

Why might one kind of hybrid fitness problem (hybrid seed sterility) snowball with divergence while another (hybrid pollen sterility) does not? The snowball prediction depends on the combinatorial pile-up of pairs, triplets, and so on, of independently accumulated substitutions, each of which has some probability of being incompatible. But if a substitution can be incompatible only with substitutions at one other specific locus, then there can be no combinatorial explosion of possible DMIs and thus no snowball [7]. There are at least two plausible ways in which substitutions might be incompatible with only one other substitution. First, a slightly deleterious mutation might be compensated by a second-site substitution, often occurring in the same gene [18]. No snowball is expected under this kind of compensatory evolution [7,14], and indeed none is found in molecular evolution studies [18,19]. Second, a special case of compensatory evolution occurs between selfish genetic elements, like meiotic drive factors that obtain transmission advantages at the expense of their bearers, and the specific genomic substitutions that evolve to suppress them (Rob Unckless and Allen Orr, personal communication).

The third big advance in speciation genetics — the recent burst of

molecular analyses of DMI genes — is especially relevant here. An emerging consensus from this work is that molecular arms races between selfish genetic elements and their suppressors often contribute to the evolution of DMIs [20]. Genetic study of one aspect of speciation — the evolution of hybrid sterility and inviability — suggests a previously unappreciated fraction of genomic evolution occurs to suppress and ameliorate the deleterious consequences of genomic parasites.

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Department of Biology, University of Rochester, Rochester, New York, 14627, USA.

E-mail: dvnp@mail.rochester.edu

DOI: 10.1016/j.cub.2010.10.056

Primateology: Monkey Bromance

Male macaques form strong social bonds that enhance competitive ability and mating success, belying theoretical predictions that mate competition should prevent males from cooperating with one another.

Dorothy L. Cheney

Recently, the Oxford English Dictionary added 'bromance' (and its bookend, 'unfriend') to its lexicon, signaling the migration of the concept of "a close but non-sexual relationship between two men" from the insular confines of beer commercials into the world at large. At about the same time, Holt-Lundstad *et al.* [1] published the results of a meta-analysis indicating that strong social bonds enhance health and longevity in both men and women. That friendships should constitute an

important component of men's, as well as women's, health might come as a surprise to some. After all, the recurring theme in bromance flicks is that men's friendships struggle to progress beyond the level of burping contests and fist-bumps. Indeed, to date most of the evidence for a link between strong social bonds and enhanced reproductive success in animals has come from studies of females [2–6]. There are good theoretical reasons for expecting this sex bias. Because males compete with each other for mating opportunities,

close, affiliative bonds are predicted to be much rarer in males than in females, and restricted primarily to species in which males are usually the philopatric sex, such as chimpanzees and humans. In recent years, however, it has become clear that cooperation among males is not always restricted to kin, and that unrelated males too may sometimes derive reproductive benefits from forming same-sexed affiliative bonds. Writing in this issue of *Current Biology*, Oliver Schülke and his colleagues [7] report a striking example of cooperation and reproductive success among unrelated male macaques.

With the exception of chimpanzees, males living in multi-male groups seldom form long-term alliances, especially when they are unrelated. Male-male alliances occur more often in contexts in which a small number

of individuals (often involving only two males) bands together to compete for and defend a group of females against other small coalitions of males. Such coalitions occur in, among other species, lions, cheetahs, horses, and howler monkeys [8–12]. As predicted by reproductive-skew theory [13], alliances among non-kin are both less stable and more equitable than alliances among kin [9]. Some of the most complex alliances ever reported for animals occur among male dolphins, where two or three closely bonded individuals form stable, long-term alliances in order to compete for females. These teams, in turn, occasionally form more transient ‘second order’ alliances with other teams in contests that involve many males [14]. Some male–male alliances may last for years. Indeed, in the long-tailed manakin, a species of lek-breeding bird in which a pair of males attracts females through coordinated dancing duets, subordinate apprentices may serve as the dominant male’s dancing partner for more than 10 years before acquiring any mating opportunities themselves [15].

Despite these examples, cooperation among males seems both sporadic and fragile when compared to cooperation among females. This is particularly true in species where males are the dispersing sex, spending their adult lives either as the sole male in a group of females, where they must defend their group against challengers, or as members of a multi-male group, where they must compete with other resident males for access to the group’s females. The latter description characterizes the social system of many Old World monkey species, including baboons and macaques. In these species, males form unstable dominance hierarchies based on fighting ability, and high-ranking males usually monopolize the most mating opportunities. Although males occasionally form alliances to challenge more dominant individuals for access to females [16] or to reinforce existing rank relations [17], these coalitions seldom result in changes to a male’s dominance rank and are rarely associated with high rates of grooming or other affiliative behaviour. In contrast to females, males seldom establish close bonds with one another, and even males who form alliances at relatively high rates



Figure 1. Achilles.

The Assamese macaque Achilles was the male with the strongest social bonds in the study of Schülke *et al.* [7]. Achilles subsequently moved all the way to the alpha position in the study group and today is still the beta-male second only to his closest social partner since 2006. Photograph: Oliver Schülke.

continue to compete with one another for mates.

Male Assamese macaques (*Macaca assamensis*) are an exception to this apparent rule (Figure 1). Schülke and his colleagues [17] studied a group of wild Assamese macaques in Thailand that included 12 unrelated males and found that most males formed strong, differentiated bonds, as measured by grooming and proximity, with two or three other resident males. Males with strong bonds frequently formed coalitions against other males. These coalitions, in turn, are linked to future dominance rank and paternity success. The relationship between high sociality and high rank was not simply due to high-ranking males being more social, because current sociality was more highly correlated with future rank than current rank was correlated with future sociality. Furthermore, less social males were more likely to drop in rank, whereas more social males were more likely to rise. Although at least one other study of macaques has shown that males are most likely to form alliances with frequent grooming partners [18], this is the first study to suggest a causal relation between male affiliation, coalitions and rank advancement.

Schülke *et al.*’s [7] data corroborate several recent studies of female

animals, including baboons, horses, and rats [2–6], suggesting that strong social bonds contribute to increased health, longevity and offspring survival, and do so even when the degree of genetic relatedness is controlled for [3,6]. Importantly, the study also corroborates findings from a number of other species indicating that close bonds are not necessarily restricted to kin [5,6,11,14,19,20]. It therefore seems likely that living with kin *per se* plays a less important role than strong social bonds in enhancing reproductive success. The motivation to form differentiated relationships may have been under strong selective pressure in many species, including humans, for many millions of years.

The study also begs an unresolved question. It is now becoming increasingly clear that males, in addition to females, benefit from establishing close bonds with same-sexed partners. It is also clear that males in many species are capable of forming transient alliances with other males in order to compete for females, even when these alliances are not based on long-term affiliative relationships, e.g. [16]. What remains most puzzling about male–male alliances is their relative rarity across species, given how efficacious they

can be in enhancing mating success. Males in many species seem unable to set aside their competitive differences to form bonds that could, over the long term, be of mutual beneficial. Why should male Assamese macaques have been able to navigate this impasse when males in so many other species remain caught in a 'bad bromance'?

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Department of Biology, University of Pennsylvania, Philadelphia, PA 19104, USA.
E-mail: cheney@sas.upenn.edu

DOI: 10.1016/j.cub.2010.11.014

Aging: miRacles of Longevity?

The inventory of processes that miRNAs regulate has continued to expand since their relatively recent discovery. A new study reveals not only that the expression of miRNAs changes with age, but also that these miRNAs can act in both pro- and anti-longevity regulatory pathways.

Coleen T. Murphy

MicroRNAs (miRNAs), the endogenous 22-nucleotide non-coding RNAs that regulate expression through translational repression or RNA degradation, were first discovered through their roles in regulating developmental decisions in *Caenorhabditis elegans* [1]. Since then, miRNAs have been found to be remarkably well-conserved in plants and animals, including humans. The regulation of developmental timing, neuronal asymmetry, germline cell division, reprogramming of induced pluripotent stem cells, p53-induced cell senescence, and cancer progression are all controlled by miRNAs [2], and it is likely that even more functions of miRNAs will be discovered. In a paper published in this issue of *Current Biology* by de Lencastre *et al.* [3], miRNAs are shown to act in regulatory

pathways that both extend and reduce lifespan, suggesting a more important role for miRNAs in the regulation of aging than had been previously appreciated.

The questions posed in the paper by de Lencastre *et al.* [3] are whether miRNA expression changes with age, and whether those miRNAs that change with age play a role in regulating longevity [3]. These two questions had been previously addressed in separate studies; Ibanez-Ventoso *et al.* [4] used microarrays to identify *C. elegans* miRNAs that change with age, while Boehm and Slack [5] showed that the heterochronic development circuit miRNAs *lin-4* and *lin-14* regulate longevity post-developmentally.

de Lencastre *et al.* [3] have elaborated on these concepts, using deep sequencing to identify miRNAs that change with age, examining young

(day 0) and middle-aged (day 10) wild-type and long-lived *daf-2* insulin signaling mutants. Notably, the use of deep sequencing allowed the discovery of 11 new miRNAs, several of which share homology with miRNAs in higher eukaryotes.

Generally, miRNA expression declines with age. However, a small group of the small RNAs showed particularly large changes in expression, and a few were upregulated with age. Most of these miRNAs have not yet been characterized fully, but *let-7*, one of the founding miRNAs that is associated with both late larval development [6] and cancer [7], showed the greatest decrease with age. Fusion of the miRNA promoters to the *gfp* gene and analysis of GFP expression revealed that many of these age-regulated miRNAs are expressed primarily in the intestine, neurons, and somatic gonad — all tissues that have been previously associated with the regulation of aging [8].

Do these miRNAs actually regulate longevity, or are they merely passive markers of age? de Lencastre *et al.* [3] used *C. elegans* knock-out consortium deletion mutants to show that some of the miRNAs that were