

LETTER

The interaction between personality, offspring fitness and food abundance in North American red squirrels

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Abstract

Animal personality is now frequently reported in wild and captive populations. It has been shown to be moderately heritable and to have potentially important fitness consequences. Variation in personality within a population may be maintained by balancing selection if different values of personality traits are favoured under different conditions. We measured personality in 98 female North American red squirrels (*Tamiasciurus hudsonicus* Erxleben), and examined whether its variation could be maintained by changing selection pressures acting via reproductive traits and yearly variation in food abundance. There was no effect of personality on parturition date or litter size, but a female's activity was correlated to the growth rate of her offspring in the nest, and her aggressiveness was correlated to their survival in the nest and overwinter. The magnitude and direction of the effects changed among life history stages and years, possibly in association with food supply in some cases, and may indicate a role for balancing selection in the maintenance of personality.

Keywords

Activity, aggressiveness, balancing selection, behavioural syndromes, cone abundance, growth rate, juvenile survival, personality, *Tamiasciurus hudsonicus*, temperament.

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INTRODUCTION

Animal personality refers to consistent individual differences in behaviour (Sih *et al.* 2004), and it has been demonstrated to be repeatable (Réale *et al.* 2000; Dingemanse *et al.* 2002; Carere *et al.* 2005), heritable (Dingemanse *et al.* 2002; Drent *et al.* 2003), and a predictor of several other ecological and social variables [e.g. dispersal distance (Dingemanse *et al.* 2003), parental care (Cleveland *et al.* 2004; Both *et al.* 2005; Duckworth 2006), territory size (Civantos 2000)]. However, we know very little about the fitness consequences of personality and about how the observed range of among-individual variation is maintained (Sih *et al.* 2004; Dingemanse & Réale 2005; B. R. Smith & D. T. Blumstein, unpublished data).

Only a handful of studies have examined the effects of personality on fitness. Bold bighorn ewes (*Ovis canadensis*) are less likely to be killed by cougars (*Puma concolor*, Réale & Festa-Bianchet 2003). The survival and reproductive success of great tits (*Parus major*) depends on an interaction between their exploration speed, sex and winter resource availability, such that the direction of selection fluctuates between years (Dingemanse *et al.* 2004). The phenotype of the pair is also

important, and assortatively mated pairs produce offspring in the best condition (Both *et al.* 2005). Reduced weaning or fledging success is associated with shyness in bighorn ewes (Réale *et al.* 2000), aggressiveness in male western bluebirds (*Sialia mexicana*, Duckworth 2006), and low concentrations of 5-hydroxyindoleacetic acid (5-HIAA, a serotonin metabolite) in rhesus macaques (*Macaca mulatta*), which is associated with low sociability, high aggressiveness, and more risk-taking behaviours (Mehlman *et al.* 1994, 1995; Westergaard *et al.* 2003).

Personality is also associated with differences in maternal behaviour that can affect fitness. Female house mice (*Mus domesticus*) selected for high aggression nurse and groom their pups more than females selected for low aggression (Benus & Røndigs 1996), but take longer to retrieve their pups in a behavioural trial (Gammie *et al.* 2006). Low 5-HIAA rhesus macaque mothers are highly protective and restrictive with their infants (Cleveland *et al.* 2004). Both *et al.* (2005) suggested that slow exploring great tits may be better parents, because they respond more easily to environmental change. Maternal behaviour has also been shown to produce persistent effects on the stress responses of offspring through epigenetic programming (Weaver *et al.*

2004). If the covariance of maternal style and personality is widespread, then it could result in important maternal effects on offspring growth and survival, leading to further fitness consequences of personality.

If personality indeed has important consequences for fitness, it would seem that selection should reduce variation in favour of all individuals having the same 'optimal' personality. However, selection could actively maintain genetic variation in personality traits through balancing selection, in which different phenotypes are favoured under different conditions, leading to identical average fitness overall (Penke *et al.* 2007). This could potentially result from fluctuations in the favoured phenotypes because of environmental heterogeneity in space or time (Mangel 1991; Dingemans *et al.* 2004), and/or because of correlations between risk-associated personality traits and life history tradeoffs (Stamps 2007; Wolf *et al.* 2007). Variation in personality traits could also be maintained by having different effects at different stages during ontogeny, or on different components of fitness (Schluter *et al.* 1991), or there could be antagonistic effects of different personality traits that are correlated as part of a behavioural syndrome. Behavioural syndromes are the correlation of personality traits in different conditions or contexts, or the correlation of different personality traits to each other, such as aggressiveness and boldness (Sih *et al.* 2004). These phenotypic correlations may result from common hormonal control of behaviours or other forms of genetic correlation, which may constrain the optimization of any one personality trait, thereby maintaining variation in both traits (Sih *et al.* 2004).

In this study, we used *Tamiasciurus hudsonicus* Erxleben (North American red squirrel) to test whether personality affects fitness in a wild population over multiple years, and if so, whether the direction of selection pressures is constant or variable. Red squirrels are diurnal tree squirrels with female-only parental care that defend non-overlapping food-based territories year-round (McAdam *et al.* 2007). They experience dramatic yearly fluctuations in their food supply resulting from mast-seeding of the dominant conifer in the region, the white spruce (*Picea glauca*, LaMontagne & Boutin 2007), and in our study area the average number of cones per tree has ranged from 0 to 982 in the last 20 years (S. Boutin, unpublished data). Squirrels store cones in a central food cache, or midden, and they rely primarily on this cached food through the winter and into the spring (Boutin *et al.* 2006). In one of the first studies to examine multiple life history traits in relation to personality in the wild, we measured personality in 98 females, and tested for effects on parturition date, litter size, offspring growth and survival in the nest, and offspring survival through their first winter, during both low- and high-cone years. We found that the optimal personality changes between years and

according to the life history trait in question, and suggest that balancing selection may play a role in maintaining variation in personality in this population.

METHODS

Study site and population

This study was conducted in conjunction with a long-term study of North American red squirrels near Kluane National Park in south-western Yukon, Canada (61 °N, 138 °W). We combined field studies of personality from summer 2005 with reproductive and life-history data of those individuals from 2003 to 2006. Individual squirrels were followed in detail as described in Boutin *et al.* (2006) and McAdam *et al.* (2007). Briefly, all individuals on three study grids (two control and one food supplemented) were marked with numbered ear tags threaded with a unique combination of coloured wires for identification at a distance. On the food supplemented grid, each squirrel in the population was provided with *ad libitum* peanut butter from fall until spring, in a bucket hung above the primary midden. Survival and reproductive status of squirrels were monitored through behavioural observations and regular live trapping with Tomahawk traps. Soon after parturition, we located females' nests with telemetry and briefly removed the young to sex, mark and weigh them. We reentered the nests when the juveniles were between 25 and 30 days old to weigh and mark them with ear tags. Juveniles emerge from the nest at approximately 40 days and wean at 70 days (McAdam *et al.* 2007). Survival of juveniles after emergence was monitored using live trapping, behavioural observations and telemetry.

Behavioural tests

We measured personality in 71 adult females and 27 juvenile (young of the year) females with three behavioural tests. The first was an open field (OF), which is used to quantify activity, exploration and stress responses in a novel environment (Walsh & Cummins 1976; Martin & Réale 2007). The second test, mirror-image stimulation (MIS), is used to assess aggressive and sociable behaviours (Svendsen & Armitage 1973). The two tests were performed in the same testing session, with the OF also serving as habituation time before the MIS (Svendsen & Armitage 1973). The testing arena was a 60 × 80 × 50 cm white box with a clear acrylic lid through which the behavioural trials were recorded with a digital video camera. A series of four blind holes in the floor aided in separating exploratory behaviours from activity, since they are generally correlated (Martin & Réale 2007). A 45 × 30 cm mirror fixed to one end of the arena was

covered during the OF and exposed for the MIS. All tests were performed at the point of capture on the territory of the focal individual, and were conducted by the same observer (AKB) using a standardized procedure.

The focal squirrel was captured, handled, and transferred to a trap leading into the arena. The 7.5-min OF trial began when the squirrel entered the arena. The 5-min MIS trial started after uncovering the mirror, when the squirrel was perceived to have seen its reflection. Its behaviour changed markedly when it saw its reflection, and generally it either froze suddenly while looking at the mirror, or approached and attacked the mirror in rapid succession (AKB, personal observation). At the conclusion of the trial, the squirrel was released and the arena cleaned with 70% ethanol. Of the 71 adult females, 55 were retested six or more weeks later; of the 16 that were not retested, seven died of natural causes, two disappeared and seven were alive but could not be recaptured. The 27 juveniles were tested as soon as they

could be trapped (mostly 70–85 days of age; range 51–108 days). Subsequent analyses showed that age of juveniles at the time of testing had no effect on personality (analysis not shown). Juveniles were tested only once because of the short time interval between first trials and the end of the field season.

The videotaped trials were analysed using THE OBSERVER VIDEO-PRO 5.0 (Noldus Information Technology, Wageningen, The Netherlands). For the OF, we used an ethogram similar to that of Martin & Réale (2007) for the Eastern chipmunk (*Tamias striatus*), and for the MIS we developed one based on our observations and previous descriptions of agonistic behaviours in the red squirrel (Ferron 1979, 1980). See Table 1 for more details of the behaviours measured.

The third behavioural test quantified the squirrel's response to handling (Carere & van Oers 2004). Immediately after transferring an individual from a trap to a handling bag, we measured struggle rate (number of seconds

Table 1 PCA loadings for behaviours in two behavioural tests, an open field (axes OF1–3) and a mirror-image stimulation (axes MIS1–2) in female North American red squirrels

Behaviour	OF1	OF2	OF3	Behaviour	MIS1	MIS2
Still	-0.49	-0.11	-0.07	Attack rate**	0.42	-0.13
Walk	0.48	0.10	-0.13	Crouch rate††	0.42	0.03
Jump rate	0.38	0.36	-0.13	Front‡‡	0.42	-0.01
Sniff*	0.34	-0.34	-0.11	Attack latency	-0.40	0.41
Hole rate†	0.29	-0.34	-0.26	Approach latency	-0.39	0.00
Rear	0.29	-0.24	-0.05	Back‡‡	-0.30	-0.35
Hang‡	0.18	0.55	0.28	Grunt§§	0.22	-0.10
Chew§	0.08	-0.30	0.56	Stretch¶¶	0.15	0.82
Scan	-0.03	0.26	-0.49			
Groom	-0.04	-0.29	-0.36			
No. pellets¶¶	0.25	-0.14	0.33			
SD	1.83	1.28	1.18		1.90	1.04
% Total variance	30.4	14.9	12.7		45.0	13.6
% Repeatability	41.0	68.2	41.5		37.4	15.2
LRT (d.f. = 1)	10.32	27.77	11.83		8.58	1.46
P-value	0.001	<0.0001	0.001		0.003	0.23

Units are the percentage of time spent in each behaviour, unless indicated otherwise, and bold type indicates behaviours that contributed importantly to a component. MIS behaviours are mirror-directed, and latencies are log-transformed. The significance of repeatability was tested by comparing mixed models including individual identity as a random effect to linear models without it, using a likelihood ratio test (LRT). See text for more information.

*Sniff the floor or walls.

†Put head in hole in the floor.

‡Hang from top of walls.

§Chew or scratch at floor or walls.

¶Number of pellets left in the arena after the tests.

**Aggressive contact, standing on back legs and striking with the front (Ferron 1979).

††Posture indicative of imminent attack; tail positioned over the back with hairs erect (Ferron 1979).

‡‡Percent time spent in the third of the arena closest to or farthest from the mirror (Front and Back).

§§Vocalization of intense threat (Ferron 1979).

¶¶Slow approach towards mirror with back legs stretched behind: characteristic of the exploration of novelty (Ferron 1980).

spent struggling in 30 s) and breathing rate (breaths per 10 s). Between one and seven samples were collected per individual, by five observers.

Statistical analyses

For the OF and MIS, we used principal components analyses (PCA; separately for the two tests) to reduce the number of behaviour variables measured to a limited number of synthetic behavioural variables, following Martin & Réale (2007). This allowed us to identify the primary differences among individuals along those behavioural axes using linear mixed models (LMM) with the synthetic variables (principal component scores) as dependant variables, plus age, reproductive condition, grid of origin, testing date and time, and trial number as fixed effects and squirrel identity (ID) as a random effect. For each synthetic variable, we used stepwise backwards elimination model selection on the mixed model, compared it with a linear model without ID using a likelihood ratio test with one degree of freedom, and determined the repeatability, or proportion of variance explained by the individual (Lessells & Boag 1987). For components with a repeatability significantly greater than zero (i.e. a significant effect of individual in the mixed model), we extracted the best linear unbiased predictors (BLUPs), which provide predictions of the random effect of each individual squirrel independent of the other terms in the model, standardized to a mean of zero (Kruuk 2004). We used these BLUPs as individual values of 'personality traits' in further analyses. To simplify the analysis and interpretation of life-history models, we chose to include only the first principal component from the OF and the MIS. These two variables represent activity/exploration (OF1) and aggressiveness (MIS1), as described in the Results section, and were chosen because of their potential importance to the ecology of squirrels in terms of energetics and the ability of a squirrel to obtain and defend food resources (M. M. Humphries, unpublished data, Stuart-Smith & Boutin 1994).

For struggle rate and breathing rate, we used LMMs in the same way to test and control for micro-environmental and individual characteristics, to estimate repeatability, and to reduce multiple observations to a single value per individual. In each model, we included squirrel ID as a random effect, plus age, grid, reproductive condition, test date and observer as fixed effects. We extracted the BLUPs and used these as the individual values of struggle and breathing rate in further analyses.

To determine whether squirrels exhibit behavioural syndromes, we tested for correlations among OF1, MIS1, struggle rate and breathing rate using Pearson's product moment correlations in a pair-wise manner among the four variables. False discovery rates were calculated to account

for multiple comparisons (Benjamini *et al.* 2001). Positive correlations among these four traits would indicate a 'proactive-reactive' syndrome (Koolhaas *et al.* 1999; Sih *et al.* 2004).

We investigated the effects of personality on the following life history traits: (i) parturition date; (ii) litter size at birth; (iii) offspring growth rate; (iv) survival of offspring in the nest; (v) overwinter survival of offspring; and (vi) territory bequeathal. In initial models, we included other variables that have previously been found to be important in this system (see McAdam *et al.* 2002; McAdam & Boutin 2003a,b) such that significant effects of personality on life-history traits would be independent of those variables. Because they were included only to avoid confounding results regarding personality, we will not discuss them in any detail. The fixed effects included in most initial models were year, grid, female's age, activity, aggressiveness and the interactions year by activity, year by aggressiveness and activity by aggressiveness. These are referred to collectively as the standard fixed effects, and any additional fixed effects are indicated in the description of each model.

We used stepwise backwards elimination model selection with variables standardized to a mean of zero, and all analyses were performed using R (R Development Core Team 2006). Sample sizes vary according to the number of individuals or litters for which we had complete data in each analysis. Because individual females were observed over multiple years, we included female ID as a random effect in all of the following analyses. This allowed us to avoid pseudoreplication and to estimate the proportion of variance of a trait that is due to individual effects. Variance among females represents genetic (both additive and non-additive) and maternal effects that could not be explained by the fixed effects included in the model (Falconer & Mackay 1996). Therefore, the effect of a personality trait on offspring fitness could be interpreted independently of other potential genetic and maternal effects.

For some of our analyses, we used generalized linear mixed models with penalized quasi-likelihood (glmmPQL function). These models are not fit using log-likelihood methods, and so likelihood ratio tests cannot be used to evaluate the strength of fixed effects. Because our initial models are complex, we used a conservative strategy of first employing a GLM to reduce the number of interactions and fixed effects. We then used the terms included in this final GLM as the baseline from which to evaluate the data using a GLMM to account for mother's ID as a random effect, and further simplified the GLMM using *t*-tests, retaining the categorical variables when at least one level differed significantly from the others, to obtain our selected model. We also verified our analyses using another method, GLMMs using the lmer function followed by Markov

Chain Monte Carlo simulation to calculate confidence intervals. We determined that (i) all fixed effects in our final GLMMPQL models are also significant in an lmer model with MCMC simulation, and (ii) our methods appear to be more conservative, but do not greatly alter the interpretations, and we feel that they allow a more intuitive understanding of the results.

To model parturition date (of a female's first litter in each year), we fit an LMM (years 2003–2006; $n = 158$ litters produced by 80 females) with the standard fixed effects. We analysed litter size at birth (years 2003–2006; $n = 175$ litters produced by 80 females) first with a GLM with quasi-Poisson errors and a log link function, and included the standard fixed effects plus parturition date. As described above, we then included the variables that remained in that model in a GLMM with the same error structure, and further simplified the model.

The effects of a female's personality on the growth rate of her offspring in the nest (i.e. gain in mass between first and second measurement divided by the number of days; years 2003–2006, $n = 348$ offspring produced by 75 females) was examined using an LMM with the standard fixed effects plus parturition date, juvenile sex, juvenile mass at first measurement, and litter size at second measurement.

The survival of juveniles in the nest (i.e. from shortly after birth until shortly before emergence; years 2003–2006, $n = 517$ offspring produced by 79 females) was analysed using a GLM followed by a GLMM, with binomial errors and a logit link function. The standard fixed effects plus parturition date, juvenile sex, and litter size and juvenile mass at first measurement were included in the initial model.

For the survival of offspring through their first winter (from weaning until May 1 of the following year; years 2003–2005, $n = 124$ offspring produced by 49 females), we also included information on territory bequeathal; mothers sometimes give their offspring part or all of the natal territory, which increases the probability of overwinter survival for the juvenile (Price & Boutin 1993; Berteaux & Boutin 2000). A juvenile was considered to have been bequeathed to if it settled on part of the natal territory. We used a GLM followed by a GLMM, with binomial errors and logit link, and the standard fixed effects plus parturition date, juvenile sex, and bequeathal.

Finally, we examined whether the tendency of a mother to bequeath territories to her offspring was related to her personality. We created a binomial variable indicating whether or not a female bequeathed part or all of her territory to at least one of her offspring, in each year for which she had at least one juvenile survive to weaning ($n = 67$ instances for 49 females). We did not include year in this analysis because of the small number of records for 2003 and 2004. We ran a binomial GLMM including

parturition date, number of offspring surviving to weaning, activity, and aggressiveness.

RESULTS

Personality

Following the PCA, we retained three components from the OF and two from the MIS, which explained 58.0% and 58.6% of the total variance respectively. The first principal component from the open field (OF1) was characterized by behaviours of locomotion and exploration (Table 1), and will be referred to as activity hereafter. OF2 was characterized primarily by behaviours representing different aspects of exploration and may be a measure of impulsiveness, while OF3 was composed of behaviours related to the stress response of the animal (Archer 1973; Martin & Réale 2007). The first component of the MIS (MIS1) separated observations with high values of Attack Rate, Crouch Rate and time in the Front of the arena, from those with high Approach Latency, Attack Latency and time in the Back (Table 1). This component will be called aggressiveness hereafter. MIS2 separated Stretch and Attack Latency from time spent far from the mirror.

The three components of the OF and first of the MIS showed significant individual repeatability ranging from 37.4% to 68.2% (Table 1), but MIS2 was not significantly repeatable. Squirrels tended to be more active (OF1 more positive) with advancing date ($F_{1,53} = 5.8$, $P = 0.02$) but less active in the second trial than in the first ($F_{1,53} = 21.6$, $P < 0.0001$). OF2 was generally more negative in second trials (decrease in Jump/Hang, increase in Sniff/Hole/Chew; $F_{1,54} = 39.0$, $P < 0.0001$), and OF3 more negative with advancing date (decrease in Chew/Pellets, increase in Scan/Groom; $F_{1,54} = 28.2$, $P < 0.0001$). Squirrels also became less aggressive (MIS1 more negative) with advancing date ($F_{1,54} = 7.7$, $P = 0.008$). Both handling tests were significantly repeatable (struggle rate: repeatability = 35.7%, LRT = 33.98, $P < 0.0001$; breathing rate: repeatability = 42.4%, LRT = 38.80, $P < 0.0001$). There was a significant effect of observer for both tests (struggle rate: $F_{4,166} = 12.5$, $P < 0.0001$; breathing rate: $F_{3,171} = 23.2$, $P < 0.0001$), and breathing rate tended to increase with advancing date ($F_{1,171} = 51.6$, $P < 0.0001$).

There were significant correlations between activity and aggressiveness ($r = 0.54$, d.f. = 96, $P < 0.0001$), activity and struggle rate ($r = 0.42$, d.f. = 94, $P < 0.0001$), activity and breathing rate ($r = 0.23$, d.f. = 95, $P = 0.02$), aggressiveness and struggle rate ($r = 0.30$, d.f. = 94, $P = 0.003$) and struggle rate and breathing rate ($r = 0.53$, d.f. = 94, $P < 0.0001$). There was no correlation between aggressiveness and breathing rate ($r = 0.07$, d.f. = 95, $P = 0.49$).

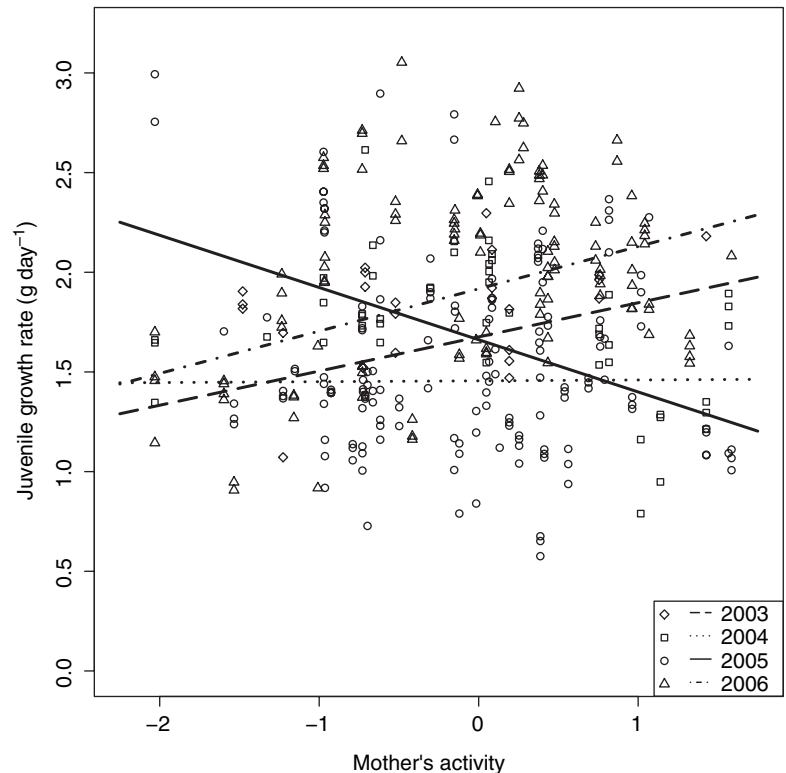


Figure 1 The nestling growth rate of North American red squirrels depends on the activity level of the mother in an open field behavioural trial and varies by year. See Table 2 for details of the linear mixed model.

None of these correlations was affected by the calculation of false discovery rates (Benjamini *et al.* 2001).

Maternal effects and fitness

There was no effect of activity or aggressiveness on parturition date or on litter size at birth (all removed with $P \geq 0.2$); the final model for parturition date included only year ($F_{3,73} = 28.2$, $P < 0.0001$), age ($F_{1,73} = 8.5$, $P = 0.005$) and grid ($F_{1,73} = 5.3$, $P = 0.02$), while only year significantly affected litter size (all years compared with 2005: 2003 = 1.03 ± 0.07 , $t_{92} = -1.73$, $P = 0.09$; 2004 = 0.99 ± 0.05 , $t_{92} = -3.14$, $P = 0.002$; 2005 = 1.16 ± 0.03 ; 2006 = 1.17 ± 0.04 , $t_{92} = 0.33$, $P = 0.74$).

The growth rates of juveniles were significantly affected by an interaction between female's activity and year, such that in some years the offspring of the most active females grew most quickly, while in other years they grew most slowly (Fig. 1; Table 2). There were also significant effects of parturition date, litter size at second measurement, and mass at first measurement. Female ID significantly improved the fit of the model (LRT = 178.1, d.f. = 1, $P < 0.0001$) and explained 70.2% of the remaining variance in growth rate, which includes heritability and maternal effects not included as fixed effects.

In 3 of 4 years, the probability of offspring survival to tagging decreased with increasing female aggressiveness, but

Table 2 Final linear mixed model* of offspring growth rate in the nest in North American red squirrels, with female identity as a random effect ($N = 348$ juveniles from 75 females)

	d.f.	F	P-value
Intercept	1, 264	432.75	< 0.0001
Year	3, 264	31.95	< 0.0001
Parturition date	1, 264	31.09	< 0.0001
Litter size at tagging	1, 264	43.66	< 0.0001
Mass at 1st marking	1, 264	7.21	0.008
OF1	1, 73	2.67	0.11
Year \times OF1†	3, 264	14.46	< 0.0001

OF1 is a synthetic variable representing the female's level of activity and exploration.

*Initial model also included as fixed effects grid, sex, mother's age, MIS1, year \times MIS1, and OF1 \times MIS1, which were removed during model selection with $P > 0.05$.

†Intercept \pm SE, slope \pm SE

2003 \times OF1: 1.68 ± 0.08 , 0.17 ± 0.10 .

2004 \times OF1: 1.46 ± 0.08 , 0.00 ± 0.10 .

2005 \times OF1: 1.49 ± 0.07 , -0.09 ± 0.10 .

2006 \times OF1: 1.92 ± 0.08 , 0.21 ± 0.10 .

the magnitude of the effect varied with year (Fig. 2a; Table 3). Juveniles born later in the season were more likely to survive to tagging. Female ID improved the fit of the model (LRT = 60.7, d.f. = 1, $P < 0.0001$) and explained 81.3% of the remaining variance in the final model.

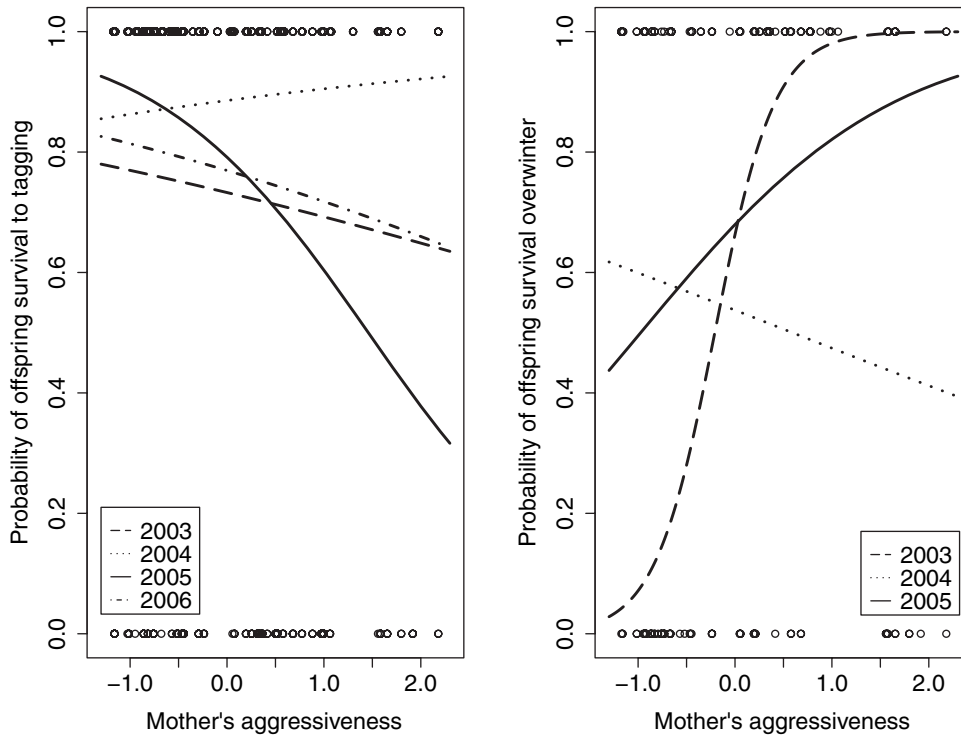


Figure 2 (a) The survival of juvenile North American red squirrels from birth until 25–30 days of age, shortly before emergence, depends on the aggressiveness of their mother and varies by year. (b) The overwinter survival of juveniles from weaning until 1 May of the following year also depends on the mother’s aggressiveness and varies by year. See Tables 3 and 4 for details of the models.

In 2003 and 2005, the offspring of the most aggressive females were most likely to survive the winter, while in 2004 they were least likely to survive (Fig. 2b; Table 4). Juveniles who received a territory from their mother had a higher chance of survival (marginally), as did juveniles born earlier in the year. All variables that remained in the final GLM were also significant in the GLMM. Female ID explained 0% of the remaining variance in the GLMM and did not improve the fit of the model (LRT = 0, d.f. = 1, $P = 1$), so we present the GLM as the final model (Table 4). A female’s personality did not affect her tendency to bequeath, but the probability of bequeathal increased with the number of juveniles successfully weaned (0.98 ± 0.40 , d.f. = 17, $t = 2.46$, $P = 0.02$).

DISCUSSION

A female red squirrel’s personality is correlated with the growth rates and survival of her offspring both in the nest and through their first winter, suggesting that personality may influence offspring phenotype and fitness. Variation in personality in this population could be maintained by opposing selection pressures at several levels. Environmental heterogeneity, such as temporally fluctuating food abundance because of mast seeding of the white spruce

Table 3 Final generalized linear mixed model* of juvenile survival in the nest (from shortly after birth until shortly before emergence) for North American red squirrels, with female identity as a random effect ($N = 517$ juveniles from 79 females)

	d.f.	<i>t</i>	<i>P</i> -value
Intercept	431	4.95	< 0.0001
2003	431	−0.76	0.45
2004	431	1.87	0.06
2006	431	−0.52	0.60
Parturition date	431	8.17	< 0.0001
MIS1	77	−2.98	< 0.0001
2003 × MIS1†	431	1.64	0.10
2004 × MIS1	431	2.58	0.01
2006 × MIS1	431	2.19	0.03

MIS1 is a synthetic variable representing the female’s aggressiveness.

*Initial model also included as fixed effects: grid, litter size at birth, mother’s age, juvenile sex, mass at first measurement, OF1, year × OF1, and OF1 × MIS1, and these variables were removed during model selection with $P > 0.05$.

†Intercept ± SE, slope ± SE

2003 × MIS1: 1.01 ± 0.43 , -0.20 ± 0.44 .

2004 × MIS1: 2.05 ± 0.38 , 0.20 ± 0.44 .

2005 × MIS1: 1.34 ± 0.27 , -0.92 ± 0.31 .

2006 × MIS1: 1.40 ± 0.25 , -0.28 ± 0.29 .

Table 4 Final generalized linear model* of juvenile overwinter survival in North American red squirrels ($N = 124$ juveniles)

	LR χ^2	d.f.	<i>P</i> -value
Year	0.49	2	0.78
Parturition date	6.31	1	0.01
MIS1	5.53	1	0.02
Bequeathed	4.39	1	0.04
Year \times MIS1†	8.39	2	0.02

Female identity, when included as a random effect in a GLMM, explained 0% of the variation and is therefore not included in this model. MIS1 is a synthetic variable representing the female's aggressiveness, and 'bequeathed' indicates that the juvenile was given a territory by its mother.

*Initial model also included as fixed effects: grid, juvenile sex, mother's age, OF1, year \times OF1, and OF1 \times MIS1, and these variables were removed during stepwise backwards elimination model selection with $P > 0.05$.

†Intercept \pm SE, slope \pm SE

2003 \times MIS1: 0.67 ± 0.86 , 3.24 ± 1.49 .

2004 \times MIS1: 0.15 ± 0.94 , -0.25 ± 1.56 .

2005 \times MIS1: 0.75 ± 0.86 , 0.77 ± 1.52 .

(Boutin *et al.* 2006; LaMontagne & Boutin 2007), may favour different values of personality traits in different years, and accordingly, the magnitude and direction of the correlations among personality and fitness traits are not consistent, in some cases reversing between years. Selection pressures also depend on the particular life-history stage and personality trait in question; while there is no effect of a female's personality on her parturition date or litter size, her offsprings' growth in the nest is affected by her activity, while their survival to tagging and overwinter are influenced by her aggressiveness. Selection pressures also appear to vary in direction or magnitude at different times during offspring development: the aggressiveness of a female can affect the survival of her offspring differently from birth to tagging than it does from weaning to spring (Fig. 2). Given the numerous opposing selection pressures, there is not one 'best' personality that leads to the highest fitness in all conditions, and balancing selection may therefore favour the maintenance of variation in these traits (Schluter *et al.* 1991; Sih *et al.* 2004; Penke *et al.* 2007). Furthermore, recent theoretical models have suggested that under variable food conditions, the involvement of personality traits in life history tradeoffs may lead to the maintenance of individual differences in personality (Stamps 2007; Wolf *et al.* 2007).

Red squirrels show consistent individual behavioural differences, and the most active squirrels also tend to be the most aggressive, to struggle the most, and to have the highest breathing rate during handling. These phenotypic correlations among personality traits are typical of the

proactive-reactive behavioural syndrome observed in other animals (Koolhaas *et al.* 1999; Sih *et al.* 2004), and have been found to be linked to physiological and neuroendocrine differences in rodents, such as plasma concentrations of adrenaline, noradrenaline and corticosterone (Koolhaas *et al.* 1999; Groothuis & Carere 2005). Although we do not have estimates of the genetic correlations, this may indicate that these traits are not evolutionarily independent.

The activity of a female affected the growth rate of her offspring, but the direction of the effect depended on the year. In 2003 and 2006, more active females had faster-growing offspring, in 2005 they were slower-growing, and in 2004 there was no effect. This may be a result of yearly differences in food availability. Both the current year's and the previous year's cone abundance have significant effects on juvenile growth rates (McAdam & Boutin 2003a). The average number of cones per tree on the two control grids combined was 84 in 2002, 17 in 2003, 24 in 2004, 502 in 2005 and two in 2006. The 2003 and 2006 breeding seasons, for which there were positive correlations between female activity and juvenile growth rate, followed the years with the highest cone numbers in the time period of this study, while 2005, in which there was a negative correlation, followed two successive years of very low cone numbers. Active females may therefore produce high juvenile growth rates in good conditions, but low growth rates in poor conditions. This could result from genetic differences in resource acquisition ability (including obtaining, processing, and transforming resources to usable energy) if high acquisition ability is costly (Reznick *et al.* 2000), such as by requiring resources to be abundant for success (Tessier *et al.* 2000). This could mean that active squirrels can acquire more resources and therefore have more energy to allocate to reproduction, as well as other aspects of life-history, relative to less active squirrels, but only when resources are abundant. When resources are scarce, they may be unable to deplete available resources to as low a level as less active squirrels [as in high vs. low acquisition *Daphnia* species (Tessier *et al.* 2000), and fast vs. slow exploring great tits (reviewed in Groothuis & Carere 2005)], leading to the observed pattern of variation in juvenile growth rates. Correspondingly, McAdam & Boutin (2003a) reported a large decrease in maternal effects on juvenile growth rates with food supplementation in this population, and suggested that even in very high natural food conditions, the ability of a female to acquire resources was a source of significant variation. In this study, we did not detect an effect of food supplementation in years of high natural food abundance. However, unpredictable mast seeding of white spruce may lead to balancing selection on activity in females due to differences in juvenile growth rates resulting from differences in the acquisition and allocation of resources among individuals. Strong inference regarding the link between

food abundance and the personality-fitness relationship would only be possible by accumulating data over multiple years with varying food conditions.

The survival of juveniles in the nest depends on the aggressiveness of their mother but not her activity. There is no clear relationship with food resources, as increasing aggressiveness corresponded to a higher probability of juvenile mortality in the nest in the year following both the smallest and the largest cone crop (2005 and 2006). These survival differences may result from other environmental effects that we did not measure in this study, or they could be because of differences in maternal style. If aggressive females provide less care or less milk to the litter relative to its needs, there may be greater competition for resources within the nest leading to greater mortality. Although aggressive female house mice spend more time nursing and grooming their pups, their offspring do not grow faster (Benus & Röndigs 1996). The authors suggest that time spent nursing may not be a reliable indication of milk transfer, or that the offspring of aggressive females may have higher metabolic rates due to higher testosterone levels, necessitating a greater quantity of milk (Benus & Röndigs 1996; Tobler *et al.* 2007). Female rhesus macaques with 5-HIAA concentrations indicative of high aggression and low sociability have higher rates of fetal and infant death despite being very protective of their offspring (Westergaard *et al.* 2003; Cleveland *et al.* 2004). Aggressive male western bluebirds feed their mates less frequently during incubation (Duckworth 2006), and male pied flycatchers (*Ficedula hypoleuca*) with experimentally increased testosterone show increased courtship and territorial activities and reduced feeding of nestlings (Silverin 1980), leading to lower fledging success in both cases. Aggressiveness is therefore associated with reduced juvenile survival in a number of species. However, in the current study, that appears to be true only in certain years, and the mechanism of the association remains unclear.

The overwinter survival of juveniles was also affected by the aggressiveness of their mother. The offspring of more aggressive females were more likely to survive the winter following the 2003 and 2005 breeding seasons, but less likely to survive following the 2004 breeding season, independently of their birth date and of whether they were bequeathed a territory or secured one independently. Similarly to juvenile survival in the nest, there is no clear relationship with food availability, but the heritability of personality or maternal effects could be important. If personality has a significant heritable component, then the offspring of aggressive females may survive better in some years because they themselves are more aggressive, such as by allowing them to compete more effectively for territories or food resources. However, this may also depend on a variety of other factors, such as population density.

If aggressive juvenile squirrels have higher testosterone concentrations, then they may also have higher metabolic rates (Tobler *et al.* 2007), which could hinder their survival when food is scarce and favour it when food is abundant, especially if there are also differences in resource acquisition ability as discussed previously (Reznick *et al.* 2000). A female's aggressiveness could also lead to maternal effects that influence juvenile overwinter survival; it has previously been demonstrated in this population that maternal nutrition prior to juvenile emergence affects juvenile overwinter survival, independently of the juvenile's body size and territory quality (Kerr *et al.* 2007). Nutritional factors or differences in maternal behaviour that are related to aggressiveness could also lead to persistent maternal effects to influence juvenile overwinter survival in this study. The relative importance of the aggressiveness of the offspring and that of the mother cannot be disentangled at this time, but in any case, the favoured maternal phenotype changes from year to year.

Personality influences life history in numerous ways in this population. Selection pressures on personality seem to act in different directions in different years and at different life history stages. Environmental heterogeneity, correlations among personality traits and trade-offs among their effects on life history may therefore be actively maintaining variation in personality via balancing selection, because there is no one value of personality that performs best in all conditions encountered.

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