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Social Evolution: Big Benefits of BFFs

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Having long-term familiar neighbors — rather than kin neighbors — can increase survival and double reproductive success in North American red squirrels. These benefits are so high they can slow senescence and may explain numerous social behaviors in this otherwise individualistic species.

Cooperation is stabilized through indirect genetics benefits from helping kin[1] or when costs of cooperating are recovered in future reciprocal interactions[2]. For example, cooperation in primates can quite literally entail 'I scratch your back, and you scratch mine' both among kin and non-kin[3]. In vampire bats, if a roost-mate goes hungry, another will vomit up blood to help it survive the day in hopes for a return favor when the tables are turned[4]. Bat roosts include kin leading to meal-sharing among relatives, but also includes reciprocation among non-relatives[3]. In such iconic cases, long-term social relationships — best friends forever (BFFs) — help stabilize cooperation and may be a key ingredient in generating big benefits of cooperation. But does that mean that less social species never cooperate or benefit from stable neighbors? Even species not typically considered social interact and maybe even cooperate to some degree; 'fences make good neighbors', after all.

Classic studies in territorial birds have shown that neighbors recognize each other's songs and respect territorial boundaries, only getting in a huff when neighbors or other intruders cross the 'fence'[5]. This so-called 'dear-enemy effect' could be considered a form of cooperation, as neighbors reduce territory maintenance costs if they respect boundaries. But in contrast to picking lice or vomiting blood for your friends over a lifetime, it is less clear if 'dear enemy' interactions benefit from long-term partnerships. In other words, do asocial animals gain fitness benefits from BFFs? In a new paper in this issue of *Current Biology*, Erin Siracusa, Andrew McAdam and colleagues[6] ask this question using an exceptional 22-year long-term dataset on red squirrels that includes information on neighborhood structure as well as survival and reproductive success.

North American red squirrels (*Tamiasciurus hudsonicus*) are essentially asocial — males and females each defend exclusive territories from intruders of both sexes[7]. They only really interact to argue with neighbors ('dear enemies') using vocalizations, to steal food or to have sex. Red squirrels hoard pine cones in middens which are critical to survival and reproductive success. While both sexes rely on their hoard to survive through winter[8], their food stores also play a critical role in reproductive success. Females require considerable energy during lactation and a full midden leads to more pups[9]. Males spend the most energy running around at -4°C in January to find mates and having a large food reserve allows them to search further and spend more time in mating chases[10]. The critical importance of these middens means that squirrels steal from each other. Because offspring do not disperse far (~100 m), and few individuals move after acquiring a territory[11], neighborhoods vary in both kin structure and long-term familiarity, which could help reduce both midden

raids and time spent on territory defense.

The Kluane Red Squirrel project was started in 1987 by Stan Boutin, and over the past 22 years the team has also gathered territory maps of known individuals and collected DNA samples to accurately measure male fitness for evolutionary studies. Armed with this impressive dataset, Siracusa and colleagues[6] were able to ask a fairly simple question that few others have been able to ask: does having kin or long-term neighbors provide fitness advantages in an asocial species? For each individual, they calculated the average relatedness with neighbors and the average familiarity (length of time two individuals have been neighbors). Neighbors were individuals whose middens were within 130 m of the focal squirrel's midden — just within vocal and pilfering range including non-adjacent territories.

Siracusa and colleagues[6] found that elevated average kinship in the neighborhood had no effect on either survival or reproductive success. This is surprising because red squirrels seem to recognize kin from their calls[12], and kin selection theory suggests that kin should cooperate more than non-kin. However, average kinship was actually pretty low, probably a consequence of fairly high turnover (i.e. extrinsic mortality) and male mating chases far from home territories which also decreases average kinship within a neighborhood. In contrast, having familiar neighbors had a massive effect on both survival and reproductive success for both sexes[6]. Having highly familiar neighbors increased annual survival by over 15% and nearly doubled the number of young produced on average. The fitness benefit of familiar neighbors is so large that it generates a huge incentive to keep neighbors alive and reduce neighborhood turnover in this otherwise ruggedly independent species. The authors show that the equivalent benefit of this familiarity under kin selection would represent cooperation among distant cousins ($r > 0.06$), which is higher than the average kinship among neighbors ($r < 0.05$).

If such strong benefits of familiarity occur in other systems, the importance of kin selection in cooperative social interactions might be less than generally expected and the importance of familiarity might be underestimated. For example, golden-crowned sparrows show very stable across-year social relationships in winter despite migration, which is not a result of kin structure[13,14]. Likewise, red-winged blackbirds benefit from having familiar neighbors[15], while dispersal means neighbors are not likely kin. While it is still possible that having close kin as neighbors could provide benefits in squirrels, birds, and other systems, the overall impact might be muted by also having non-kin neighbors leading to negligible effects at the population level. While more work is needed to understand how exactly having familiar neighbors improves fitness in red squirrels, Siracusa and colleagues suggest that having familiar neighbors increases survival through lower costs of territoriality and less pilfering of middens[16], which in turn allows males to search longer and farther for mates[6,10] (Figure 1). More broadly, our current focus on slightly reduced costs of territory defense in other 'dear-enemy' systems may similarly blind us to benefits of having more time for other activities that together produce an important fitness advantage.

The Kluane red squirrel long-term dataset provides a unique opportunity to measure fitness effects and social structure under natural conditions, but correlative studies are also open to confounding effects. With this knowledge, Siracusa and colleagues[6] dove into their data to make sure their results were not spurious. For example, it is possible that good territories increase both reproductive success and survival, which leads to all neighbors surviving better, and therefore an increase in familiarity. However, there was no spatial autocorrelation in survival or reproductive success. Likewise, younger individuals by definition will not have highly familiar neighbors and often have lower fitness than more experienced individuals, which could also lead to a spurious pattern. By restricting the dataset to older, senescent individuals (older than four years), in which age and familiarity are decoupled, Siracusa and colleagues[6] show that the benefits to survival and reproductive success are even more striking than the population average. In fact, the increase in survival among older senescent individuals that the authors measured is so large that keeping familiar neighbors nullifies the steady drop in annual survival of aging squirrels. It seems that red squirrels may have found the fountain of youth: keeping the same neighbors over time. Unfortunately for squirrels, extrinsic



Figure 1. Benefits of having familiar neighbors for individually marked red squirrels.
Red squirrels interact primarily through 'rattle calls' (top left) used to defend territories and food stores called middens. Having familiar neighbors allows individuals to decrease time spent on territory defense and is hypothesized to decrease loss of food stores, which should allow males more opportunities to mate (bottom left), females to raise more pups (top right) and both sexes to better survive winter (bottom right). (Photos: Ryan Taylor.)

mortality (i.e. predation) is high enough that very few individuals (4%) manage to have enough long-term neighbors, meaning that this fountain of youth has little impact at the population level, and much less on the evolutionary dynamics of senescence.

Together, these exciting findings in red squirrels bring up a number of new questions about how social structure impacts fitness. While the group found strong effects of average familiarity on fitness, it is quite possible that interactions with specific familiar individuals are key or that the pattern of familiar and less familiar neighbors matters. Measures of variation in familiarity such as effective degree[17] from neighborhood familiarity networks might be particularly appropriate to evaluate how familiarity structure impacts fitness. Likewise, the pattern of turnover among neighbors impacts both familiarity and kinship and it is possible that the exact pattern of who is lost and when could have important impacts on neighborhood strife, access to mates, and fitness[18]. Regardless of these details, a strong effect of familiarity with neighbors on fitness suggests we may have often overlooked the importance of territorial stability and 'hidden sociality' in explaining both specific behaviors and variance in fitness in less social species. It may also mean that reciprocal cooperation — through neighborhood stability in asocial species — may be more common than generally thought[19].

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Taste: A Scattered Affair

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***In vivo* two photon calcium imaging in the gustatory cortex of alert mice reveals that taste-responsive cells can vary in their breadth of tuning across taste qualities and that they are sparse and spatially distributed across the cortex.**

In all sensory systems, the neural pathway from the periphery through the brain ends in the cortex. For vision, audition and somatosensation, there is an orderly, topographic representation of stimuli along the surface of their respective, specialized cortices. For olfaction, the cortical representation is more broadly distributed, likely because there is no obvious way to organize odors. What about taste? Taste stimuli are organized as groups called 'taste qualities' based on data from humans suggesting that they taste alike. There are five widely recognized taste qualities: sweet, salty, sour, bitter and umami (savory). Just how these taste qualities are represented in the responses of cortical neurons remains a subject of intense debate. Essentially, there is evidence for two disparate points of view. There are some who argue for a gustotopic map[1], with cells that respond to each taste quality segregated into discreet areas of the cortex, called 'hot spots'. Others suggest that taste-responsive cells are distributed across