Territorial red squirrels live longer when they're friendly with their neighbors

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A North American red squirrel. Credit: Dr Erin Siracusa

Though red squirrels are a solitary and territorial species, a 22-year study of these squirrels in the Yukon suggests that they have a higher chance of survival and a greater number of offspring when living near the same

neighbors year after year. Surprisingly, the findings—appearing December 17 in the journal *Current Biology*—show that it didn't matter whether the squirrels' neighbors were related to them; these fitness benefits instead depended on familiarity, or the length of time the same squirrels lived next to each other. These benefits were even more pronounced in older squirrels, whom the data suggested could sharply offset the effects of aging by maintaining all of their neighbors from one year to the next.

"Red squirrels live on their individual territory, and they rarely come into physical contact with one another, but given the value of familiar neighbors, our study raises this really interesting possibility that they might cooperate with their competitors," says first author Erin Siracusa, a postdoctoral researcher at the University of Exeter, who conducted this research as a doctoral candidate at the University of Guelph. "What this cooperation looks like, whether it's sharing of food resources, or actively alarm-calling to warn their neighbors of predators, or potentially even forming coalitions to protect the neighboring territories from usurpers, we don't know. But I would argue based on our findings that despite their solitary nature, red squirrels do engage in social interactions and can have important social relationships."

While it's known that social relationships play a key role for animals that live in groups, Siracusa was interested in learning how social relationships affect solitary, territorial species—who rarely physically interact with their own kind. Through the Kluane Red Squirrel Project, Siracusa and her colleagues from the University of Guelph (Andrew G. McAdam), the University of Alberta (Stan Boutin), the University of Saskatchewan (Jeffrey E. Lane), and the University of Michigan (Ben Dantzer) followed 1,009 individuals over 22 years. Each summer, every squirrel was given colored ear tags so researchers could record who lived where and who shared territory boundaries.

Siracusa had previously observed that red squirrels with stable social relationships—established in part through defensive calls known as "rattles" that the squirrels make to identify themselves—were less likely to intrude on each other's territories and pilfer each other's cache. "Once they live next to each other long enough to agree on these territory boundaries, they sort of enter into this gentleman's agreement, saying, 'Okay, we've established these territory boundaries. We know where they are. We're not going to waste our time and energy fighting over these boundaries anymore,'" she says. This reduced aggression in familiar neighbors, known as the "dear enemy" phenomenon, has been established in many species previously, but researchers haven't been able to easily tie the phenomenon to a fitness advantage.

In this project, Siracusa and her team set out to discover whether there were any survival and reproduction benefits for squirrels who lived near their blood relatives or lived near non-related squirrels over a number of years. What they found was that living near relatives didn't provide any biological benefits—which was surprising, since animals that share the same genes are generally more likely to act altruistically toward one another. But they did find that regardless of relatedness, the longer squirrels lived with each other, the more likely they were to survive into the next year and produce more offspring.

The benefits of this familiarity among older squirrels were even more pronounced. "The benefits of familiarity were strong enough to completely offset the negative effects of aging," Siracusa says. "For example, for a four-year-old red squirrel that ages by one year, their survival probability decreases from 68% to 59%. But if that same squirrel that ages one year also maintains all of their neighbors, that probability of survival actually increases from 68% to 74%." However, she notes that only a small percentage of squirrels maintain their neighbors from one year to the next, so not all squirrels experience the benefits of familiarity in old age.

North American red squirrel pups. Credit: Dr Erin Siracusa

To make sure their results reflected the effects of familiarity among neighbors rather than localized areas with a particularly good habitat or low risk of predators, Siracusa and her team tested for spatial correlation in survival and reproductive success and found that it was rare and inconsistent.

More broadly, she suggests that these findings might help us better understand the evolution of territorial systems. They might help explain territorial behaviors such as migratory species returning to the same place year after year, sedentary species maintaining relatively stable

territories or home ranges throughout their lifetime, and animal mothers only rarely giving up their territory for the sake of their offspring—all of which could relate to animals not wanting to renegotiate social relationships. "In order for territorial systems to arise, the benefit of being territorial has to outweigh the costs of defending those resources, so it's not surprising that we should see the evolution of a mechanism that works to minimize those costs of territoriality," says Siracusa.

"At the risk of waxing poetic about squirrels," she says, "I think there is a sort of interesting lesson here that red squirrels can teach us about the value of social relationships. Red squirrels don't like their neighbors. They're in constant competition with them for food and mates and resources. And yet, they have to get along to survive. In the world right now, we're seeing a lot of strife and division, but perhaps this is a lesson worth bearing in mind: red squirrels need their neighbors, and maybe we do too."

The study, published in the journal *Current Biology*, is entitled: "Familiar neighbors, but not relatives, enhance fitness in a territorial mammal."

More information: *Current Biology*, Siracusa et al.: "Familiar neighbors, but not relatives, enhance fitness in a territorial mammal" www.cell.com/current-biology/f … 0960-9822(20)31615-8 , DOI: 10.1016/j.cub.2020.10.072

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