased
536   growth in subordinate female meerkats. *Ecol. Evol.* 9, 1127-1134.
537   59. Reed, C. *et al.* (2019) Competitive growth in a social fish. *Biol. Lett.* 15,
538   20180737.
539   60. Desrochers, L. *et al.* (2020) Sensory cues underlying competitive growth in the
540   clown anemonefish (*Amphiprion percula*). *Behav. Proc.* 181, 104276.
541   61. Clutton-Brock, T.H. *et al*. (2001b) Cooperation, control, and concession in
542   meerkat groups. *Science* 291, 478-481.
543   62. Buston, P.M. and Cant, M.A. (2006) A new perspective on fish size hierarchies
544   in nature: patterns, causes and consequences. *Oecologia* 149, 362-372.
545   63. Wong, M.Y.L. *et al.* (2016) The four elements of within group conflict in animal
546   societies: an experimental test using the clownfish. *Behav. Ecol. Sociobiol.* 70,
547   1467-1475.
548   64. Branconi, R. et al. (2020) Ecological and social constraints combine to promote
549   the evolution of non-breeding strategies in clownfish. *Nature Comms Biol.* 3, 649.

550 65. Wong, M.Y.L. *et al.* (2007) The threat of punishment enforces peaceful
551 cooperation and stabilises queues in a coral-reef fish. *Proc. R. Soc. B* 274, 1093-
552 1099.
553 66. Wong, M.Y.L. *et al.* (2008) Fasting or feasting in a fish social hierarchy. *Curr.*
554 *Biol.* 18, R372-R373.
555 67. Taborsky, M. (1984) Broodcare helpers in the cichlid fish *Lamprologus*
556 *brichardi*: their costs and benefits. *Anim. Behav.* 32, 1236–1252.
557 68. Hamilton, I.M. *et al.* (2005) Size differences within a dominance hierarchy
558 influence conflict and help in a cooperatively breeding cichlid. *Behaviour* 142,
559 1591-1613.
560 69. Kokko, H. and Johnstone, R.A. (1999) Social queuing in animal societies: a
561 dynamic model of reproductive skew. *Proc. R. Soc. B* 266, 571-578.
562 70. Buston, P.M. and Zink, A.G. (2009) Reproductive skew and the evolution of
563 conflict resolution: a synthesis of transactional and tug-of-war models. *Behav. Ecol.*
564 20, 672-684.
565 71. Johnstone, R.A. and Cant, M.A. (1999) Reproductive skew and the threat of
566 eviction: a new perspective. *Proc. R. Soc. B* 266, 275-279.
567 72. Johnstone, R.A. and Cant, M.A. (2009) Models of reproductive skew: outside
568 options and the resolution of reproductive conflict. In Reproductive skew in
569 vertebrates: Proximate and ultimate causes (Hager, R. and Jones, C.B. eds), pp. 3-
570 23, Cambridge University Press.
571 73. Cant, M.A. (2011) The role of threats in animal cooperation. *Proc. R. Soc. B* 278,
572 170-178.
573 74. Fisher, H.S. (2019) Unravelling the evolution of complex reproductive traits
574 with phenotypic engineering. *Molec. Ecol.* 28, 3461-3463.
575 75. Nugent, B.M. *et al.* (2019) Experimentally induced variation in neuroendocrine
576 processes affects male reproductive behaviour, sperm characteristics and social
577 interactions. *Molec. Ecol.* 28, 3464-3481.
578 76. Pfennig, D. (1990) The adaptive significance of an environmentally-cued
579 developmental switch in an anuran tadpole. *Oecologia* 85, 101-107.
580 77. Pfennig, D.W. (1992) Polyphenism in spadefoot toad tadpoles as a locally
581 adjusted evolutionarily stable strategy. *Evolution* 46, 1408-1420.
582 78. Zamudio, K.R. and Chan, L.M. (2008) Alternative reproductive tactics in
583 amphibians. In Alternative reproductive tactics: an integrative approach (Oliveira,
584 R.F. et al. eds), pp. 300-331, Cambridge University Press.
585 79. Given, M.F. (1988) Growth rate and the cost of calling in male carpenter frogs,
586 *Rana virgatipes*. *Behav. Ecol. Sociobiol.* 22, 153-160.
587 80. Chapple, D.G. (2003) Ecology, life-history, and behavior in the Australian scinid
588 genus *Egernia*, with comments on the evolution of complex sociality in lizards.
589 *Herpetol. Monogr.* 17, 145-180.
590 81. Gardner, M.G. *et al.* (2008) Molecular systematics of social skinks: phlogeny
591 and taxonomy of the *Egernia* group (Reptilia: Scinidae). *Zool. J. Linn. Soc.* 154, 781-
592 794.
593 82. Davis, A.R. *et al.* (2010) Convergent evolution of kin-based sociality in a lizard.
594 *Proc. R. Soc. B* 278, 1507-1514.
595 83. Duffield, G.A. and Bull, C.M. (2002) Stable social aggregations in an Australian
596 lizard, *Egernia stokesii*. Naturwissenschaften 89, 424-427.
597 84. McAlpin, S. *et al.* (2011) Lizards cooperatively tunnel to construct a long-term
598 home for family members. *PLoS ONE* 6, e19041.

599   85. Royle, N.J. *et al.* (1999) Sibling competition and the evolution of growth rates
600   in birds. *Proc. R. Soc. B* 266, 923-932.
601   86. Remes, V. (2006) Growth strategies of passerine birds are related to brood
602   parasitism by the brown-headed cowbird (*Molothrus ater*). *Evolution* 60, 1692-
603   1700.
604   87. Remes, V. (2010) Explaining postnatal growth plasticity in a generalist brood
605   parasite. *Naturwissenschaften* 97, 331-335.
606   88. Winnicki, S.K. *et al.* (2021) Developmental asynchrony and host species
607   identity predict variability in nestling growth of an obligate brood parasite: a test
608   of the "growth-tuning" hypothesis. *Can. J. Zool.* 99.
609   89. Gil, D. *et al.* (2008) Adaptive developmental plasticity in growing nestlings:
610   sibling competition induces differential gape growth. *Proc. R. Soc. B* 275, 549-554.
611   90. Mainwaring, M.C. and Hartley, I.R. (2012) Causes and consequences of
612   differential growth in birds: A behavioral perspective. In Advances in the Study of
613   Behavior (Brockmann, H.J. et al. eds), pp. 225-277, Academic Press.
614   91. Alonso, J.C. *et al.* (2010) Correlates of male mating success in great bustard
615   leks: the effects of age, weight, and display effort. . *Behav. Ecol. Sociobiol.* 64, 1589-
616   1600.
617   92. Alonso, J.C. *et al.* (2009) The most extreme sexual size dimorphism among
618   birds: Allometry, selection, and early juvenile Ddvelopment in the Great Bustard
619   (*Otis tarda*). *The Auk* 126, 657-665.
620   93. Elo, I.T. and Preston, S.H. (1992) Effects of early-life conditions on adult
621   mortality: A Review. *Population Index* 58, 186-212.
622   94. Gluckman, P.D. *et al.* (2008) Effect of in utero and early-life conditions on adult
623   health and disease. *N. Engl. J. Med.* 359, 61-73.
624   95. Hermanussen, M. *et al.* (2018) Stunting, starvation and refeeding: a review of
625   forgotten 19th and early 20th century literature. *Acta Paediat.* 107, 1166-1176.
626   96. Hermanussen, M. *et al.* (1988) Periodical changes of short term growth
627   velocity ('mini growth spurts) in human growth. *Annals Hum. Biol.* 15, 103-109.
628   97. Bogin, B. *et al.* (2018) Human life course biology: A centennial perspective of
629   scholarship on the human pattern of physical growth and its place in human
630   biocultural evolution. *Ameri. J. Phys. Anthropol.* 165.4, 834-854.
631   98. Koziel, S. *et al.* (2019) Social mobility of the father influences child growth: A
632   three-generation study. *Amer. J. Hum. Biol.* 31, e23270.
633   99. Peeters, C. and Ito, F. (2001) Colony dispersal and the evolution of queen
634   morphology in social Hymenoptera. *Annu. Rev. Entomol.* 46, 601-630.
635   100. Schwander, T. *et al.* (2010) Nature versus nurture in social insect caste
636   differentiation. *Trends Ecol. Evol.* 25, 275-282.
637   101. Ayre, D.J. and Grosberg, R.K. (2005) Behind anemone lines: factors affecting
638   division of labour in the social cnidarian *Anthopleura elegantissima*. *Anim. Behav.*
639   70, 97-110.
640   102. Ayre, D.J. and Grosberg, R.K. (1996) Effects of social organisation on inter-
641   clonal dominance relationships in the sea anemone *Anthopleura elegantissima*.
642   *Anim. Behav.* 51, 1233-1245.
643   103. Chak, S.T.C. *et al.* (2015) Social control of reproduction and breeding
644   monopolization in the eusocial snapping shrimp *Synalpheus elizabethae. Amer.*
645   *Nat.* 186, 660-668.
646   104. Duffy, J.E. and Macdonald, K.S. (1999) Colony structure of the social snapping
647   shrimp *Synalpheus filidigitus* in Belize. *J. Crustacean Biol.* 19, 283-292.

648 105. Thorne, B.L. *et al.* (2003) Evolution of eusociality and the soldier caste in
649 termites: influence of intraspecific competition and accelerated inheritance. *Proc.*
650 *Nat. Acad. Sci. USA* 100, 12808-12813.
651 106. Thorne, B.L. (1997) Evolution of eusociality in termites. *Amer. Rev. Ecol. Syst.*
652 28, 27-54.
653 107. Schwinning, S. and Weiner, J. (1998) Mechanisms determining the degree of
654 size asymmetry in competition among plants. *Oecologia* 113, 447-455.
655 108. Falster, D.S. and Westoby, M. (2003) Plant height and evolutionary games.
656 *Trees* 18, 337-343.
657 109. Canham, C.D. (1988) Growth and canopy architecture of shade-tolerant trees:
658 response to canopy gaps. *Ecology* 69, 786-795.
659 110. Canham, C.D. (1989) Different responses to gaps among shade tolerant trees.
660 *Ecology* 70, 548-550.
661 111. Poulson, T.L. and Platt, W.J. (1996) Replacement patterns of beech and sugar
662 maple in Warren Woods, Michigan. *Ecology* 77, 1234-1253.
663 112. Marks, P.L. and Gardescu, S. (1998) A case study of sugar maple (*Acer*
664 *saccharum*) as a forest seedling bank species. *J. Torrey Bot. Soc.* 125, 287-296.
665 113. Johnston, R.A. *et al*. (2021) Morphological and genomic shifts in mole-rat
666 'queens' increase fecundity but reduce skeletal integrity. *eLife* 2021;10:e65760
667 114. Berglund, A. 1991. Egg competition in a sex-role reversed pipefish:
668 subdominant females trade reproduction for growth. *Evolution* 45, 770-774.
669 115. Lansade, L. *et al.* (2014) Behavioral and transcriptomic fingerprints of an
670 enriched environment in horses (*Equus caballus*). *PLoS ONE* 9, e114384.
671 116. Dantzer, B. et al. (2013) Density triggers maternal hormones that increase
672 adaptive offspring growth in a wild mammal. *Science* 340, 1215-1217.
673
674

Strategic growth in social vertebrates

Highlights

• Phenotypic plasticity is the ability of a genotype to express different phenotypes in response to variation in environmental conditions.

• Plasticity of body size, both adaptive and non-adaptive, in response to contrasts in ecological conditions is taxonomically widespread and widely recognized.

• Adaptive plasticity of body size in response to fine-grain changes in social conditions (strategic growth) is less well-known and harder to comprehend.

• We review examples of strategic growth in social vertebrates, e.g., the ability of clownfish to decrease growth as they approach the size of their dominants to avoid eviction from their social group and the ability of meerkats to increase growth in response to the growth of rivals to maintain their social rank.

• Circumstantial evidence suggests that strategic modifications of growth and size may be taxonomically widespread, occurring in many other social vertebrates, including humans, as well as social invertebrates and social plants, enabling individuals to resolve social conflicts and confront social challenges.

Strategic growth in social vertebrates

Outstanding Questions

• What are the general social conditions under which strategic growth will evolve by natural selection? Are there other, more relaxed social conditions?

• In which other taxa might these social conditions lead to the convergent evolution of strategic growth? How widespread is strategic growth in nature?

• Do domestic animals, e.g., horses [115], exhibit strategic growth and, if so, what are the consequences of the way they are raised for their competitive ability?

• Do humans exhibit strategic growth and, if so, what are the repercussions of using growth hormone to treat short stature of "unknown cause" in children?

• Can parents modify the growth and size of their offspring in response to cues regarding the social conditions that their offspring will experience [e.g., 116]?

• What other body systems, e.g., circulatory or nervous systems, might show cryptic, adaptive responses to fine-grain changes in social conditions?

• What are the proximate mechanisms underlying strategic growth? The problem is a complex one: individuals must assess their own size, the size of others, process that information, and change their gene expression, hormones, or behaviour to achieve an appropriate growth response. Subordinates are not passive players in these social groups. So, one must ask, how do dominant individuals suppress subordinates, how do subordinate individuals respond to suppression, and how does this vary across social contexts and across taxa?

1
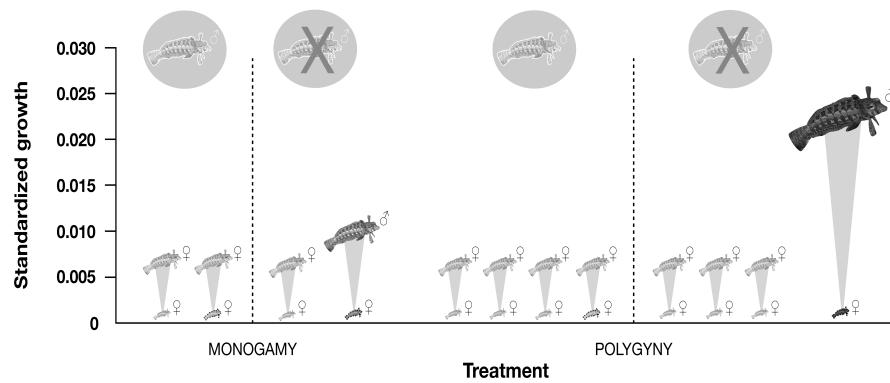
2

3

4 **Figure 1.** Strategic increases of growth and size of individual cylindrical

5 sandperch (*Parapercis cylindrica*) in response to acquisition of male breeding

6 position: individuals that undergo sex change and acquire the male breeding

7 position (dark and medium gray sandperch) grow more than individuals that do

8 not undergo sex change and do not acquire the male breeding position (light gray

9 sandperch); individuals that acquire the male breeding position when the

10 polygyny potential is high (dark gray sandperch) grow more than individuals that

11 acquire the male breeding position when the polygyny potential is low (medium

12 gray sandperch). (Adapted from Walker & McCormick [27]; original photo by

13 Rickard Zerpe; subsequent artwork by Rebecca Branconi).

14
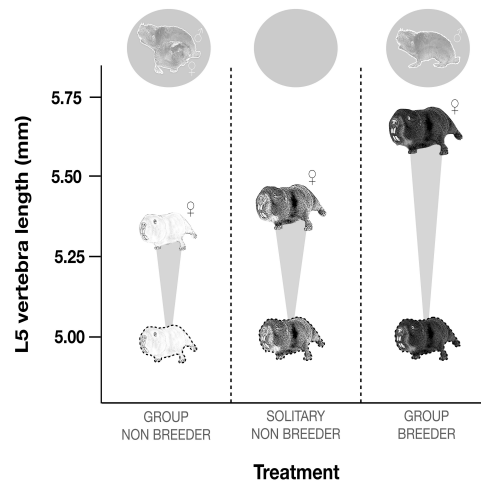
Figure 2. Strategic increases of growth and size of female Damaraland mole-rats (*Fukomys damarensis*) in response to acquisition of female breeding position: individuals that are placed in a new tunnel system with an unfamiliar male to become a breeder (dark gray mole-rats) show greater growth of individual vertebrae and overall lengthening of the spinal column than do individuals that are placed in a new tunnel system as a solitary non-breeder (medium gray mole-rats) or individuals that remain in their natal group as non-breeders (light gray mole-rats). (Adapted from Thorley et al. [40]; original photo © Joel Sartore / National Geographic Photo Ark; subsequent artwork by Rebecca Branconi).
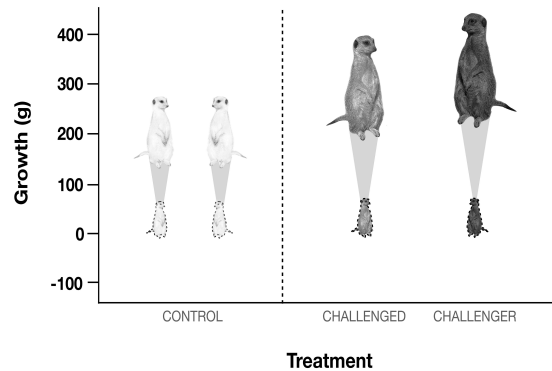
Figure 3. Strategic increases of growth and size of non-breeding Kalahari meerkats (*Suricata suricatta*) in response to experimentally induced increases in growth of same sex rivals: individuals referred to as 'challengers' are fed a hard-boiled egg each day and they grow a lot (dark gray meerkats); individuals referred to as 'challenged' are unfed littermates who grow in response to the challenger (medium gray meerkats); individuals referred to as 'controls' are from other litters where the feeding manipulation was not conducted and they grow less than challenged individuals (light gray meerkats). (Adapted from Huchard et al. [21]; original photo by Roberto Vavassori; subsequent artwork by Rebecca Branconi).

40
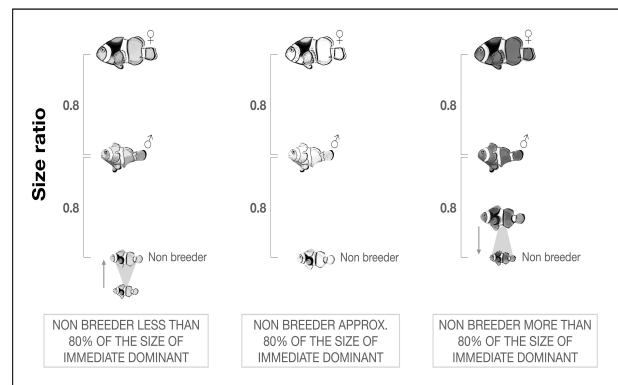
41

42

43 **Figure 4.** Strategic decrease of growth and maintenance of size differences by

44 non-breeding clown anemonefish (*Amphiprion percula*) in response to the threat

45 of eviction by their dominants: individuals a lot smaller than their immediate

46 dominant (less than 80% of the size) grow more than their immediate dominant

47 and have a low risk of eviction (medium gray clownfish); individuals smaller than

48 their immediate dominant (approximately 80% of the size) grow in lock-step with

49 their immediate dominant (light gray clownfish); individuals only a little smaller

50 than their immediate dominant (greater than 80% of the size), which is relatively

51 rare under natural conditions, grow less than their immediate dominant and have

52 a high risk eviction (dark gray clownfish). (Adapted from Buston [19], Buston &

53 Cant [62], and Branconi et al. [64]; original photo by Rebecca Branconi;

54 subsequent artwork by Rebecca Branconi).

55

56

57

58

59

60
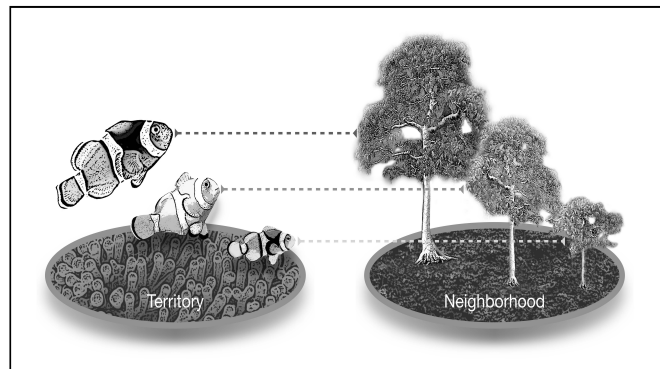
Figure 5. General conditions under which strategic growth occurs and potential convergent evolution of strategic growth. Social settings where one or a few individuals are able to monopolize resources and reproductive competition is intense provide conditions in which the relative fitness of alternative growth and size tactics varies strongly with social position. Stable social settings, involving long-lived individuals with little or no movement between groups, provide conditions in which individuals can reliably assess their social position and predict the outcome of adjusting their growth and size. These conditions are shared by organisms across the tree of life including **a**. animals, e.g., clown anemonefish (*Amphiprion percula*) and naked-mole rats (*Heterocephalus glaber*) and **b**. plants, e.g., beech (*Fagus grandifolia*) and sugar maple (*Acer saccharum*). (Artwork by Rebecca Branconi).

Strategic Growth in Social Vertebrates

Peter Buston[1*], Tim Clutton-Brock[2]

1. Department of Biology, Boston University; Boston, MA 02215, USA.

   E-mail: buston@bu.edu

   ORCID iD: https://orcid.org/0000-0001-5513-8259

   Twitter: @BustonLab

   * Corresponding author.

2. Department of Zoology, University of Cambridge; Cambridge CB3 9EJ, UK.

   E-mail: thcb@cam.ac.uk

   ORCID iD: https://orcid.org/0000-0001-8110-8969

Table S1. Strategic growth of vertebrates in response to fine grain changes in social context. Evidence is considered *experimental* when it compares individuals in alternative experimental contexts using statistics, *observational* when it compares individuals in alternative natural contexts using statistics, *anecdotal* when it compares individuals in alternative contexts without statistics, and *hypothetical* when the individuals and context are intriguing but there are no data.

Type of Plasticity	Species	Social Context	Phenotype	Evidence	Reference
Increase of growth and size in males	Saddleback wrasse (*Thalassoma duperrey*)	Polygynous mating system	Length	Experimental	Ross 1987 [S1]
	Cylindrical sandperch (*Parapercis cynlindrica*)	Polygynous mating system	Length	Experimental	Walker & McCormick 2009 [S2]
	Orangutans (*Pongo sp.*)	Polygynous mating system	Weight	Observational	Knott & Kahlenberg 2007 [S3]
	Puku (*Kobus vardoni*)	Polygynous mating system	Weight	Observational	Rosser 1990 [S4]
	Iberian red deer (*Cervus elaphus hispanicus*)	Polygynous mating system	Antlers	Experimental	Carranza *et al.* 2020 [S5]
	Great bustards (*Otis tarda*)	Polygynous mating system	Size	Hypothetical	Alonso *et al.* 2009, 2010 [S6,S7]
Increase of growth and size in females	Naked mole-rat (*Heterocephalus glaber*)	Cooperative breeding system	Length	Observational	O'Riain *et al.* 2000 [S8]
	Naked mole-rat (*Heterocephalus glaber*)	Cooperative breeding system	Length/weight	Experimental	Dengler-Crish & Catania 2007 [S9]
	Damaraland mole-rats (*Fukomys damarensis*)	Cooperative breeding system	Length	Observational	Young & Bennett 2010 [S10]
	Damaraland mole-rats (*Fukomys damarensis*)	Cooperative breeding system	Length	Experimental	Thorley *et al.* 2018 [S11]
	Kalahari meerkats (*Suricatta suricata*)	Cooperative breeding system	Length	Observational	Russell *et al.* 2004 [S12]
	Kalahari meerkats (*Suricatta suricata*)	Cooperative breeding system	Weight	Experimental	Huchard *et al.* 2016 [S13]
	Pink anemonefish (*Amphiprion perideraion*)	Cooperative breeding system	Length	Anecdotal	Allen 1972 [S14]
	Tomato clownfish (*Amphiprion frenatus*)	Cooperative breeding system	Length	Experimental	Hattori 1991 [S15]
	Clown anemonefish (*Amphiprion percula*)	Cooperative breeding system	Length/weight	Observational	Buston personal observation
Increase of growth in non-breeders	Kalahari meerkats (*Suricatta suricata*)	Cooperative breeding system	Weight	Experimental	Huchard *et al.* 2016 [S13]
	Clown anemonefish (*Amphiprion percula*)	Cooperative breeding system	Length	Experimental	Reed et al. 2019 [S16]
Decrease of growth in non-breeders	Clown anemonefish (*Amphiprion percula*)	Cooperative breeding system	Length	Experimental	Buston 2003 [S17]
	Clown anemonefish (*Amphiprion percula*)	Cooperative breeding system	Length	Observational	Buston & Cant 2006 [S18]
	Emerald coral goby (*Paragobiodon xanthosoma*)	Cooperative breeding system	Length	Observational	Wong *et al.* 2007 [S19]
	Emerald coral goby (*Paragobiodon xanthosoma*)	Cooperative breeding system	Length	Experimental	Wong *et al.* 2008 [S20]
	Tanganyika cichlids (*Neolamprologus pulcher*)	Cooperative breeding system	Length/weight	Experimental	Heg *et al.* 2004 [S21]
Leapfrog growth in males and females	Poeciliid fish males (*Xiphophorus variatus*)	Polygynous mating system	Length	Experimental	Borowsky 1973 [S22]
	African cichlid fish males (*Haplochromis burtoni*)	Polygynous mating system	Length	Experimental	Hofmann *et al.* 1999 [S23]
	Carpenter frog males (*Rana virgatipes*)	Polygynous mating system	Weight	Observational	Given 1988 [S24]
	Pipefish females (*Syngnathus typhle*)	Polygamous mating system	Length	Experimental	Berglund 1991 [S25]
Increase of growth in nestlings	Brown-headed cowbird (*Molothrus ater*)	Nestlings	Mass	Observational	Winnicki *et al.* 2021 [S26]
	Spotless starling (*Sturnus unicolor*)	Nestlings	Gape width	Experimental	Gil *et al.* 2008 [S27]

Supplemental References

S1. Ross, R.M. (1987) Sex-change linked growth acceleration in a coral-reef fish, *Thalassoma duperrey*. *J. Exper. Zool.* 244, 455-461.

S2. Walker, S.P.W. and McCormick, M.I. (2009) Sexual selection explains sex-specific growth plasticity and posiitve allometry for sexual size dimorphism in a reef fish. *Proc. R. Soc. B* 276, 3335-3343.

S3. Knott, C.D. and Kahlenberg, S.M. (2007) Orangutans in perspective: forced copulations and female mating resistance. In Primates in Perspective (Campbell, C. et al. eds), pp. 290-304, Oxford University Press.

S4. Rosser, A.M. (1990) A glandular neckpatch secretion and vocalizations act as signals of territorial status in male puku (*Kobus vardoni*). *African J.Ecol.* 28, 314-321.

S5. Carranza, J. *et al.* (2020) Social environment modulates investment in sex trait versus lifespan: red deer produce bigger antlers when facing more rivalry. *Nature Sci. Rep.* 10, 9234.

S6. Alonso, J.C. *et al.* (2010) Correlates of male mating success in great bustard leks: the effects of age, weight, and display effort. . *Behav. Ecol. Sociobiol.* 64, 1589-1600.

S7. Alonso, J.C. *et al.* (2009) The most extreme sexual size dimorphism among birds: Allometry, selection, and early juvenile Ddvelopment in the Great Bustard (*Otis tarda*). *The Auk* 126, 657-665.

S8. O'Riain, M.J. *et al.* (2000) Morphological castes in a vertebrate. *Proc. Nat. Acad. Sci. USA* 97, 13194-13197.

S9. Dengler-Crish, C.M. and Catania, K.C. (2007) Phenotypic plasticity in female naked mole-rats after removal from reproductive suppression. *J. Exper. Zool.* 210, 4351-4358.

S10. Young, A.J. and Bennett, N.C. (2010) Morphological divergence of breeders and helpers in wild Damaraland mole-rat societies. *Evolution* 64, 3190-3197.

S11. Thorley, J. *et al.* (2018) Reproduction triggers adaptive increases in body size in female mole-rats. *Proc. R. Soc. B* 285, 20180897.

S12. Russell, A.F. *et al.* (2004) Adaptive size modification by dominant female meerkats. *Evolution* 58, 1600-1607.

S13. Huchard, E. *et al.* (2016) Competitive growth in a cooperative mammal. *Nature* 533, 532-534.

S14. Allen, G.R. (1972) The Anemonefishes: Their classification and biology, 2nd edn., TFH Publications.

S15. Hattori, A. (1991) Socially controlled growth and size-dependent sex change in the anemonefish *Amphiprion frenatus* in Okinawa, Japan. *Japan J. Ichthyol.* 38, 165-177.

S16. Reed, C. *et al.* (2019) Competitive growth in a social fish. *Biol. Lett.* 15, 20180737.

S17. Buston, P. (2003) Social hierarchies: size and growth modification in clownfish. *Nature* 424, 145-146.

S18. Buston, P.M. and Cant, M.A. (2006) A new perspective on fish size hierarchies in nature: patterns, causes and consequences. *Oecologia* 149, 362-372.

S19. Wong, M.Y.L. *et al.* (2007) The threat of punishment enforces peaceful cooperation and stabilises queues in a coral-reef fish. *Proc. R. Soc. B* 274, 1093-1099.

S20. Wong, M.Y.L. *et al.* (2008) Fasting or feasting in a fish social hierarchy. *Curr. Biol.* 18, R372-R373.

S21. Heg, D. *et al.* (2004) Strategic growth decisions in helper cichlids *Proc. R. Soc. B* 271, 5505-5508.

S22. Borowsky, R.L. (1973) Social control of adult size in males of *Xiphophorus variatus*. *Nature* 245, 332-335.

S23. Hofmann, H.A. *et al.* (1999) Social status regulates growth rate: Consequences for life-history strategies. *Proc. Nat. Acad. Sci. USA* 96, 14171-14176.

S24. Given, M.F. (1988) Growth rate and the cost of calling in male carpenter frogs, *Rana virgatipes. Behav. Ecol. Sociobiol.* 22, 153-160.

S25. Berglund, A. 1991. Egg competition in a sex-role reversed pipefish: subdominant females trade reproduction for growth. *Evolution* 45, 770-774.

S26. Winnicki, S.K. *et al.* (2021) Developmental asynchrony and host species identity predict variability in nestling growth of an obligate brood parasite: a test of the "growth-tuning" hypothesis. *Can. J. Zool.* 99.

S27. Gil, D. *et al.* (2008) Adaptive developmental plasticity in growing nestlings: sibling competition induces differential gape growth. *Proc. R. Soc. B* 275, 549-554.