Benefits of living closer to kin vary by genealogical relationship in a territorial mammal

Sam F. Walmsley[1*†], Stan Boutin[2], Ben Dantzer[3,4], Jeffrey E. Lane[5], David W. Coltman[2,6], Andrew G. McAdam[1].

[1]Department of Ecology and Evolutionary Biology, University of Colorado, 1900 Pleasant Street, Boulder, CO 80309, USA

[2]Department of Biological Sciences, University of Alberta, 11455 Saskatchewan Drive, Edmonton, AB, T6G 2E9, CA

[3]Department of Psychology, University of Michigan, 500 S State St, Ann Arbor, MI 48109, USA

[4]Department of Ecology and Evolutionary Biology, University of Michigan, 500 S State St, Ann Arbor, MI 48109, USA

[5]Department of Biology, University of Saskatchewan, 112 Science Pl, Saskatoon, SK, S7N 5E2, CA

[6]Biology Department, Western University, 1151 Richmond Street, London, ON, N6A 5B7, CA

*Correspondence: sam.walmsley@dal.ca

[†] Current address: Department of Biology, Dalhousie University, 1355 Oxford Street, Halifax, Canada, NS B3H 4J1.

Abstract

While cooperative interactions among kin are a key building block in the societies of group-living mammals, their importance for species with more variable social environments is unclear. North American red squirrels (*Tamiasciurus hudsonicus*) defend individual territories in dynamic neighbourhoods and are known to benefit from living among familiar conspecifics, but not relatives. However, kin-directed behaviours may be restricted to specific genealogical relationships or strongly mediated by geographic distance, masking their influence at broader scales. Using distance between territories as a proxy for the ability of individuals to interact, we estimated the influence of primary kin (parents, offspring, siblings) on the annual survival and reproductive success of red squirrels. Contrary to previous work, this approach revealed large fitness effects of living closer to kin, but only for certain genealogical relationships and fitness components. For example, females had enhanced annual survival when living closer to their daughters, though the reverse was not true. Most surprising was the finding that males had higher annual reproductive success when living closer to their father, raising new questions about cooperation among fathers and sons. Together, these findings reveal unexpected nuance in the fitness consequences of kinship dynamics for a species that is territorial and largely solitary.

Keywords

Cooperation ▪ kinship ▪ reproductive success ▪ survival ▪ social evolution ▪ territoriality

Introduction

How individuals disperse, settle, and die has important consequences for cooperative group-living, constraining the mechanisms by which affiliative relationships evolve [1,2]. For example, in most group-living mammals, female-biased philopatry results in social units composed of matrilineal relatives [3]. Here, kin selection provides the opportunity for the development of stable and cooperative groups, bolstered by the additional benefits of inclusive fitness [4,3]. While the challenges of navigating group dynamics can be significant, members often rely on predictable dominance and kinship-based hierarchies to structure their interactions. For example, spotted hyenas (*Crocuta crocuta*) are born into matrilineal clans and inherit the social rank and network of their mother, a key determinant of lifelong fitness [5–7]. Less understood is how cooperative relationships form in species where access to kin is more variable [8–10], especially those lacking obvious social units, such as solitary species [11].

Non-traditional co-operative relationships may be particularly difficult to study if they rely on more cryptic forms of cooperation among kin. For example, kin-directed behaviours in Galápagos sea lions (*Zalophus wollebaeki*) or gray squirrels (*Sciurus carolinensis*) may simply involve increased spatial tolerance [12], or subtle reductions in antagonism [13]. An important follow-up question is whether these subtler processes should translate into meaningfully large effects on individual variation in survival and reproductive success. Quantifying the fitness consequences of these less-conspicuous interactions is a crucial step towards understanding whether the benefits of living with kin are mirrored in species with highly variable social environments.

Evidence from group-living species suggests that variable access to kin can result in a compensatory investment in mutualistic relationships with non-relatives. Vampire bats (*Desmodus rotundus*) rely on regular food sharing, which typically occurs among close kin [14]. However, to mitigate the risk of resting at a different roost from these preferred partners, individuals “hedge their bets” by simultaneously developing affiliative relationships with unrelated conspecifics. Similar strategies are found in baboons: female yellow baboons (*Papio cynocephalus*) preferentially associate with their mothers or daughters but rely on bonds with non-kin when necessary [15], and female Chacma baboons (*Papio ursinus*) increase investment in new grooming relationships when a preferred kin partner dies [16]. These findings demonstrate that cooperation with unrelated individuals can buffer individuals from the risks of temporarily or permanently losing access to a close relative. In other words, despite lacking the advantage of inclusive fitness benefits, group-living animals may choose to invest in mutualistic bonds with non-kin if it leads to a more predictable social environment [17,18]. So, while kin selection is typically considered the lower-threshold pathway to prosocial bonds [19], mammals living in less-structured social environments may instead prioritise mutualistic bonds with potentially unrelated individuals.

North American red squirrels (*Tamiasciurus hudsonicus*; hereafter red squirrels) defend exclusive territories containing a central hoard of stored food resources (midden) from nearby conspecifics. Populations are characterized by fluctuating membership, driven by an influx of juveniles in the summertime [20], particularly during periodic resource pulses. Red squirrels sometimes establish territories near their parents [20,21], creating the spatial scaffolding for kin cooperation. However, mean relatedness among neighbours remains low, meaning that prior to recruitment, an individual's ability to access to kin is highly unpredictable. The analogy from group-living mammals raises the question: are red squirrels exploiting their rare access to kin, or does the unpredictability of the social environment lead to a prioritization of mutualistic bonds with available neighbours, regardless of relatedness?

Siracusa et al. (2021) found that familiarity, defined as the amount of time two individuals lived in the same area, enhanced the survival and reproductive success of red squirrels whereas the mean relatedness of neighbouring conspecifics within a 130 m radius had no effect [22]. Though consistent with predictions from group-living species with variable access to kin, this is surprising given evidence of rare but seemingly cooperative kin-biased behaviour: related red squirrels sometimes nest communally for warmth [23], adopt orphaned juveniles [24], and even bequeath entire territories to their offspring [20]. Possible explanations for this discord could be that benefits of kin-directed behaviour only occur at finer spatial scales [22], or perhaps, that kin benefits are limited to specific genealogical relationships (e.g., mother-daughter) [25,26], especially if kin recognition and/or affiliation are contingent on early associations in the natal nest [27,28].

Leveraging a long-term study of wild red squirrels in Yukon, Canada, we ask whether kinship plays a role in structuring fitness-enhancing interactions in a highly unpredictable social neighbourhood. Red squirrels risk intrusions from neighbours when away from their territory [29], likely making it costly to interact with individuals that are far away. Following studies on kin benefits in humans [30], we aimed to exploit the spatial limitations of any affiliative behaviours, hypothesizing that the influence of kin on annualized survival and reproductive success would be mediated by geographic distance. Given the possibility that beneficial kin-directed behaviours vary by genealogical relationship [25,31], we focused our analysis on primary kin (mothers, fathers, sons, daughters, full siblings), estimating separate influences for each kinship class. We predicted that any influences of kin on annual survival or annual reproductive success would dissipate as a function of distance. And while we were interested in possible interactions among male-male kin dyads, we expected that benefits were more likely to occur among female kin or mother-son dyads.

Materials and methods

Study site and long-term data collection

All data used in this study were collected as part of the Kluane Red Squirrel Project (KRSP), a long-term research project investigating populations of wild red squirrels living in southwestern Yukon, Canada (61°N, 138°W). Since 1987, individual red squirrels in this region have been tagged with alphanumeric ear tags (Monel #1; National Band and Tag, Newport, KY, USA), enumerated, and monitored throughout their lives. Red squirrel territories are typically centred on caches or "middens" containing hoarded white spruce cones (*Picea glauca*). White spruce trees periodically undergo masting events (every 4-7 years), leading to a resource pulse for red squirrels. Our analysis focused on two study areas ("Kloo" and "Sulphur"). Both study areas were staked at 30 m intervals, with locations identified to tenths of a stake length, meaning that any spatial position could be specified within approximately 3 m. Both male and female red squirrels are exclusively territorial, and typically defend the same territory year-round for life, allowing us to reliably locate individuals and map out the distances between them. Territory ownership was determined during a census each May through repeated live-trapping at each midden or nest on the study area (Tomahawk Live Trap Co., Tomahawk, WI, USA), and by behavioural observations (principally, evidence that an individual consistently used its territorial "rattle" vocalization at a given location [29]). Pregnant females are regularly monitored in the spring so that juveniles can be tagged and linked to their maternal pedigree. Previous work has confirmed that these linkages are unlikely to be biased by rare adoption events [24]. Starting in 2003, all individuals have also been genotyped at 16 microsatellite loci. These data have been used to supplement maternal linkages with paternities (99% confidence, CERVUS 3.0 [32]), resulting in a comprehensive, long-term pedigree including nearly every individual living on each study area [33]. For additional information on the study site and long-term data collection protocols, see [20,34,35].

Study subjects

For all known red squirrels living on the Kloo or Sulphur study areas between 2003-2014, we identified pairwise relationships among close kin (mother, father, son, daughter, full sibling) using the multigenerational pedigree and the *pedantics* package [36]. Full sibling relationships were not partitioned by sex due to a lack of data: high rates of both multiple paternity [37], and juvenile mortality meant that it was relatively rare for full siblings to persist in the population (median 2 sibling dyads per study area per year, range 0-7). Given our interest in estimating annual survival, we only included individuals with known birth years, and excluded any squirrels that died of un-natural causes, as these deaths were expected to be unrelated to influences of the social environment. Geographic distance between kin territories was measured as the linear distance between the centre of the primary midden (cone cache) of each squirrel, which is typically situated at the centre of the

territory. We included territory locations of several individuals who lacked full, established middens but were known to defend a nest in the study area ($n_{territories} = 4$). For individuals without any primary kin in the study area in a given year, we calculated their distance to the territory of a randomly selected individual, coded as "Non-kin". Note that this category could include more distantly related kin, but no full siblings, parents, or offspring. These "Non-kin" observations served as a reference category, anchoring estimated influences of primary kin in subsequent models to a meaningful baseline.

Estimating influences of kin on survival

We measured annual survival as the detection of an individual on or after January 1st of the following calendar year. Because red squirrels rarely change territory locations [38], individuals were assumed to have died if they disappeared from the study area and were never seen or trapped again. Previous work on this population has estimated the probability of re-detecting living adults to be 100% [39]..

Prior to analysis, we subset the data to only include observations of the *nearest* nuclear relative for each focal-year combination, resulting in a dataset with distances to different types of kin. This allowed us to directly test whether influences on fitness differed by kin relationship, while also focusing on the smallest distance values, expecting that any behaviourally mediated influences should be most apparent when squirrels were close together. First, we used generalized additive models (GAMs) to investigate possible non-linearities in the relationships between fitness and distance to specific types of primary kin. This was important given the expectation that influences of other squirrels might be negligible at very large distances, meaning that a linear fit may not be justified for the full spatial extent of the data. We fitted GAMs with a binomial family, logit link, and basis dimension of 3 to relate annualized survival as the response variable. Crucially, we fitted an interaction between relationship type and linear distance. This allowed us to test whether the fitness-distance relationship was significantly different between different types of primary kin, compared to the reference category ('Non-kin'). We also included mast year (yes/no) as a predictor, expecting that resource pulses could be a common cause influencing survival, and potentially, access to primary kin. Lastly, we included quadratic effects of age given the expectation that the probability of annual survival should decrease for both juveniles and senescent adults [22].

These preliminary GAMs indicated potentially non-linear relationships between fitness and distance to specific types of close kin. However, relationships within the previously defined "social neighbourhood" in this population [22,27], i.e., up to a maximum distance between territories of 130m, tended to be linear, with apparent changes in the relationship typically occurring at or beyond this point. Accordingly, we fitted GLMMs with linear effects of distance to the restricted, "social

neighbourhood" datasets, only including distance records less than or equal to 130 m. These models were fitted with binomial family and a logit link function and used the same response and predictor structure as above, explaining survival as a function of mast year, age (linear and quadratic terms), and an interaction between genealogical relationship and geographic distance. Though within-neighbourhood (i.e., < 130m) influences of kin were most relevant for our research question, we also provide additional GLMMs in the supplement which include distances spanning the full range of each study area as well as a quadratic effects of distance to account for apparent non-linear associations at this scale (See electronic supplementary material).

All GLMMs were fitted with crossed random effects to account for the inclusion of multiple measures of the focal squirrel (focal ID) across years and of possibly bi-directional records of the same dyad of squirrels (dyad ID). We also included a random effect for year of the study period to account for any additional annual variation in fitness measures not captured by the mast-year fixed effect. Because we were interested in the annual influences of primary kin on the probability of survival, we did not use Cox proportional hazard models, which instead model time to death across each individual's lifetime. Accordingly, there was no need to account for right-censoring in our data

Estimating influences of kin on reproductive success

Following previous work on this population [22], we calculated separate metrics of annual reproductive success (ARS) for males and females to reflect differences in parental care. For females, we defined annual reproductive success as the number of pups that were successfully recruited (i.e., were confirmed alive for at least 200 days), excluding any non-breeding individuals. To test the sensitivity of our results to this exclusion, we also fitted identical GAMs including non-breeding females (n = 181), attributing them ARS values of 0. Because male red squirrels provide no paternal care, annual reproductive success for males was measured as the number of pups sired per year.

As with measures of annual survival, we first used GAMs to visualize any non-linear influences of each type of primary kin on annual reproductive success. We similarly identified linear relationships within the social neighbourhood, with possible non-linearities apparent when considering the full spatial extent of each study area. Here, we used GLMMs with Poisson family and log link function to explain reproductive success as a function of distance to primary kin, fitted with an interaction between distance and genealogical relationship type. As before we also included mast year, linear and quadratic effects of age, and crossed random intercepts representing individual, dyad-level, and annual variation.

The model with male reproductive success as the response variable showed moderate overdispersion, so was re-fitted using a zero-inflated distribution. For all GLMMs, measures of distance were $\log_{10}$-

transformed, reducing the leverage of very large distance values. No additional mean-centering or scaling was applied, so that main effect coefficients correspond to benefits of each type of primary kin having a separate territory at very close distances (1 m). Note though that such close distances do not occur biologically: in our study, the closest distance between two squirrels with distinct territories was 9.5 m. Given our aim to explain rather than predict variation in fitness, no model selection procedures were performed.

Prior to analysing any data, we developed and publicly uploaded an analysis plan to avoid inadvertently hypothesizing after results are known ("HARKing") [40]. This plan is available at https://github.com/KluaneRedSquirrelProject/Analysis-Plans. Some changes to our approach were made during analysis, such as the inclusion of a year-specific random effect. All analyses were conducted in R version 4.0.5 [41]. GAMs were fit using the *mgcv* package while GLMMs were fit using *glmmTMB* [42]. Model diagnostics were assessed using *DHARMa* [43]. Coding scripts are available at github.com/KluaneRedSquirrelProject/Walmsley-Projects.

Results

In total, our main analysis included observations of annualized fitness from 679 individuals between 2003 and 2014. We found that female red squirrels generally lived nearer to their closest primary kin than did males (median for females = 101 m, median for males = 137 m; electronic supplementary material, Figure S1). As expected, the individuals in our study had highly variable access to primary kin. In any given year, it was common for red squirrels not to have any close relatives in their social neighbourhood (mean 0.56 primary kin within 130m, range 0-6). These associations were also transient, with kin dyads remaining in the same social environment for just 1.4 years on average (range 1-4; for 130 m neighbourhood). Access to kin was not much improved when considering the larger spatial scale of each study area (approx. 40 ha), with each squirrel having a mean of 0.83 primary kin in the study area (range 0-7) in a given year, and with overlap among kin lasting 1.5 years on average (range 1-4). Visualizations suggested that the number of kin relationships varied in tandem with changes in population density attributable to resource pulses. Specifically, both density and the number of kin relationships tended to increase immediately after mast years, gradually declining thereafter (Figure 1; electronic supplementary material, Figure S2).

Influences of kin on survival

For females, annual survival was strongly influenced by access to daughters. At the scale of the social neighbourhood, females whose nearest primary kin was a daughter were more likely to survive when that daughter was closer, reflected in the significantly more negative distance-survival relationship for daughters compared to the reference category, "non-kin" ($\beta = -4.92 \pm 1.51$ s.e., $p = 0.001$; Table 1).

Note that this effect was estimated while controlling for quadratic influences of age, which, as expected, were also a significant predictor of survival (β^2 = -0.11 ± 0.04 s.e., p = 0.007). The additional GLMM including distance measures greater than 130 m did not identify a significant effect of the proximity of daughters on female survival. However, the coefficient for the quadratic distance-survival relationship was positive, consistent with the shape of the fitted GAM (Fig. 1), suggesting that daughter-induced fitness benefits may not be linear across such large distances.

Males were less likely to survive during mast years (β = -0.67 ± 0.33 s.e., p = 0.045) and showed a negative quadratic trend in the probability of survival with age (β = -0.08 ± 0.04 s.e., p = 0.035). However, there were no significant differences in the distance-survival relationship for any types of primary kin, compared to the reference effect calculated for non-kin conspecifics (Table 2) indicating no effect of kin proximity on male survival. Results were similar when including the entire study area, however the quadratic component of the daughter-distance interaction was statistically significant and negative (β = -28.08 ± 11.91 s.e., p = 0.018; electronic supplementary material, Table S2).

Influences of kin on reproductive success

For females, annual reproductive success was strongly influenced by masting events, with breeding females producing approximately 3 times as many recruiting offspring during mast years vs. non-mast years, on average (β = 1.16 ± 0.18 s.e., p < 0.001). However, reproductive success was not influenced by distance to any type of primary kin, relative to non-kin (Table 3; electronic supplementary material, Figure S3). These results were similar for models including distances to kin across the entire study area (here, quadratic; electronic supplementary material, Table S3). The additional analysis including non-breeding individuals (attributing them 0 pups recruited) revealed the same pattern whereby distance to kin did not affect female reproductive success (electronic supplementary material, Fig. S4), so we proceeded to interpret values from GLMMs using ARS of breeders alone.

In contrast, we found clear links between annual reproductive success and distance to kin territories for males. Outputs from the GAMs suggested that these trends varied with the sex of the nearby relative: males sharing their social neighbourhood with a father or son sired more pups when living *closer* to that individual (Figure 3). Oppositely, distance to a mother or daughter's territory appeared to be positively associated with male reproductive success (i.e., implying a relative cost of living closer to female kin). This pattern was supported by the parametric outputs from a GLMM (Table 4). There was strong evidence that among males whose nearest primary kin was their father, those living *closer* to their father sired more pups, reflected in a more negative distance-survival relationship for fathers compared to non-kin (β = -6.44 ± 2.19 s.e., p = 0.003). Oppositely, among males whose nearest primary kin was their mother, those living *farther* from their mother were more successful (β = 2.77 ± 1.37 s.e., p = 0.042), though this effect was smaller in magnitude than the influence of

fathers. As before, these effects were estimated while conditioning on masting events and age (linear and quadratic terms), all of which also had statistically significant influences on male ARS (Table 4).

Discussion

In this study, we used the geographic distance between territories of solitary red squirrels to test whether access to kin influenced individual fitness. We found that red squirrels had improved survival and reproductive success when living near primary kin, though these effects were surprisingly nuanced, hinging on genealogical relationship, sex, and fitness measure. The dilution of these fitness consequences from nearby kin across relatively short distances (0-130 m) is consistent with the hypothesis that these benefits are caused by kin-specific behaviours, though other explanations are possible. Together, our findings reveal complex kinship effects on survival and reproductive success in a solitary mammal, highlighting the value of multigenerational datasets for uncovering otherwise cryptic social dynamics.

The increased survival of mothers living closer to daughters converges with similar findings from other mammals, where philopatry facilitates further cooperative or tolerative interactions [11,44]. This includes a growing literature documenting female-biased kin benefits in less social mammalian species. For example, Eurasian lynx (*Lynx lynx*) mothers and daughters appear to share space when resources are patchy [28]. It is worth noting the magnitude of the effect of proximity to daughters in red squirrels. For example, among females whose nearest primary kin was a daughter, having that daughter 30m away rather than 130m away corresponded to a change in the mother's predicted probability of overwinter survival from approximately 36% to 82% (calculated for non-mast year with focal age 2; Table 1). Interestingly, daughters did not appear to receive similar benefits from access to their mother. We also note the lack of any influences of nearby kin on annual reproductive success in females. Social thermoregulation is a possible mechanism driving these kin-based increases in survival, which is known to occur among females whose territories are close together (mean of 43.4±18.0 m SD apart) [23]. However, we would generally expect the benefits of social thermoregulation to be reciprocal, i.e., also increase survival for daughters living near mothers [45]. Previous work has shown that territorial intrusions (possible to pilfer cones) sometimes involve mothers invading offspring territories, and again is more likely to occur when distances between territories are small [27]. Thus, a seemingly more likely explanation for these unidirectional benefits is that mothers increase their survival by maintaining access to the resources of nearby daughters. It is important to note though that generally, pilfered cones appear to make up a very small proportion of an individual's food stores in this population [46].

Much more surprising was the finding that male red squirrels had increased reproductive success when living closer to their fathers. First, while red squirrels appear to discriminate kin and non-kin based on rattle vocalizations [47], it is not clear to what extent recognition relies on early life (natal) experience [48], which does not include fathers. Second, male red squirrels have been found to have enhanced lifetime reproductive success as immigrants to a new population [49], congruent with the expectation that they are avoiding competition with related males. In a similar vein, evidence in this study of reduced male reproductive success when closer to mothers (Table 4), could reflect the costs of reduced access to unrelated mates (but see [57], which suggests limited inbreeding avoidance in the population).

In some mammals, males form reproductive alliances to cooperate in securing and defending mating opportunities with females, leading to improved reproductive success [50–52]. Alliance members are often related, leading to indirect benefits for individuals that do not enjoy increased mating opportunities themselves. Much rarer associations between fathers and sons have been linked to reproductive benefits in Red Howler Monkeys (*Alouatta seniculus*) [53] and yellow baboons (*Papio cynocephalus*) [54], for example. And while male-male alliances are typically found in group-living species, it has been suggested that rudimentary aspects of coalitionary behaviour may be exhibited in otherwise solitary males [55]. So, could the observed ARS benefits observed among father-son dyads in red squirrels be evidence of cryptic coalitions? Theory suggests that male reproductive coalitions are more likely to form when 1) females are receptive for short periods of time and 2) cannot be monopolized by a single mate [55,56]. Both are true of the “scramble” polygynous mating system of red squirrels, where estrus lasts just a single day, during which an estrous female mates with an average of 6 males [33,57]. However, male red squirrels are not known to engage in any observable affiliative interactions, making even basic aspects of coalitionary behaviour unlikely. Perhaps more likely is that is that fathers and sons are simply less likely to disrupt one another’s copulations during mating chases. Hypothetically, related males living together could also benefit from socially transmitted information about the locations of receptive females. One avenue for future work would be to investigate where proximity between fathers and sons predicts co-parentage of offspring in the same litter (above and beyond any influences of distance to the mother), expected if male kin are somehow facilitating mating opportunities. Alternatively, increased tolerance among fathers and sons could reduce the need for defense and thereby allow males to exert more energy searching for mates.

More generally, these findings place an even greater emphasis on territory acquisition as a determinant of fitness for reds squirrels [58], by increasing the stakes of co-locating with certain types of kin. Red squirrels are one of very few species known to exhibit bequeathal, where an adult female undergoes breeding dispersal thus allowing an offspring (with a slight bias for daughters over sons) to inherit her territory and resource cache [20,59]. Such an extreme display of nepotism is puzzling, especially given the critical importance of territory ownership for survival. Interestingly then,

previous work in this population has not identified a survival cost for bequeathing mothers [60]. Theory suggests that if a mother can secure a new territory near their previous site, increased access to offspring might lead to greater downstream fitness benefits via kin cooperation [61]. Consistent with this hypothesis, our findings suggest that bequeathal may provide additional, direct benefits to mothers in addition to enhancements in offspring survival [60], at least when the inheritor is a daughter. Compared to females, male red squirrels tend to live farther from primary kin, with no obvious pattern of father-son dyads living closer together than father-daughter dyads, for example (See electronic supplement, Figure S1). Thus, at first glance we find no obvious indication of "kin-biased dispersal" [62], whereby males might be expected to preferentially acquire territories near male kin, though a thorough test of this possibility may be a worthwhile direction for future work.

Leveraging geographic distance among kin as a proxy for their ability to interact allowed us to directly measure fitness consequences without a clear sense of the specific behaviours that are important [30]. Beyond age and resource pulses (which were controlled for in our models), we are unaware of any likely confounds of proximity among kin and individual fitness in the population. Moreover, the importance of small differences in distance to kin (i.e., within the 130m social neighbourhood) and the variation in effects across genealogical relationship are difficult to explain without distance-constrained social behaviours. It is possible however that a more complex story remains to be told linking kinship and demographic responses to resource availability, which could hypothetically contribute to these patterns, in addition to behavioural effects. Our hope is that further work will investigate the hypothesized mechanisms of these benefits, particularly for the male-male dyads, where there has been no previous evidence of affiliative interactions.

The idiosyncratic nature of our results suggests that consequences of proximity to kin may be overlooked in systems where associations are not parsed into specific genealogical relationships. It also suggests that squirrels require kin recognition to maintain these relationships, contrary to many species where spatial heuristics (e.g., "cooperate with those around you") are sufficient for cooperation [63,64]. In tandem with previous studies, our work contributes to an increasingly complex depiction of sociality in a mostly solitary species. For red squirrels then, biological fitness is strongly influenced by relationships with both familiar neighbours [22], as well as with primary kin. Though further work is needed to understand the specific mechanisms causing these benefits, it appears that kinship can have multifaceted and impactful contributions to fitness in solitary mammals.

Acknowledgements

We thank Agnes MacDonald and her family for long-term access to her trapline, and the Champagne and Aishihik First Nations for allowing us to conduct our work within their traditional territory. We are grateful to each of the field technicians who have contributed to the long-term Kluane Red Squirrel Project database over the years. We thank Dr. Erin Siracusa and Dr. April Martinig for providing helpful advice regarding analysis and interpretation. We also thank members of the McAdam lab including Shelby Bohn, Dr. David Delaney, Simon Denomme-Brown, Alex Hare, Katie Kariatsumari, and Dr. Quinn Webber for valuable and supportive commentary on an earlier version of this work.

Funding

This work was supported by Fulbright Canada (Special Foundation Fellowship to S.F.W.), the USA National Science Foundation (DEB-0515849 to A.G.M, IOS-1110436 to A.G.M. and B.D., IOS-1749627 to B.D.), the Natural Sciences and Engineering Research Council of Canada (Discovery Grants RGPIN-371579-2009 and RGPIN-2015-04707 to A.G.M, RGPIN 2020-06781 to J.E.L.; RGPIN-2018-04354 to D.W.C.; RGPIN-2014-05874 to S.B.) and the Ontario Ministry of Research and Innovation (ER08-05-119 to A. G. M).

References

1. Silk JB. 2007 The adaptive value of sociality in mammalian groups. *Philosophical Transactions of the Royal Society B: Biological Sciences* , 539–559. (doi:10.1098/rstb.2006.1994)

2. Mitani JC, Watts DP, Pepper JW, Merriwether DA. 2002 Demographic and social constraints on male chimpanzee behaviour. *Animal Behaviour* , 727–737. (doi:10.1006/anbe.2002.4014)

3. Clutton-Brock TH, Lukas D. 2012 The evolution of social philopatry and dispersal in female mammals. *Molecular Ecology* **21**, 472–492. (doi:10.1111/j.1365-294X.2011.05232.x)

4. Thompson ME. 2019 How can non-human primates inform evolutionary perspectives on female-biased kinship in humans? *Philosophical Transactions of the Royal Society B: Biological Sciences* **374**. (doi:10.1098/rstb.2018.0074)

5. Holekamp KE, Smale L. 1991 Dominance acquisition during mammalian social development: The 'inheritance' of maternal rank. *Integrative and Comparative Biology* **31**, 306–317. (doi:10.1093/icb/31.2.306)

6. Turner JW, Robitaille AL, Bills PS, Holekamp KE. 2021 Early-life relationships matter: Social position during early life predicts fitness among female spotted hyenas. *Journal of Animal Ecology* **90**, 183–196. (doi:10.1111/1365-2656.13282)

7. Ilany A, Holekamp KE, Akçay E. 2021 Rank-dependent social inheritance determines social network structure in spotted hyenas. *Science* **373**, 348–352. (doi:10.1126/science.abc1966)

8. Shah SS, Rubenstein DR. 2021 Prenatal environmental variation, alternative reproductive tactics and the formation of a mixed-kin cooperative society. *bioRxiv Preprint* (doi:doi.org/10.1101/2021.02.10.430612)

9. Croft DP, Weiss MN, Nielsen MLK, Grimes C, Cant MA, Ellis S, Franks DW, Johnstone RA. 2021 Kinship dynamics: Patterns and consequences of changes in local relatedness. *Proceedings of the Royal Society B: Biological Sciences* **288**. (doi:10.1098/rspb.2021.1129)

10. Cantor M *et al.* 2021 The importance of individual-to-society feedbacks in animal ecology and evolution. *Journal of Animal Ecology* **90**, 27–44. (doi:10.1111/1365-2656.13336)

11. Holekamp KE, Sawdy MA. 2019 The evolution of matrilineal social systems in fissiped carnivores. *Philosophical Transactions of the Royal Society B: Biological Sciences* **374**. (doi:10.1098/rstb.2018.0065)

12. Wolf JBW, Trillmich F. 2008 Kin in space: Social viscosity in a spatially and genetically substructured network. *Proceedings of the Royal Society B: Biological Sciences* **275**, 2063–2069. (doi:10.1098/rspb.2008.0356)

13. Koprowski JL. 1993 The role of kinship in field interactions among juvenile gray squirrels (Sciurus carolinensis). *Canadian Journal of Zoology* **71**, 224–226. (doi:10.1139/z93-031)

14. Carter GG, Farine DR, Wilkinson GS. 2017 Social bet-hedging in vampire bats. *Biology Letters* **13**, 1–4.

15. Silk JB, Altmann J, Alberts SC. 2006 Social relationships among adult female baboons (*papio cynocephalus*) I. Variation in the strength of social bonds. *Behavioral Ecology and Sociobiology* **61**, 183–195. (doi:10.1007/s00265-006-0249-2)

16. Engh AL, Beehner JC, Bergman TJ, Whitten PL, Hoffmeier RR, Seyfarth RM, Cheney DL. 2006 Behavioural and hormonal responses to predation in female chacma baboons (*Papio hamadryas ursinus*). *Proceedings of the Royal Society B: Biological Sciences* **273**, 707–712. (doi:10.1098/rspb.2005.3378)

17. Chakrabarti S, Kolipakam V, Bump JK, Jhala YV. 2020 The role of kinship and demography in shaping cooperation amongst male lions. *Scientific Reports* , 1–13. (doi:10.1038/s41598-020-74247-x)

18. Moor DD, Roos C, Ostner J, Schülke O. 2020 Bonds of bros and brothers: Kinship and social bonding in postdispersal male macaques. *Molecular Ecology* , 3346–3360. (doi:10.1111/mec.15560)

19. West SA, Cooper GA, Ghoul MB, Griffin AS. 2021 Ten recent insights for our understanding of cooperation. *Nature Ecology and Evolution* **5**, 419–430. (doi:10.1038/s41559-020-01384-x)

20. Bertaux D, Boutin S. 2000 Breeding Dispersal in Female North American Red Squirrels. *Ecology* **81**, 1311–1326.

21. Larsen KW, Boutin S. 1994 Movements, Survival, and Settlement of Red Squirrel (*Tamiasciurus Hudsonicus*). *Ecology* **75**, 214–223.

22. Siracusa E, Boutin SA, Dantzer B, Lane JE, Coltman DW, McAdam AG. 2019 Familiar neighbors, but not relatives, enhance fitness in a territorial mammal. *Current Biology* **31**. (doi:10.1016/j.cub.2020.10.072)

23. Williams CT, Gorrell JC, Lane JE, McAdam AG, Humphries MM, Boutin S. 2013 Communal nesting in an 'asocial' mammal: Social thermoregulation among spatially dispersed kin. *Behavioral Ecology and Sociobiology* **67**, 757–763. (doi:10.1007/s00265-013-1499-4)

24. Gorrell JC, McAdam AG, Coltman DW, Humphries MM, Boutin S. 2010 Adopting kin enhances inclusive fitness in asocial red squirrels. *Nature Communications* **1**, 22. (doi:10.1038/ncomms1022)

25. Wright BM, Stredulinsky EH, Ellis GM, Ford JKB. 2016 Kin-directed food sharing promotes lifetime natal philopatry of both sexes in a population of fish-eating killer whales, *Orcinus orca*. *Animal Behaviour* **115**, 81–95. (doi:10.1016/j.anbehav.2016.02.025)

26. Emigh H, Truax J, Highfill L, Vonk J. 2020 Not by the same token: A female orangutan (*Pongo pygmaeus*) is selectively prosocial. *Primates* **61**, 237–247. (doi:10.1007/s10329-019-00780-7)

27. Siracusa E, Boutin S, Humphries MM, Gorrell JC, Coltman DW, Dantzer B, Lane JE, McAdam AG. 2017 Familiarity with neighbours affects intrusion risk in territorial red squirrels. *Animal Behaviour* **133**, 11–20. (doi:10.1016/j.anbehav.2017.08.024)

28. Aronsson M, Åkesson M, Low M, Persson J, Andrén H. 2020 Resource dispersion and relatedness interact to explain space use in a solitary predator. *Oikos* **129**, 1174–1184. (doi:10.1111/oik.07258)

29. Siracusa E, Morandini M, Boutin S, Humphries MM, Dantzer B, Lane JE, McAdam AG. 2017 Red squirrel territorial vocalizations deter intrusions by conspecific rivals. *Behaviour* **154**, 1259–1273. (doi:10.1163/1568539X-00003467)

30. Engelhardt SC, Bergeron P, Gagnon A, Dillon L, Pelletier F. 2019 Using geographic distance as a potential proxy for help in the assessment of the grandmother hypothesis. *Current Biology* **29**, 651-656.e3. (doi:10.1016/j.cub.2019.01.027)

31. Ellis S, Franks DW, Weiss MN, Cant MA, Domenici P, Balcomb KC, Ellifrit DK, Croft DP. 2021 Mixture models as a method for comparative sociality: social networks and demographic change in resident killer whales. *Behavioral Ecology and Sociobiology* **75**. (doi:10.1007/s00265-021-03006-3)

32. Kalinowski ST, Taper ML, Marshall TC. 2007 Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology* **16**, 1099–1106. (doi:10.1111/j.1365-294X.2007.03089.x)

33. Lane JE, Boutin S, Gunn MR, Coltman DW. 2009 Sexually selected behaviour: red squirrel males search for reproductive success. *Journal of Animal Ecology* **78**, 296–304. (doi:10.1111/j.1365-2656.2008.01502.x)

34. McAdam AG, Boutin S, Sykes AK, Humphries MM. 2007 Life histories of female red squirrels and their contributions to population growth and lifetime fitness. *Ecoscience* **14**, 362.

35. Dantzer B, McAdam AG, Humphries MM, Lane JE, Boutin S. 2020 Decoupling the effects of food and density on life-history plasticity of wild animals using field experiments: Insights from the steward who sits in the shadow of its tail, the North American red squirrel. *Journal of Animal Ecology* **89**, 2397–2414. (doi:10.1111/1365-2656.13341)

36. Morrissey MB, Wilson AJ. 2010 PEDANTICS: an r package for pedigree-based genetic simulation and pedigree manipulation, characterization and viewing. *Molecular Ecology Resources* , 711–719.

37. Lane JE, Boutin S, Gunn MR, Slate J, Coltman DW. 2008 Female multiple mating and paternity in free-ranging North American red squirrels. *Animal Behaviour* **75**, 1927–1937. (doi:10.1016/j.anbehav.2007.10.038)

38. Larsen KW, Boutin S. 1995 Exploring territory quality in the North American red squirrel through removal experiments. *Canadian Journal of Zoology* **73**, 1115–1122. (doi:10.1139/z95-133)

39. Descamps S, Boutin S, McAdam AG, Berteaux D, Gaillard JM. 2009 Survival costs of reproduction vary with age in North American red squirrels. *Proceedings of the Royal Society B: Biological Sciences* **276**, 1129–1135. (doi:10.1098/rspb.2008.1401)

40. Kerr NL. 1998 HARKing: Hypothesizing after the results are known. *Personality and Social Psychology Review* **2**, 196–217. (doi:10.1207/s15327957pspr0203_4)

41. R Core Development Team. 2021 *R: A language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing.

42. Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Mächler M, Bolker BM. 2017 glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R Journal* **9**, 378–400. (doi:10.32614/rj-2017-066)

43. Hartig F. 2018 *DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models*. See https://cran.r-project.org/web/packages/DHARMa/vignettes/DHARMa.html.

44. Ashbury AM, Willems EP, Suci S, Atmoko U, Saputra F, Schaik CPV. 2020 Home range establishment and the mechanisms of philopatry among female Bornean orangutans (*Pongo pygmaeus wurmbii*) at Tuanan. *Behavioral Ecology and Sociobiology* , 1–21.

45. Lutermann H, Schmelting B, Radespiel U. 2006 The role of survival for the evolution of female philopatry in a solitary forager, the grey mouse lemur (*Microcebus murinus*). *Proceedings of the Royal Society B: Biological Sciences* **273**, 2527–2533. (doi:10.1098/rspb.2006.3603)

46. Donald JL, Boutin S. 2011 Intraspecific cache pilferage by larder-hoarding red squirrels (Tamiasciurus hudsonicus). *Journal of Mammalogy* **92**, 1013–1020. (doi:10.1644/10-MAMM-A-340.1)

47. Wilson DR, Goble AR, Boutin S, Humphries MM, Coltman DW, Gorrell JC, Shonfield J, McAdam AG. 2015 Red squirrels use territorial vocalizations for kin discrimination. *Animal Behaviour* **107**, 79–85. (doi:10.1016/j.anbehav.2015.06.011)

48. Shonfield J, Gorrell JC, Coltman DW, Boutin S, Humphries MM, Wilson DR, McAdam AG. 2017 Using playback of territorial calls to investigate mechanisms of kin discrimination in red squirrels. *Behavioral Ecology* **28**, 382–390. (doi:10.1093/beheco/arw165)

49. Martinig AR, McAdam AG, Dantzer B, Lane JE, Coltman DW, Boutin S. 2020 The new kid on the block: immigrant males win big whereas females pay fitness cost after dispersal. *Ecology Letters* **23**, 430–438. (doi:10.1111/ele.13436)

50. Parsons KM, Durban JW, Claridge DE, Balcomb KC, Noble LR, Thompson PM. 2003 Kinship as a basis for alliance formation between male bottlenose dolphins, Tursiops truncatus, in the Bahamas. *Animal Behaviour* **66**, 185–194. (doi:10.1006/anbe.2003.2186)

51. Wiszniewski J, Corrigan S, Beheregaray LB, Mo LM. 2012 Male reproductive success increases with alliance size in Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). *Journal of Animal Ecology* , 423–431. (doi:10.1111/j.1365-2656.2011.01910.x)

52. Williams DA, Rabenold KN. 2005 Male-biased dispersal, female philopatry, and routes to fitness in a social corvid. *Journal of Animal Ecology* **74**, 150–159. (doi:10.1111/j.1365-2656.2004.00907.x)

53. Pope TR. 1990 The reproductive consequences of male cooperation in the red howler monkey: Paternity exclusion in multi-male and single-male troops using genetic markers. *Behavioral Ecology and Sociobiology* **27**, 439–446.

54. Charpentier MJE, Van Horn RC, Altmann J, Alberts SC. 2008 Paternal effects on offspring fitness in a multimale primate society. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 1988–1992. (doi:10.1073/pnas.0711219105)

55. Olson LE, Blumstein DT. 2009 A trait-based approach to understand the evolution of complex coalitions in male mammals. *Behavioral Ecology* **20**, 624–632. (doi:10.1093/beheco/arp040)

56. Teichroeb JA, Wikberg EC, Ting N, Sicotte P. 2014 Factors influencing male affiliation and coalitions in a species with male dispersal and intense male-male competition, *Colobus vellerosus*. *Behaviour* **151**, 1045–1066. (doi:10.1163/1568539X-00003089)

57. Lane JE, Boutin S, Gunn MR, Slate J, Coltman DW. 2007 Genetic relatedness of mates does not predict patterns of parentage in North American red squirrels. *Animal Behaviour* **74**, 611–619. (doi:10.1016/j.anbehav.2006.12.017)

58. Hendrix JG, Fisher DN, Martinig AR, Boutin S, Dantzer B, Lane JE, McAdam AG. 2020 Territory acquisition mediates the influence of predators and climate on juvenile red squirrel survival. *Journal of Animal Ecology* **89**, 1408–1418. (doi:10.1111/1365-2656.13209)

59. Fisher DN, Boutin S, Dantzer B, Humphries MM, Lane JE, McAdam AG. 2017 Multilevel and sex-specific selection on competitive traits in North American red squirrels. *Evolution* **71**, 1841–1854. (doi:10.1111/evo.13270)

60. Lane JE, Mcadam AG, Charmantier A, Humphries MM, Coltman DW, Fletcher Q, Gorrell JC, Boutin S. 2015 Post-weaning parental care increases fitness but is not heritable in North American red squirrels. *Journal of Evolutionary Biology* **28**, 1203–1212. (doi:10.1111/jeb.12633)

61. Clarke PMR, McElreath MB, Barrett BJ, Mabry KE, McElreath R. 2018 The evolution of bequeathal in stable habitats. *Ecology and Evolution* **8**, 10594–10607. (doi:10.1002/ece3.4549)

62. Pollack L, Rubenstein DR. 2015 The fitness consequences of kin-biased dispersal in a cooperatively breeding bird. *Biology Letters* **11**, 2–5. (doi:10.1098/rsbl.2015.0336)

63. Langer P, Nowak MA, Hauert C. 2008 Spatial invasion of cooperation. *Journal of Theoretical Biology* **250**, 634–641. (doi:10.1016/j.jtbi.2007.11.002)

64. Rand DG, Nowak MA. 2013 Human cooperation. *Trends in Cognitive Sciences* **17**, 413–425. (doi:10.1016/j.tics.2013.06.003)

Table 1. Results from generalized linear mixed effects model estimating the influences of distance to primary kin on annual survival in female North American red squirrels.

Female annual survival						
Model		Variable	Estimate	95% CI	*z*	*p*
Within social neighbourhood						
n_{Obs}	617	Intercept	-2.51	(-5.79, 0.77)	-1.5	0.134
n_{Focal}	315	$\log_{10}$Distance	1.65	(-0.02, 3.33)	1.93	0.053
n_{Dyad}	414	Daughter	8.27	(3.04, 13.5)	3.1	0.002
		Mother	2.79	(-1.71, 7.28)	1.22	0.224
		Sibling	3.69	(-2.97, 10.35)	1.09	0.278
		Son	10.31	(-0.37, 20.99)	1.89	0.059
		Father	0.93	(-6.99, 8.85)	0.23	0.818
		Age	0.5	(-0.04, 1.04)	1.81	0.07
		Age^2	-0.11	(-0.19, -0.03)	-2.68	0.007
		Mast year (Y)	-0.09	(-0.92, 0.75)	-0.2	0.84
		$\log_{10}$Distance × Daughter	-4.92	(-7.87, -1.97)	-3.26	0.001
		$\log_{10}$Distance × Mother	-1.44	(-3.91, 1.03)	-1.14	0.254
		$\log_{10}$Distance × Sibling	-1.81	(-5.51, 1.89)	-0.96	0.337
		$\log_{10}$Distance × Son	-5.36	(-10.97, 0.24)	-1.88	0.061
		$\log_{10}$Distance × Father	-0.33	(-4.68, 4.02)	-0.15	0.882
		Focal ID (random effect variance)	2.78×10^{-8}			
		Dyad ID (random effect variance)	0.227			
		Year (random effect variance)	0.264			

Table 2. Results from generalized linear mixed effects model estimating the influences of distance to primary kin on annual survival in male North American red squirrels.

Male annual survival						
Model		Variable	Estimate	95% CI	*z*	*p*
Within social neighbourhood						
n_{Obs}	707	Intercept	0.76	(-1.72, 3.24)	0.6	0.547
n_{Focal}	354	$\log_{10}$Distance	0.2	(-1.02, 1.42)	0.32	0.745
n_{Dyad}	555	Daughter	-5.52	(-12.57, 1.52)	-1.54	0.124
		Mother	0.32	(-5.78, 6.41)	0.1	0.919
		Sibling	21.28	(-15.21, 57.77)	1.14	0.253
		Son	-1.13	(-10.99, 8.73)	-0.22	0.822
		Father	3.3	(-7.53, 14.14)	0.6	0.55
		Age	0.24	(-0.24, 0.73)	0.99	0.323
		Age^2	-0.08	(-0.15, -0.01)	-2.1	0.035
		Mast year (Y)	-0.67	(-1.32, -0.02)	-2.01	0.045
		$\log_{10}$Distance × Daughter	3.12	(-0.76, 7.01)	1.58	0.115
		$\log_{10}$Distance × Mother	-0.47	(-3.71, 2.78)	-0.28	0.779
		$\log_{10}$Distance × Sibling	-11.23	(-30.27, 7.81)	-1.16	0.248
		$\log_{10}$Distance × Son	0.25	(-4.91, 5.42)	0.1	0.924
		$\log_{10}$Distance × Father	-2.0	(-7.62, 3.61)	-0.7	0.485
		Focal ID (random effect variance)	2.93×10^{-5}			
		Dyad ID (random effect variance)	2.12×10^{-4}			
		Year (random effect variance)	0.141			

Table 3. Results from generalized linear mixed effects model estimating the influences of distance to primary kin on annual reproductive success (number of pups successfully recruited) in female North American red squirrels.

Female annual reproductive success						
Model		Variable	Estimate	95% CI	*z*	*p*
Within social neighbourhood						
n_{Obs}	465	Intercept	-2.27	(-4.39, -0.14)	-2.09	0.037
n_{Focal}	259	$\log_{10}$Distance	0.75	(-0.3, 1.8)	1.4	0.16
n_{Dyad}	335	Daughter	1.83	(-0.8, 4.47)	1.36	0.173
		Mother	0.87	(-2.02, 3.76)	0.59	0.554
		Sibling	0.31	(-4.32, 4.95)	0.13	0.895
		Son	1.67	(-2.3, 5.65)	0.82	0.41
		Father	2.95	(-1.71, 7.61)	1.24	0.215
		Age	0.17	(-0.14, 0.48)	1.08	0.28
		Age^2	-0.03	(-0.07, 0.02)	-1.26	0.209
		Mast year (Y)	1.16	(0.8, 1.52)	6.36	< 0.001
		$\log_{10}$Distance × Daughter	-0.94	(-2.41, 0.53)	-1.25	0.212
		$\log_{10}$Distance × Mother	-0.5	(-2.06, 1.07)	-0.63	0.532
		$\log_{10}$Distance × Sibling	-0.22	(-2.71, 2.27)	-0.18	0.86
		$\log_{10}$Distance × Son	-0.96	(-3.08, 1.15)	-0.89	0.373
		$\log_{10}$Distance × Father	-1.51	(-4, 0.98)	-1.19	0.235
		Focal ID (random effect variance)	0.070			
		Dyad ID (random effect variance)	0.035			
		Year (random effect variance)	0.047			

Table 4. Results from generalized linear mixed effects model estimating the influences of distance to primary kin on annual reproductive success (number of pups sired) in male North American red squirrels.

Male annual reproductive success						
Model		Variable	Estimate	95% CI	*z*	*p*
Within social neighbourhood						
n_{Obs}	698	Intercept	-0.58	(-2.02, 0.86)	-0.79	0.429
n_{Focal}	346	$\log_{10}$Distance	-0.17	(-0.86, 0.52)	-0.49	0.622
n_{Dyad}	548	Daughter	-2.21	(-5.44, 1.02)	-1.34	0.18
		Mother	-5.63	(-10.76, -0.5)	-2.15	0.031
		Sibling	-4.67	(-19.14, 9.79)	-0.63	0.526
		Son	2.54	(-2.04, 7.12)	1.09	0.278
		Father	11.35	(3.53, 19.16)	2.85	0.004
		Age	0.9	(0.63, 1.18)	6.41	< 0.001
		Age^2	-0.13	(-0.17, -0.09)	-5.88	< 0.001
		Mast year (Y)	0.82	(0.61, 1.04)	7.48	< 0.001
		$\log_{10}$Distance × Daughter	1.34	(-0.38, 3.07)	1.53	0.127
		$\log_{10}$Distance × Mother	2.77	(0.1, 5.45)	2.03	0.042
		$\log_{10}$Distance × Sibling	2.48	(-5.48, 10.44)	0.61	0.541
		$\log_{10}$Distance × Son	-1.29	(-3.72, 1.14)	-1.04	0.298
		$\log_{10}$Distance × Father	-6.18	(-10.43, -1.92)	-2.85	0.004
		Focal ID (random effect variance)	0.225			
		Dyad ID (random effect variance)	0.185			
		Year (random effect variance)	3.43×10^{-9}			

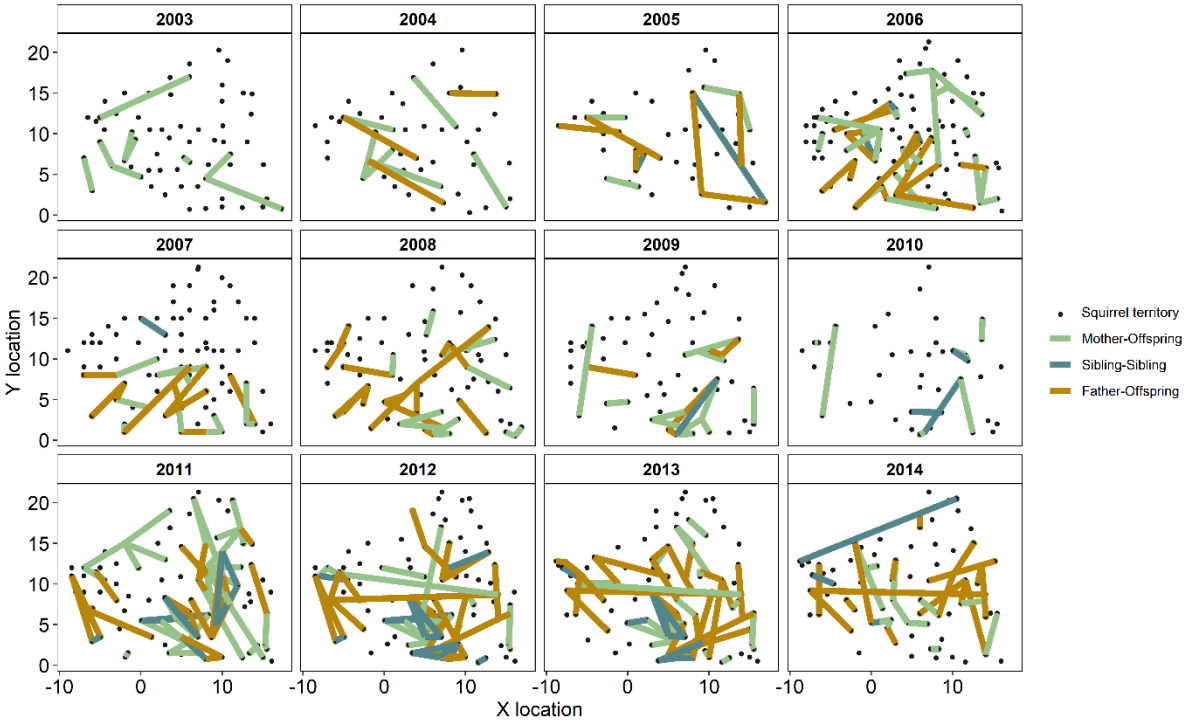

Figure 1. Spatial overview of kin relationships on "Kloo" study area. Note that location units represent a staked distance of 30 m. Lines linking certain individuals represent relationships among primary kin, with colors distinguishing dyads as a sibling pair or by the sex of the parent. Mast years (resource pulses) occurred in 2005, 2010, and 2014.

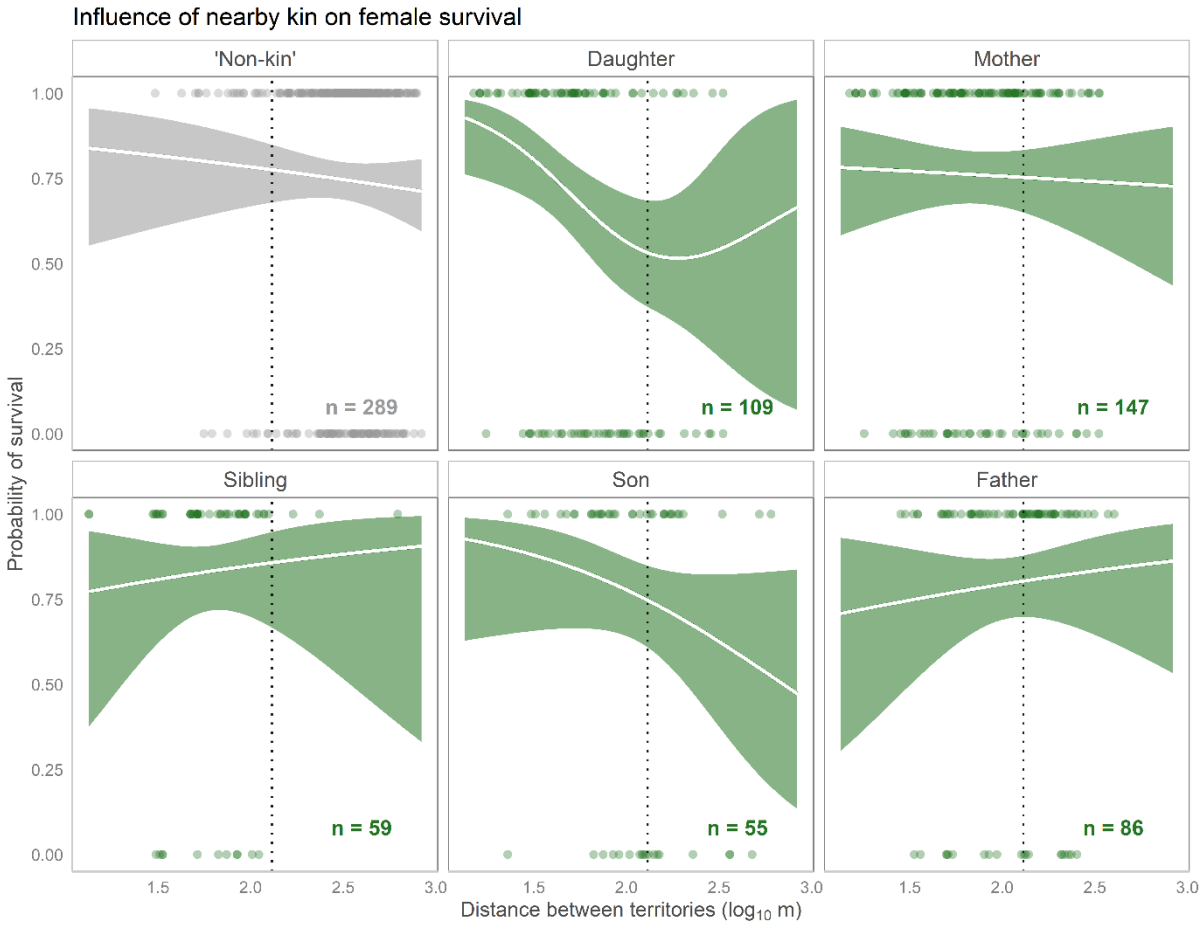

Figure 2. Lines represent predicted probabilities of female survival, estimated with GAMs while controlling for the influences of age (linear and quadratic) and resource pulses. Here, probabilities are shown for a focal individual of age 2 in a non-mast year. Dots represent raw data, so are not an exact reflection of the partial smooth. Shaded bands show 95% confidence intervals. The dotted vertical line corresponds to 130m, a commonly used radius of red squirrels' social neighbourhoods. 'Non-kin' records are made up of individuals with no nuclear relatives in the study area, for which distances were calculated to a randomly chosen individual.

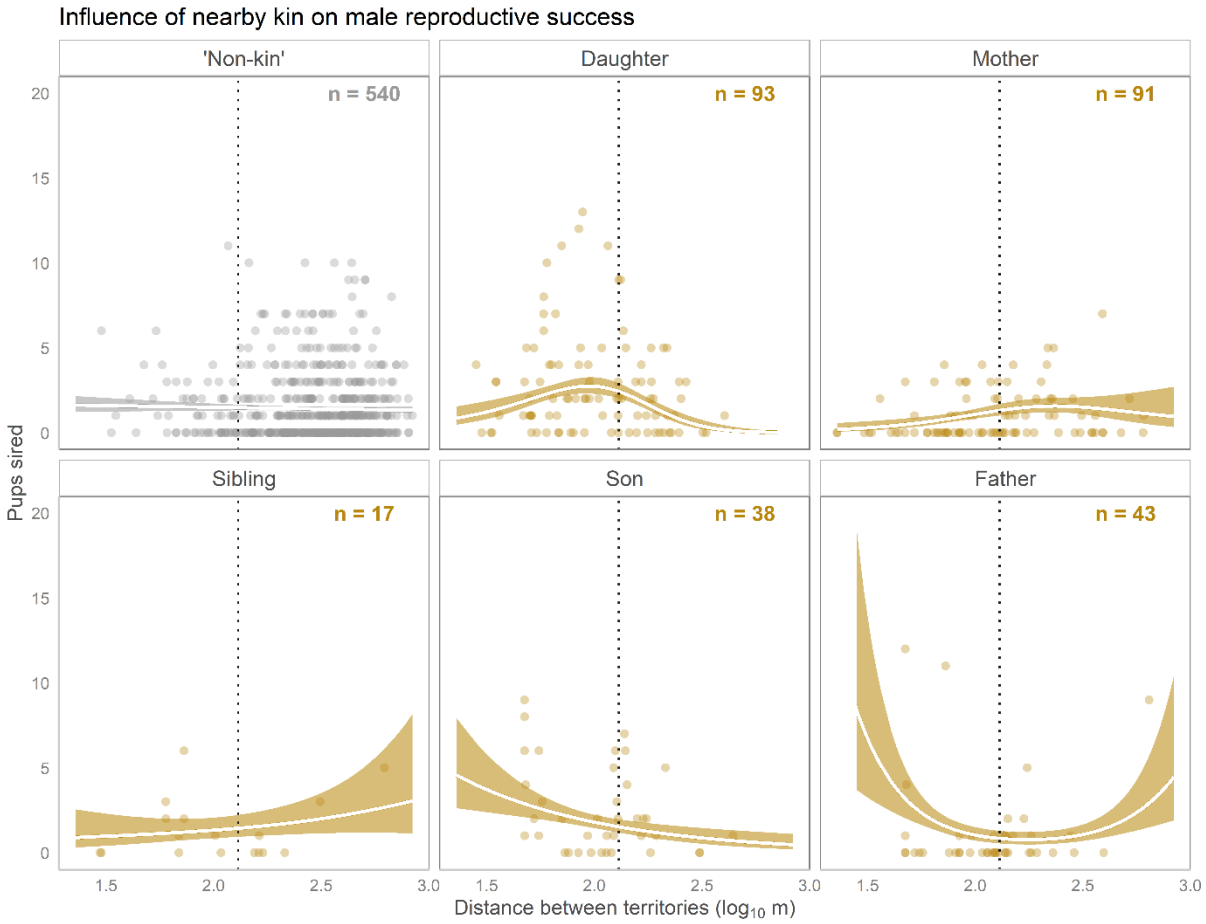

Figure 3. Lines represent predicted probabilities of male annual reproductive success, estimated with GAMs, controlling for the influences of age (linear and quadratic) and resource pulses, with shaded bands representing 95% confidence intervals. Here, probabilities are shown for a focal individual of age 2 in a non-mast year. The dotted vertical line corresponds to 130m, a commonly used radius of red squirrels' social neighbourhoods. Non-kin records are made up of individuals with no nuclear relatives in the study area, and distances were calculated relative to a randomly chosen individual.