



Personality, habitat use, and their consequences for survival in North American red squirrels *Tamiasciurus hudsonicus*

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Personality affects many aspects of an individual's behaviour, life history and fitness, and has been shown to be moderately heritable in wild populations. Correlations between personality and risk-taking that lead to life history tradeoffs could act to maintain variation in personality within a population, but this has not yet been tested. In this study, we used females from a marked population of North American red squirrels in Kluane, Yukon, to determine whether personality predicts risk-taking in the wild, and whether these risk-taking behaviours result in life history tradeoffs. We measured personality in open field and mirror image stimulation tests and extracted two traits, activity and aggressiveness, using principal component analysis and mixed model techniques. Using trapping records for individuals from February to September 2005, we obtained three measures of risk-taking: the number of trapping events, the number of different trapping locations, and the maximum distance between the home territory and a trapping event. We used GLMs to determine whether the activity and aggressiveness of individuals are related to these risk-taking behaviours, and found that active squirrels were trapped significantly more frequently and at a greater number of locations. There was also a significant interaction between activity and aggressiveness to affect the maximum capture distance. To determine if there are fitness tradeoffs associated with these risk-taking behaviours, we examined female bequeathal behaviour and survival. Bequeathing a territory increases offspring probability of overwinter survival, and we found that an increasing number of trapping locations was associated with an increasing tendency to bequeath. Active females were less likely to survive until the following spring. Risk-taking is therefore predicted by personality in this population, and they affect both survival and territorial bequeathal. These fitness tradeoffs may therefore lead to the maintenance of variation in personality.

Individuals of many species behave in a characteristic manner, such as by being aggressive, shy, or active in a variety of contexts (Wilson et al. 1994, Sih et al. 2004). This tendency of an individual to behave in a predictable way is referred to as its personality (Gosling 2001), temperament (Réale et al. 2007), or behavioural syndrome (Sih et al. 2004). Personality may be reflected in many aspects of an animal's behaviour and ecology, including its habitat use, interactions with conspecifics, and willingness to take risks. For example, highly exploratory individuals tend to disperse farther than less exploratory individuals (Fraser et al. 2001, Dingemanse et al. 2003, Bremner-Harrison et al. 2004), and social individuals move away from low density populations or groups and towards high density populations, while asocial individuals do the opposite (Svendsen 1974, Cote and Clobert 2007). Additionally, individuals in populations that are invading new areas (Martin and Fitzgerald 2005), and individuals living in human-disturbed areas (Martin and Réale 2008) tend to be more bold than those in either established populations, or undisturbed habitats.

Personality can affect fitness via both reproductive success and survival (Réale and Festa-Bianchet 2003, Biro

et al. 2004, Bremner-Harrison et al. 2004, Dingemanse et al. 2004, Both et al. 2005, Boon et al. 2007), but the maintenance of variation in personality within a population is not well understood. It may result from balancing selection due to variable selection pressures (Mangel 1991, Boon et al. 2007, Penke et al. 2007), or to differences in life-history strategy that affect risk-taking behaviours (Biro et al. 2004, Stamps 2007, Wolf et al. 2007). For example, the willingness to take risks, such as by intruding on the territories of neighbours or moving long distances, may lead to some of the observed fitness consequences of personality by affecting an individual's habitat use (Fraser et al. 2001, Biro et al. 2004, Bremner-Harrison et al. 2004). The exploration of the habitat at increasing distances from an individual's core area may be both beneficial and hazardous. Exploratory movements may be used to evaluate potential mates or seek extra-pair copulations (Neudorf et al. 1997, Pedersen et al. 2006), to gain knowledge of the quality of nearby habitat and territories (Bruinzeel and van de Pol 2004, Fedy and Stutchbury 2004), or as foraging opportunities when food is scarce (Fedy and Stutchbury 2004). However, moving through unfamiliar areas also increases

the risk of predation (Metzgar 1967, Larsen and Boutin 1994, Fraser et al. 2001), and being absent from the core area may result in the loss of cached food to pilfering (Gerhardt 2005) or the loss of offspring to predation (Schmidt and Whelan 2005). Therefore, there may be a tradeoff associated with risk-taking behaviour in terms of exploratory movements, and could lead to the maintenance of variation in personality.

An individual's willingness to enter a baited trap may be another indication of its propensity for risk-taking, because it accepts the risks associated with trapping and handling in order to obtain a food reward (Réale et al. 2000). Tuytens et al. (1999) found that individual European badgers *Meles meles* tended to be either trap-happy (captured three times out of three trapping sessions) or trap-shy (captured 0 out of three times). In bighorn ewes *Ovis canadensis*, Réale et al. (2000) found individual consistency across years in the number of captures. Since there are consistent individual differences in the likelihood of entering a trap, and these differences are correlated to other dimensions of personality, such as docility and other measures of boldness (Wilson et al. 1993, Réale et al. 2000), individual trappability could be considered as a measure of risk-taking.

North American red squirrels *Tamiasciurus hudsonicus* are diurnal tree squirrels that defend individual food-based territories year-round with a central cache, or primary midden, as its physical and activity centre (Gurnell 1984, McAdam et al. 2007). At low population densities, squirrels may also defend several secondary middens. Parental care is solely maternal, and mothers sometimes bequeath territories, by giving part or all of their territory to one or more of their offspring, which increases the offsprings' probability of overwinter survival (Boutin et al. 1993, 2000, Price and Boutin 1993, Berteaux and Boutin 2000, Boon et al. 2007). Activity, aggressiveness, struggle rate, and breathing rate during handling are correlated in a proactive-reactive behavioural syndrome in this population (Boon et al. 2007).

In this study, we investigated whether risk-taking of female red squirrels was related to their personality as measured in behavioural trials. We used trapping data to obtain three proxies of risk-taking behaviour and related them to the individual's activity and aggressiveness. We predicted that increasing activity and aggressiveness would be associated with an increase in the total number of captures, in the number of capture locations (an indication of the diversity of exploration, and how often the individual intrudes on the territories of others), and in the maximum distance between the individual's primary midden and a capture event. We also predicted that females may use forays away from their primary middens to search for new territories before bequeathing a territory to their offspring. If so, then individuals that explore more extensively (i.e. are trapped in a greater number of different locations and farther from home) may be more likely to bequeath. However, we predict that these behaviours are costly as well, and are associated with an increased mortality risk.

Methods

This study was conducted in 2005 using 71 adult female North American red squirrels as part of a long-term study population near Kluane National Park in southwestern Yukon, Canada (61°N, 138°W). Details of the study population and monitoring techniques are described in detail by Boutin et al. (2006) and McAdam et al. (2007). Three study grids, two control (40 ha each) and one experimental food addition (60 ha), are staked at 30 m intervals and the locations of middens are recorded at 15 m intervals. All individuals on the study grids were marked with numbered ear tags and a unique combination of coloured wires. Their survival and reproduction were monitored using behavioural observations and targeted live trapping on middens with Tomahawk traps baited with peanut butter. Generally traps were set on each grid six days per week between the middle of February and the end of September (2005). The time of day and number of hours per day that traps were open depended primarily on season, as we tried to match trapping to the squirrels' activity patterns; in winter, traps were open during most of the day, while in summer trapping was restricted to the morning (07:00–13:00) and sometimes the evening (approximately 19:00–22:00). Traps were checked every 90 min and were closed after the target squirrel had been captured. Squirrels were targeted for capture on their own middens, but were also captured as intruders on middens within the territories of others. Non-breeding, lactating, and post-weaning females were targeted approximately every two weeks, while pregnant females were targeted every 10 days early in the pregnancy and up to every three days near the end to accurately pinpoint the parturition date.

Field technicians set a variable number of traps on a variable number of middens owned by the target squirrel. One or two traps were set on the primary midden for most individuals, but technicians would set more traps and more middens for individuals that they knew to be hard to capture, or for individuals that they had already targeted without success for one or more days. We have not corrected for this variation in trapping effort because it should act to increase the variation in trapping success among individuals; those that were hard to trap were targeted more frequently (on more days) and with greater effort (on more middens and with more traps), while those who were frequently caught as intruders were rarely targeted directly. Some squirrels lived on the study grids for longer periods of time than others (due to immigration, emigration or death), and to account for this we included in all trapping analyses the number of days that the individual was present in the study population as an independent variable, calculated as the number of days between the first capture of 2005 and the last sighting, capture, or confirmation of death.

We used three indices of boldness and exploration related to trapping success: the total number of captures, the number of different locations where the individual was captured (regardless of whether those locations were on its territory or not), and the farthest distance from home that the squirrel was captured, measured as the straight-line distance to its primary midden. Since each squirrel owns an

average of 2.5 middens, an increasing number of trapping locations indicates that they are intruding on the territories of an increasing number of other individuals. All statistics were performed using R ver. 2.5. For all analyses, we used stepwise backwards elimination model selection at $p = 0.05$ with dependent variables standardized to a mean of zero.

Measuring personality

We used two behavioural tests to measure personality: an open field test to quantify behaviours related to activity and exploration in a novel environment (Walsh and Cummins 1976, Martin and Réale 2008), and a mirror-image stimulation to measure aggressiveness towards a conspecific (Svendsen and Armitage 1973). The complete ethogram and further details are provided in Boon et al. (2007). We captured the test subjects on their territory, read their numbered eartags, weighed them and checked their reproductive condition, then transferred them to a trap leading into the $60 \times 80 \times 50$ cm white plastic arena with a clear lid and four blind holes in the floor. The 7.5 min open field trial started when the squirrel entered the arena, and ended when we uncovered a mirror on one wall and continued with a 5 min mirror image stimulation, then released the squirrel and cleaned the arena with 70% ethanol. We videotaped the squirrels' movements and behaviours during these behavioural trials and later analysed them using The Observer Video-Pro 5.0 software. In the open field trial, we measured the percentage of time spent sitting or standing still, walking, rearing, sniffing the walls or floor, hanging from the top of the walls, chewing or scratching at the walls or floor, scanning, and grooming, plus the frequency (number per minute of observation) of jumps and putting its head in the holes in the floor, and the number of pellets left in the arena at the end of the trials. In the mirror image stimulation, we measured the latency to approach and to attack the mirror, the rate of attacks against the mirror and of crouch (aggressive) postures, and the percentage of time spent grunting (vocalization of intense threat), stretching (exploration of novelty), and in the third of the arena closest to and farthest from the mirror. Fifty-five of the 71 squirrels were measured twice at least six weeks apart, and of the remaining 16 individuals, seven died of natural causes before retesting, two disappeared and probably also died, and seven were alive but could not be recaptured.

Using principal components analyses (PCA), separately for the open field and mirror image stimulation, we reduced the measured behavioural variables to a smaller number of synthetic variables. To simplify the analyses and interpretations, we chose to include only the first principal component from each test in further analyses. In the open field, the first principal component, called activity hereafter, explained a total of 33% of the variance, and represents the individual's level of activity and exploration. The behaviours loading most heavily on this component in the positive direction were walk, jump, sniff (walls or floor) and rear, and in the negative direction was sitting or laying still. In the mirror image stimulation, the first principal component, called aggressiveness hereafter, explained 45.4% of the total variance. The behaviours loading most

heavily on this component in the positive direction were attack rate, crouch rate, and time spent in the third of the arena closest to the mirror, and in the negative direction were latency to approach and latency to attack the mirror. We performed a linear mixed model on the principal component scores to test for effects of date, grid, age, reproductive status, time of day, and trial number, with the individual's identity included as a random effect. In the open field, trial number was the only significant fixed effect, with squirrels generally being less active in the second trial than the first ($F = 10.85$, $DF = 1, 54$, $p = 0.002$), and this model including identity was significantly better than a restricted linear model without it (likelihood ratio = 11.11, $DF = 1$, $p < 0.001$). The repeatability, the proportion of total variance that was due to the individual (Lessells and Boag 1987), of this component was 44.3%. In the mirror image stimulation, there were no significant fixed effects in the final mixed model, but this model was significantly better than the restricted linear model (likelihood ratio = 7.84, $DF = 1$, $p = 0.005$). The repeatability of this component was 39.0%. We extracted the best linear unbiased predictors (BLUPs) from the final mixed models, which provide predictions of the random effects independent of the other terms in the model, standardized to a mean of zero (Kruuk 2004), and used these values as the individual personality values of activity and aggressiveness in further analyses.

The relationship between personality and trapping success

To determine whether the number of middens owned by a squirrel in May was influenced by her personality or other characteristics, we used a generalized linear model (GLM) with a Poisson distribution and square-root link, and the squirrel's age, the grid on which it lived, activity, aggressiveness, and the interaction between activity and aggressiveness as fixed effects.

Because squirrels that live on the edges of the grids have fewer marked neighbours and could consequently be exposed to a smaller number of traps and diversity of trapping locations, we tested for differences in mean activity and aggressiveness values between squirrels with their primary midden less than 60 m from the edge of the grid ('edge', who would be unlikely to have a marked neighbour between them and the edge of the grid) versus those more than 60 m from the edge ('centre', who would most likely have a neighbour closer to the edge). We also included this binomial 'location' variable as a fixed effect in other models, as indicated below.

We tested for correlations among the three indices of trapping success using Kendall nonparametric correlations, and calculated false discovery rates (Benjamini et al. 2001) to control for multiple comparisons. To analyse the influence of personality on the total number of captures and the number of different capture locations, we used GLMs with a negative binomial distribution and a square-root link. In both models, we included as independent variables the squirrel's age, its grid, its midden location (edge or centre), the number of middens it owned in May, the total number of days that the squirrel was present in the

study population, its activity and aggressiveness, and the interaction between activity and aggressiveness. We calculated the proportion of variance explained by the model as $r^2 = (\text{null deviance} - \text{residual deviance})/\text{null deviance}$, and partial r^2 for each variable as the change in r^2 when the variable in question was removed from the model.

To model the relationship between personality and the maximum capture distance from a squirrel's primary midden, we used a linear model on square-root transformed distances and included the same independent variables as in the previous two models. We calculated the partial r^2 (adjusted) as above.

We tested whether indices of personality or trappability affected the tendency of females to bequeath territories to their offspring. For the 45 females that had at least one offspring survive to weaning in 2005, we considered them to have bequeathed a territory if at least one of their offspring settled on the natal territory (i.e. settled in an area that the mother defended previously by giving territorial rattle calls, Smith 1968). We used a binomial GLM with logit link, and age, grid, number of middens owned, maximum capture distance, number of captures per time (i.e. number of captures divided by the number of days present in the population), number of capture locations per time, and activity, aggressiveness, and their interaction as independent variables.

Finally, we investigated whether there were survival costs associated with either personality or capture success. Using a binomial GLM with a logit link, we analysed female survival to May 1, 2006 (the spring following the study year), with the same independent variables as in the bequeathal model above.

Results

Individual female red squirrels were captured an average of 21.6 times (range 6 to 48), or 0.13 captures per day present in the population (range 58 to 218 days, and 0.06 to 0.31 captures per day). They were caught at an average of 6.6 different locations (range 1 to 17), and the average maximum capture distance was 136 m from the primary midden (range 0 to 378 m). The average territory size for squirrels in this population in 2004 (a comparable year) was 0.401 ± 0.033 ha (or radius of approximately 35 ± 10 m, J. LaMontagne and S. Boutin, unpubl.), and so to reach its maximum capture distance, the average squirrel would have crossed the territory of its nearest neighbour and been captured on that of the next squirrel. Squirrels owned an average of 2.5 middens in May, so the average squirrel, caught in 6.6 different locations, would have been captured on the territory of at least two other individuals.

The number of middens owned by a squirrel in the spring was not influenced by her personality, her age, or the study population in which she lived (all variable removed with $p > 0.2$). The mean activity and aggressiveness values did not differ between squirrels living on the edge or in the centre of the grids (t-tests: activity, $t = 0.06$, $DF = 69$, $p = 0.96$; aggressiveness, $t = 0.01$, $DF = 69$, $p = 0.99$).

The total number of captures, the number of capture locations and the maximum capture distance were all significantly positively correlated to each other (Kendall,

$n = 71$, number of captures to number of locations, $\tau = 0.49$, $p < 0.0001$; number of captures to maximum distance, $\tau = 0.17$, $p = 0.03$; number of locations to maximum distance, $\tau = 0.43$, $p < 0.0001$). None of these correlations was affected by the calculation of false discovery rates (Benjamini et al. 2001).

After correcting for the number of days that an individual spent in the population, squirrels that were more active, lived on the food supplemented grid, and owned a greater number of middens were captured a greater number of times (Table 1, Fig. 1a), but age, edge versus central location, aggressiveness and the interaction between activity and aggressiveness were not significant (all $p > 0.1$). The r^2 for the selected model was 0.36. Squirrels that were more active and squirrels that were older were also captured at a greater number of different locations (Table 1, Fig. 1b), after correcting for the number of days, but grid, number of middens owned, edge versus central location, aggressiveness, and the interaction between activity and aggressiveness were removed from the model with $p > 0.1$. The r^2 for the selected model was 0.19. The maximum capture distance was significantly related to an interaction between activity and aggressiveness (Fig. 2, Table 1), which are correlated ($r = 0.54$) in this population (Boon et al. 2007). Maximum capture distance is highest for high activity/aggressiveness (proactive) individuals, but at low and moderate activity values, maximum distance increases as aggressiveness

Table 1. Three aspects of trappability are affected by personality in 71 adult female North American red squirrels in Yukon, Canada. All initial models included activity, aggressiveness, and their interaction, as well as grid, location on the grid (edge or central), age, the number of middens owned, and the number of days that the squirrel was present in the study population, and non-significant terms were removed using stepwise backwards model selection with $p > 0.05$. The number of captures and number of capture locations were analysed using a GLM with negative binomial distribution. The r^2 for the selected models was 0.29 and 0.19 respectively. Maximum distance from home was a linear regression with a square-root transformed response variable, and the adjusted r^2 for the selected model was 0.23.

Number of captures	Partial r^2	LR χ^2	DF	p
activity ¹	0.10	10.85	1	0.001
grid	0.17	18.66	2	<0.0001
days present	0.22	23.69	1	<0.0001
number of middens owned	0.06	6.86	1	0.009
Number of capture locations	Partial r^2	LR χ^2	DF	p
activity ²	0.07	6.25	1	0.01
age	0.05	4.14	1	0.04
days present	0.10	8.17	1	0.004
Maximum capture distance	Partial r^2	F	DF	p
activity ³	0.05	4.68	1	0.03
aggressiveness ⁴	0.03	1.64	1	0.21
activity \times aggressiveness ⁵	0.04	4.15	1	0.05
grid	0.11	5.50	2	0.006
age	0.04	4.04	1	0.05
location	0.06	5.82	1	0.02

¹ coefficient = 0.29 ± 0.09 .

² coefficient = 0.20 ± 0.08 .

³ coefficient = 1.40 ± 0.61 .

⁴ coefficient = -1.23 ± 0.69 .

⁵ coefficient = 1.20 ± 0.59 .

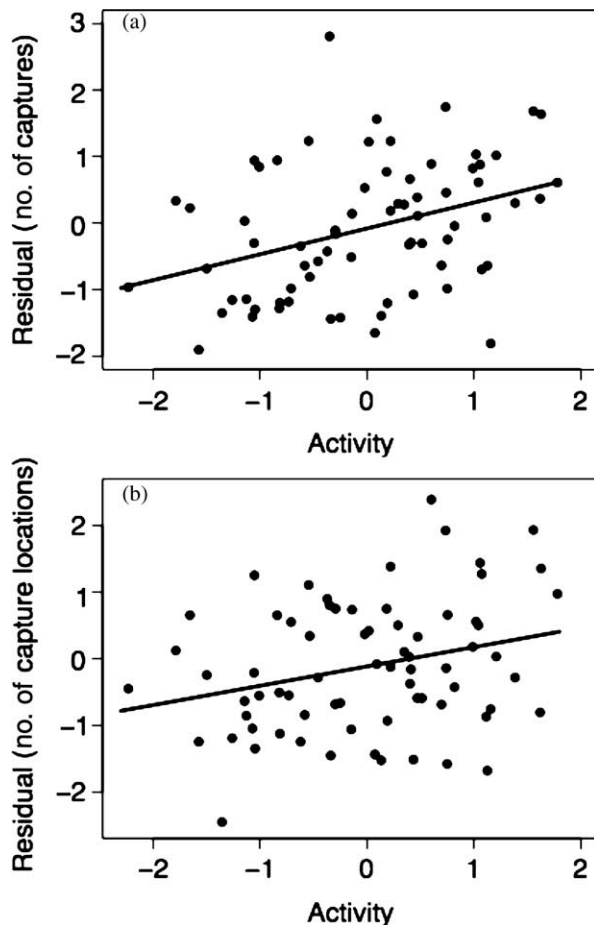


Figure 1. In female North American red squirrels, increasing activity in an open field behavioural trial is associated with (a) an increasing number of trapping events (after correcting for grid, number of middens owned, and number of days present in the population) and (b) an increasing number of different capture locations (after correcting for age and number of days present in the population), between February and September 2005.

declines (Fig. 2). Older squirrels, those that live in the centre of the grid, and those from one of the two control grids also tended to be caught farther from their primary midden than other squirrels, but time spent in the population, and number of middens owned were not significant ($p > 0.1$). The adjusted multiple r^2 for the selected model was 0.23.

Forty-five squirrels had at least one offspring survive to weaning, and 31 of them bequeathed a territory while 14 did not. Squirrels that were trapped at a greater number of different middens per time present in the population were more likely to bequeath a territory to their offspring (LR $\chi^2 = 7.00$, $DF = 1$, $p = 0.008$, partial $r^2 = 0.13$; Fig. 3), after controlling for grid (LR $\chi^2 = 25.00$, $DF = 2$, $p < 0.001$, partial $r^2 = 0.45$) and age (older squirrels were less likely to bequeath; LR $\chi^2 = 6.36$, $DF = 1$, $p = 0.01$, partial $r^2 = 0.11$). There was no effect of the number of captures per time, the maximum capture distance, the number of middens owned in May, activity, aggressiveness, or the activity by aggressiveness interaction (all removed with $p > 0.1$). The r^2 for the selected model was 0.47.

Forty-five squirrels survived until the following spring and 26 died, of which six were confirmed predations. Squirrels that were older and squirrels that were more active were more likely to die (age: LR $\chi^2 = 8.77$, $DF = 1$, $p = 0.003$, partial $r^2 = 0.09$; activity: LR $\chi^2 = 5.52$, $DF = 1$, $p = 0.02$, partial $r^2 = 0.06$; r^2 of selected model = 0.13; Fig. 4). The grid, number of captures per time, number of capture locations per time, number of middens owned, maximum capture distance, aggressiveness, and the interaction of activity by aggressiveness were not significant (all $p > 0.08$).

Discussion

This study suggests that personality can influence risk-taking and habitat use, and provides further evidence for fitness consequences of personality in wild populations. In female red squirrels, increasing activity was associated with an increasing propensity to enter traps, to intrude on the territories of others, and to move farther from their own territory, all of which represent risk-taking behaviours. The maximum capture distance was also affected by an interaction between activity and aggressiveness, but we detected no relationship between aggressiveness and the number of captures or number of capture locations. It is not clear why both proactive and reactive individuals tend to move farther from their middens than do intermediate individuals. It is possible that reactives are sometimes forced off of their territories while proactives are exploratory and leave their territories voluntarily.

In this study, we did not distinguish between on- and off-territory movements for two reasons. First, because we target individuals at a limited number of locations within their territory (i.e. on middens), which is controlled for by including the number of middens owned in the analyses, an increasing number of trapping locations is necessarily associated with an increasing number of extra-territorial forays, and not confounded by variation in territory size. The average maximum capture distance of 136 m would take a squirrel off of its own territory, across that of its neighbour, and to the centre of the next squirrel's territory. It is clear, therefore, that a large proportion of the movements that we detected were off-territory. Secondly, we think it is likely that many costs and benefits increase with distance moved from the primary midden, even if not actually on the territory of another individual. However, much of the previous research has focused on on- versus off-territory movements or events, and so we use that terminology in this discussion at times.

For an adult female red squirrel, there are both costs and benefits associated with venturing away from her primary midden. Those that were trapped at a greater number of other middens were more likely to bequeath a territory to their offspring, but more active squirrels were less likely to survive until the spring of the following year. We did not know the cause of death in enough cases to determine whether there was an influence of personality or exploration on the likelihood of being depredated, but other studies have found relationships between predation and movement away from familiar areas. Juvenile red squirrels are more likely to be killed while off their natal territory (Larsen and Boutin 1994,

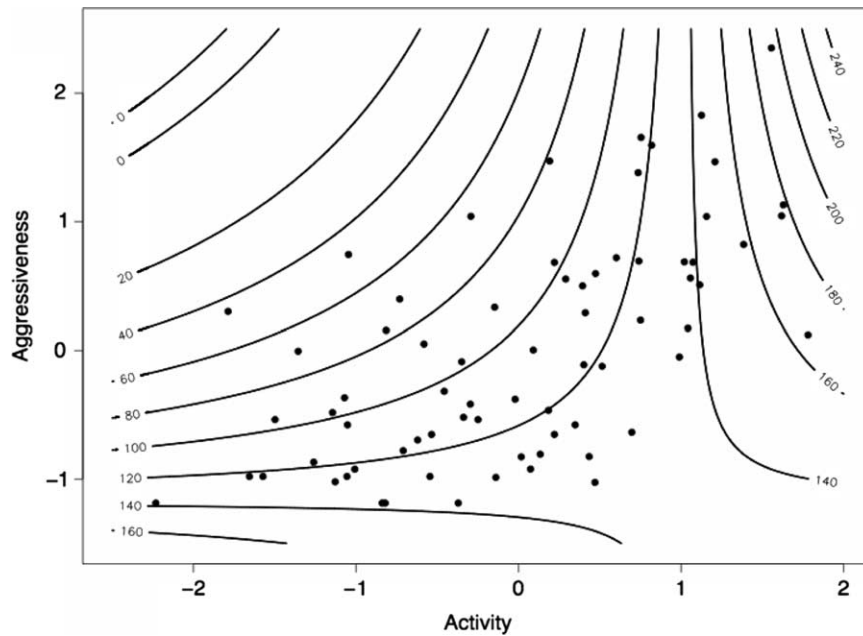


Figure 2. The interaction between activity and aggressiveness significantly affects the maximum capture distance from the primary midden for female North American red squirrels, after controlling for her age, the grid on which she lived, and her midden location on that grid (in the centre or near the edge of the monitored area).

Stuart-Smith and Boutin 1995), and transient white-footed mice *Peromyscus leucopus* are more likely to be depredated than are residents (Metzgar 1967). In reintroduced swift fox *Vulpes velox*, bold individuals move greater distances from the point of release and are more likely to die (Bremner-Harrison et al. 2004). The chances of being killed when in unfamiliar areas may be higher owing to lower familiarity with escape routes and refuges, and being engaged in exploratory behaviours that reduce vigilance and increase exposure (Metzgar 1967). Intruding on the territories of others may also increase predation risk due to increased conspicuousness and decreased vigilance during chases (Price et al. 1990). Since active squirrels tend to take more risks, such as by entering traps more frequently and at a greater variety of locations, they may be less cautious in general and engage in riskier behaviours like spending less time resting or vigilant and more time in exposed locations, both of which increase the probability of depredation in juvenile red squirrels (Stuart-Smith and Boutin 1995, Anderson and Boutin 2002). Survival could also be affected by energetic factors: active squirrels may have higher resource requirements due to higher metabolic rates, leading them to be more prone to starvation (Ros et al. 2004, 2006, Tobler et al. 2007). There could also be other risks, not considered in this study, to leaving the primary midden unattended for long periods of time, such as by traveling very long distances or by being in a trap, including the predation of offspring (Schmidt and Whelan 2005) or pilfering from food caches (Gerhardt 2005).

The benefits to exploring habitat away from the primary midden, and especially off-territory, may include knowledge of other individuals and the availability of territories and resources. Squirrels sometimes change territories; in females, this occurs most frequently after bequeathing her former territory to an offspring, although she may also bequeath just a portion and stay on the remainder herself

(Boutin et al. 1993, 2000, Price and Boutin 1993, Berteaux and Boutin 2000). In the current study, females who were caught at a greater number of different locations were more likely to bequeath a territory to their offspring, regardless of the number of middens owned, and so they may have been prospecting for a new territory. Juveniles that receive a territory from their mother are more likely to survive the winter (Boutin et al. 1993, Berteaux and Boutin 2000, Boon et al. 2007), and so bequeathal has a positive effect on the mother's fitness. In other species, an individual's movements have also been observed to provide important knowledge regarding the quality of nearby habitat and territories, as well as foraging opportunities (Bruinzeel and van de Pol 2004, Fedy and Stutchbury 2004). Collared flycatchers *Ficedula albicollis* use public information

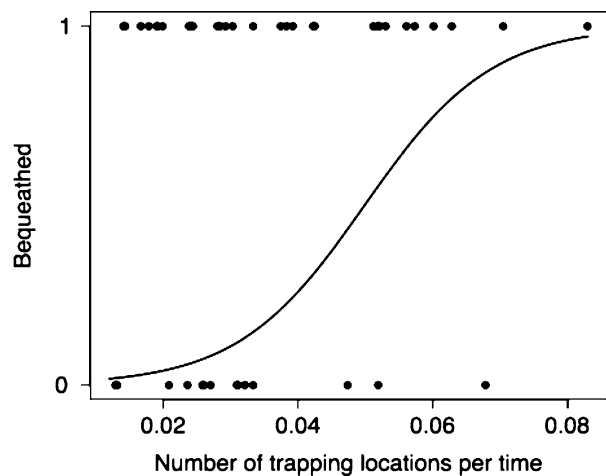


Figure 3. Female North American red squirrels that were trapped at a greater number of locations were significantly more likely to bequeath a territory to their offspring.

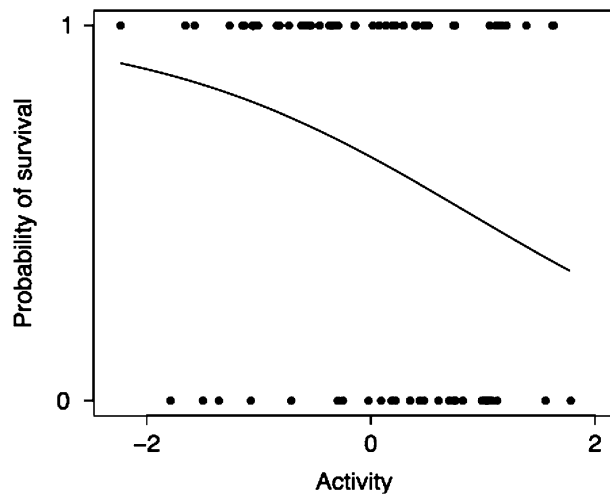


Figure 4. More active female North American red squirrels were significantly less likely to survive until the following spring (from June 2005 to May 2006).

regarding the breeding success of conspecifics to assess the quality of breeding habitat and inform future breeding-site decisions (Doligez et al. 2002), and movements onto the territories of others may allow the gathering of such information. Gerhardt (2005) observed very high rates of food pilfering from the caches of other individuals in an eastern population of red squirrels, and so extraterritorial movements may also permit the stealing of food. In birds, extra-territorial movements can also facilitate extra-pair copulations and permit the evaluation of potential mates (Neudorf et al. 1997, Pedersen et al. 2006). During the breeding season, male red squirrels move large distances in search of estrous females, and both sexes may seek information on the quality of potential mates (J. E. Lane and S. Boutin, unpubl.).

There are several potential biases in our data, but we believe that they would act to reduce rather than increase the probability of finding significant effects of personality on risk-taking behaviours, or of either of these on life history parameters. We did not correct for variation in trapping effort, as discussed previously, but as a result, the true variations in number of captures between trap-shy and trap-happy individuals should be larger than seen here. Similarly, the true maximum distances traveled from home are likely greater than those detected, given the stochastic nature of this measurement and the low probability of a squirrel encountering a trap when at its greatest displacement. Another potential bias relates to our use of trapping data to measure exploration rather than a method that allows the random sampling of behaviour, especially if squirrels are less likely to enter a trap when far from home. Our three measures of risk-taking are all, in a sense, estimations of the willingness of the squirrel to enter a trap, and as such are not independent measures. We would not detect the movements of trap-shy individuals that move long distances from their territories, for example.

On the other hand, our power to detect effects of personality and trapping indices on life history traits may be low, and there could be additional effects that we did not detect. Our measures of risk-taking are likely quite noisy, and so their effects on survival, for example, may not

emerge as being statistically significant even if they are biologically more important than the correlated personality measures. Additionally, because our study was performed in a single year, a female's trappability and habitat use could be influenced by her state in that year as well as her personality (Dingemanse et al. 2002, Drent et al. 2003). This may explain why we see bequeathal to be correlated with the number of capture locations but not with activity, for example.

A squirrel's personality affects her habitat use and her fitness. Increasing activity is associated with an increasing tendency to be risk-prone, and although those individuals had a lower chance of survival in the time period of this study, they enhanced their fitness by allowing their offspring to remain on the natal territory. This tradeoff associated with risk-taking behaviour suggests that variation in personality could be maintained via correlations with life history strategies (Stamps 2007, Wolf et al. 2007).

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