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Personality is correlated with natal dispersal in North American red squirrels (*Tamiasciurus hudsonicus*)

Eve B. Cooper [a,*], **Ryan W. Taylor** [b], **Amanda D. Kelley** [c],
April Robin Martinig [c], **Stan Boutin** [c], **Murray M. Humphries** [d],
Ben Dantzer [e,f], **Jeffrey E. Lane** [g] **and Andrew G. McAdam** [a]

[a] Department of Integrative Biology, University of Guelph, Guelph, ON, Canada
[b] Department of Biology, Stanford University, Stanford, CA, USA
[c] Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada
[d] Department of Natural Resource Sciences, Macdonald Campus, McGill University, Ste-Anne-de-Bellevue, QC, Canada
[e] Department of Psychology, University of Michigan, Ann Arbor, MI, USA
[f] Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI, USA
[g] Department of Biology, University of Saskatchewan, Saskatoon, SK, Canada
*Corresponding author's e-mail address: eve.cooper@anu.edu.au

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Abstract

Individual natal dispersal behaviour is often difficult to predict as it can be influenced by multiple extrinsic and intrinsic factors. Individual differences in personality have been shown to be an important correlate of dispersal behaviour. However, the relationships between personality traits and dispersal are often inconsistent within and across studies and the causes of these discrepancies are often unknown. Here we sought to determine how individual differences in activity and aggression, as measured in an open-field trial, were related to natal dispersal distance in a wild population of North American red squirrels (*Tamiasciurus hudsonicus*). For 14 cohorts, while individual aggression consistently had no association with dispersal distance, the association between activity and dispersal fluctuated through time, mediated by population density. The environmental-dependence of the relationship between personality and dispersal in this population is indicative of the importance of considering external conditions when predicting dispersal behaviour.

Keywords

animal personality, behaviour, dispersal, natal dispersal, personality, population density, *Tamiasciurus hudsonicus*, temperament.

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1. Introduction

Natal dispersal, defined as movement by individuals from their birthplace to new locations, represents the mechanism by which individuals become spatially distributed within populations (Cote et al., 2010). As such, dispersal has important consequences for population structure, range expansion, and the maintenance of genetic diversity, which can facilitate the ability of populations to cope with both naturally fluctuating and climate-change-driven environmental changes (Stenseth & Lidicker, 1992; Clobert et al., 2009; Cote et al., 2010). The effects of both extrinsic and intrinsic factors on dispersal have been widely studied, including habitat heterogeneity, resource availability, population density, and individual morphology and physiology (Greenwood, 1980; Clobert et al., 2009).

More recently, the role of personality, the term used to describe consistent individual differences in behaviour (Réale et al., 2007; Wolf et al., 2007), has been explored in relation to its effect on dispersal outcomes (Cote et al., 2010). Individual personality can be measured using standardized behavioural tests (Svendsen & Armitage, 1973; Walsh & Cummins, 1976; Réale et al., 2007), and is often interpreted in the context of general axes of behavioural variation such as activity, exploration, boldness, aggression, and sociability (Bell, 2007; Réale et al., 2007). Across a variety of taxa, personality has a heritable genetic basis and individual fitness consequences, leading to the expectation that personality traits can evolve (Dingemanse et al., 2004; Sih et al., 2012; Taylor et al., 2012, 2014).

Although increased interest in personality has resulted in an increase in personality-dependent dispersal research, uncertainty still remains over how specific personality traits affect dispersal (Cote et al., 2010). For example, the effects of aggression on dispersal distance are variable depending on the environmental conditions and social structure of the population studied (Cote et al., 2010; Wey et al., 2015). In some species, less aggressive individuals were more likely to disperse (Schradin & Lamprecht, 2002; Pocock et al., 2005; Guerra & Pollack, 2010), while in other species, more aggressive individuals were more dispersive (Duckworth & Badyaev, 2007; Aguillon & Duckworth, 2015). In addition, within-population variability in the effects of aggression on dispersal have also been documented (Cote et al., 2010; Wey et al., 2015). For example, the direction of the effect of aggression on dispersal has been found to fluctuate with population density (Myers & Krebs, 1971) and the social landscape (Aguillon & Duckworth, 2015). Even for personalities directly related to higher levels of locomotion such as high activity and fast exploration (Réale et al., 2007), an association between these traits and dispersal behaviour has not been universally found. Although many studies have documented a positive relationship between activity or exploration and either dispersal propensity or dispersal distance (Dingemanse et al., 2003; Bonte et al., 2004; Bremner-Harrison et al., 2004; Debeffe et al., 2014; Zavorka et al., 2015), some studies have found no effect (Cote et al., 2011; Truhlar & Aldridge, 2015).

One potential reason for these discrepancies is that relatively few studies have considered possible interactions between extrinsic variables and personality when predicting dispersal behaviour (Spiegel et al., 2017). This overall lack of attention is surprising given the strong indications that many extrinsic variables, such as predation risk, density, and the social landscape should influence the relationship between personality and dispersal (Wey et al., 2015; Spiegel et al., 2017). For example, in western bluebirds (*Sialia mexicana*), the social landscape, measured through the personality of kin, mediates the relationship between individual aggression and natal dispersal distance (Aguillon & Duckworth, 2015). In mosquitofish (*Gambusia affinis*), increased predation risk negates the effect of sociability on dispersal propensity (Cote et al., 2013). Density had a significant effect on the relationship between sociality and dispersal propensity in common lizards (*Laerta vivipara*; Cote & Clobert, 2007), and on aggression and dispersal propensity in meadow voles (*Microtus pennsylvanicus*; Myers & Krebs, 1971), but density did not affect personality-dependent dispersal in mosquitofish (*Gambusia affinis*; Cote et al., 2011). Further investigation of how the relationships between personality and dispersal can change with extrinsic factors is needed if we are to understand how personality affects dispersal in complex ecological systems.

A population of North American red squirrels (*Tamiasciurus hudsonicus*, hereafter ‘red squirrels’) located in southwestern Yukon has been previously demonstrated to exhibit consistent individual differences in behaviour, or personality (Boon et al., 2007; Taylor et al., 2012; Kelley et al., 2015). Specifically, personality has been quantified using open field (OF) trials, and mirror-image stimulation (MIS) tests, which, respectively, provide repeatable measures of activity and aggression (Boon et al., 2007; Taylor et al., 2012; Kelley et al., 2015). Previous work has demonstrated that red squirrel personality affects the fitness of individuals (Boon et al., 2007, 2008; Taylor et al., 2014), and is heritable (Taylor et al., 2012). The OF test used to measure activity is similar to measures of exploration in other systems (e.g., Walsh & Cummins, 1976; Dingemanse et al., 2002; Careau et al., 2008; Martin & Réale, 2008). Additionally, in this population of red squirrels, activity exhibits a positive genetic correlation with aggression (Taylor et al., 2012), and activity measured in adults has been shown to be associated with trappability, considered a measure of risk-taking behaviour in ecologically realistic conditions (Boon et al., 2008). These findings are suggestive of a 'proactive-reactive' behavioural syndrome (Koolhaas et al., 1999).

Red squirrels typically disperse only once in their lifetimes, as juveniles, from their natal territory to their exclusive adult territory (but see Berteaux & Boutin, 2000; Lane et al., 2015). In this population, on average, 27% of juvenile red squirrels are non-dispersers and acquire their adult territory philopatrically as a result of their mother relinquishing a part, or all, of her territory to be used exclusively by the juvenile (Berteaux & Boutin, 2000). The remainder of surviving juveniles disperse and obtain a territory that is spatially distinct from their natal territory (Berteaux & Boutin, 2000). The distance from natal territory to adult territory, hereafter referred to as dispersal distance, is thus variable among individuals. Reported dispersal distances for red squirrels in this population range from 0 to 600 m (Berteaux & Boutin, 2000). Prior to weaning, both dispersing and philopatric juveniles make frequent forays away from their mother's territory, and these forays are thought to allow juveniles to scout for their own territory (Larsen & Boutin, 1994). Haughland & Larsen (2004) previously documented a positive relationship between dispersal distance and mean distance of exploratory forays. Kelley (2014) demonstrated that, in one cohort of red squirrels, maximum foray distance had a significant positive association with aggression, and a marginally significant association with activity. In an isolated red squirrel population (Mt. Graham red squirrels; *Tamiasciurus hudsonicus grahamensis*), Merrick & Koprowski (2017) found that activity measured in an OF trial was positively associated with dispersal distance, although the effect was only significant for males in this population. It is not clear, however, how naturally-occurring fluctuations in environmental conditions affect these personality-dispersal relationships.

Red squirrels in the southwestern Yukon provide an excellent opportunity to study how extrinsic environmental conditions affect relationships between personality and dispersal distance. Squirrels in this area experience a high degree of temporal variation in environmental conditions between cohorts caused by the episodic synchronized mast seed production of white spruce cones (*Picea glauca*; Lamontagne & Boutin, 2007), which is an important food item for red squirrels (Smith, 1968). In years when the white spruce trees mast, once every 2 to 7 years, trees produce orders of magnitude more cones, where generally only 10% of cones are harvested and cached by red squirrels (Fletcher et al., 2010). This is in contrast to non-masting years, in which annual white spruce cone production is often not enough to sustain all individuals, resulting in a food-limited population (Fletcher et al., 2010). This extreme fluctuation of food availability influences the propensity of mothers to bequeath their territory to offspring. When the current hoarded capital is low, and when the upcoming crop of cones is expected to be high, mothers are more likely to bequeath their territory to offspring (Berteaux & Boutin, 2000; Lane et al., 2015). Bequeathal directly affects juvenile dispersal propensity and overall dispersal distance. The availability of food resources is also mirrored by fluctuations in population density among cohorts (Dantzer et al., 2013). Differences in population density affect the availability of territories, and this causes shifts in the proportion of recruiting juveniles and subsequent survivorship between cohorts (McAdam & Boutin, 2003).

We hypothesized that if higher activity is indicative of higher levels of locomotion in the wild, and a more ‘proactive’ behavioural-syndrome, then highly active individuals should be more prone to longer exploratory forays whilst searching for available territory, and should thus be more likely to find and secure a territory farther from their natal site. From this hypothesis we predicted a positive association between activity and natal dispersal distance. Second, we hypothesized that increased aggression would positively influence a juvenile’s ability to compete with siblings to secure philopatric territories, while having less influence on a juvenile’s ability to secure dispersive territories. This is because successful recruitment through dispersive territory acquisition is heavily dependent on a prompt initial discovery of a recently vacated territory (Boutin & Price, 1993), and thus likely to be less reliant on a juvenile’s intrinsic competitive ability. From this, we predicted aggression would be positively associated with philopatry, and, as such, negatively associated with overall natal dispersal distance. Finally, we explored the interactive effects between environmental factors (food availability and population density) and personality on dispersal distance. To do so, we measured personality traits using standardized behavioural assays and quantified dispersal distance across 14 cohorts (between 1998 to 2014) that experienced large variation in spruce cone production and population density.

2. Methodology

2.1. Study population

We studied individually marked red squirrels on two 40-ha study areas in southwestern Yukon (61°N, 138°W). Although the population in these study areas has been tracked since 1987, personality measures were only available for a sample of individuals born between 1998 and 2014. Our dataset is thus restricted to these cohorts. The habitat in this area is Boreal forest, dominated primarily by white spruce (*P. glauca*), with a willow (*Salix* spp.) understory (Boutin et al., 1995).

We monitored red squirrels annually throughout their breeding season from March to August. All adult red squirrels occupy exclusive year-round territories, which have a typical radius of 30 ± 10 m in this population (La-Montagne et al., 2013). Territories contain a central hoard of white spruce cones (i.e., a 'midden'), used as their primary food cache (Smith 1968; Price et al., 1986; Steele, 1998), which remains in a stable location over time (Lamontagne et al., 2013). We trapped breeding females routinely on their territory using Tomahawk live-traps baited with peanut butter, and determined reproductive status by palpating the abdomen and assessing nipple condition. We fitted pregnant females with radio-collars (model PD-2C, 4 g, Holohil Systems, Carp, ON, Canada) to locate nest sites and temporarily removed and marked pups with unique ear tags so they could be followed throughout their lifetime.

We followed territorial movements of individuals born within the study sites from their birth to death using semi-annual territory censuses. During each census, we identified squirrels as territory owners through consistent observations of territorial behaviours, including 'rattle' vocalizations (Smith, 1978), and feeding, following established protocols (see Berteaux & Boutin, 2000; McAdam et al., 2007). We considered the point location of an individual's food cache as the centre point of that individual's territory.

We calculated dispersal distance as the linear distance, in meters, between the central food cache of an individual's natal territory, and the central food cache of their first exclusively defended adult territory. In addition to determining the dispersal distance of all individuals, we categorized each individual as either philopatric or dispersive. Since the average radius of a red squirrel territory in this population is approximately 30 m (Lamontagne et al., 2013), we classed individuals with dispersal distances under 30 m as philopatric, having been bequeathed at least some portion of their natal territory in acquiring their adult territory. Following from this, individuals with dispersal distances over 30 m were classed as dispersive. We still calculated dispersal distances for philopatric squirrels based on the distance between the food caches on their natal territory and their first adult territory. Thus, philopatric individuals had dispersal distances between 0 and 30 m, dependent on what proportion of their natal territory they were bequeathed, with a dispersal distance of 0 reflecting a full territory bequeathal.

The use of a 30 m cut-off for dispersal distance should reliably differentiate philopatric from dispersive individuals in our study population. In our sample, 16% ($N = 28$) of individuals dispersed within ± 10 m of this cut-off. Some of this fraction of individuals may have been inaccurately categorized if their natal territory was abnormal in size, or if the food cache of their natal or adult territory was not centrally located. However, since the majority of red squirrels within our sample can be accurately categorized as either philopatric or dispersive with high confidence, this cut-off is considered adequate and is used in further modelling of dispersal propensity.

2.2. Behavioural trials

We used behavioural trials to measure activity and aggression in red squirrels (see also Boon et al., 2007; Taylor et al., 2012; Kelley et al., 2015). To measure activity, we used an open field (OF) trial, which quantifies the behaviours of an individual in a standardized novel environment (Walsh & Cummins, 1976). To measure aggression, we used a mirror-image stimulation (MIS) trial, which assesses the behavioural response towards the individual's own reflection in a mirror (Svendsen & Armitage, 1973). We followed established scoring methodology protocols for the behavioural trails (Boon et al., 2007; Taylor et al., 2012). Briefly, the OF and MIS trials occurred consecutively within the same testing arena, a 60 (w) × 80 (l) × 50 (h) cm white box with 4 false exploratory holes. We trapped the target individuals on their territories using Tomahawk live-traps baited with peanut butter. Red squirrels underwent testing within two hours of capture. We erected the trial arena directly on the individual's territory. The OF trial began immediately upon release of the subject in the arena and lasted for 7.5 min. The MIS trial began subsequent to the OF trial, with the latter serving as a habituation period for the MIS trial. The 5-min MIS trial began once a mirror within the arena was revealed to the subject. The arena had a clear lid through which the trial was recorded with a digital video camera mounted approximately 60 cm above the arena.

We scored each individual through review of the taped trial, where the latency, proportion of time, and frequency of a range of behaviours were recorded using JWatcher Video 1.0 (Blumstein & Daniel, 2007). The OF trial considered the proportion of time and frequency of engagement in activities including walking, standing still, exploring false holes within the trial arena, and jumping rate. We used the MIS trial to measure the latency, proportion of time, and frequency of engagement in activities that are directly related to the presence of the mirror, including latency to approach the mirror, latency to attack the mirror, frequency of attacks towards the mirror, and time spent in an offensive crouching posture towards the mirror. For a full description of all the behaviours considered in the ethogram, see Boon et al. (2007). The trials were scored between the years 2005 and 2015 by 8 observers. Between-observer reliability in recording of each of the specific behaviours has been previously calculated by Taylor et al. (2012, their Table 2.1) for a larger dataset of trials that included all trials in this study except for those conducted in 2012 and 2015. Following Taylor et al. (2012), only behaviours with a between-observer reliability greater than 0.7 were used in further analysis.

The sample for this study consisted of all individuals who underwent OF and MIS trials as adults, and who were born on one of the two study areas. Each individual underwent 1 personality trial, resulting in a sample size of 176 individuals born between 1998 and 2014. Trials were conducted in the years 2005 ($N = 88$), 2008 ($N = 29$), 2009 ($N = 18$), 2010 ($N = 5$), 2012 ($N = 30$), and 2015 ($N = 6$).

Since OF and MIS trials were performed exclusively on adults, post-dispersal, it is important to consider the possibility that experiences during the process of settlement could have affected adult behaviour. In red squirrels, aggression remains stable through ontogeny, however, individual activity scores do shift, regressing towards the population mean between the juvenile and adult life-stages. As a result, low activity juveniles generally become more active as adults, while high activity juveniles generally become less active. However, the amount of change in activity through ontogeny is not large enough to change the individuals' rank-level of activity, relative to others within their age class (Kelley et al., 2015). This suggests that adult red squirrels scored as being more active relative to other adults were also most likely to have held a comparable ranking of activity relative to other juveniles when they were a juvenile. Since the relative activity score between individuals is comparable between the two life-stages, and we only compared adults to other adults in our models, any possible change in absolute values of activity level from pre- to post-dispersal are not expected to affect the interpretation of our findings.

One consequence of measuring personality post-settlement is that individuals that did not successfully acquire a territory could not be included in the sample. On average, only 34% of red squirrels born within the study site successfully recruit into the population in a given cohort (McAdam & Boutin, 2003). Dispersal events outside the study area are rare due to the large size of the study areas (40 ha each) relative to red squirrel dispersal distances, and the poor quality of the habitat surrounding the study areas (McAdam et al., 2007). As such, this low level of recruitment is primarily caused by a high mortality rate in juvenile red squirrels, and not by an inability to adequately capture juvenile dispersal events. Natural selective pressures occurring pre-dispersal result in adult personality measures representing a non-random sample of each cohort at the time they were dispersing as juveniles (Hadfield, 2008). If selection removes juveniles with specific levels of activity or aggression prior to recruitment, this will affect any association between personality and dispersal distance as they appear in our results. If extreme personalities are selected against pre-dispersal, the effect size of any association between personality and dispersal will be reduced among the group of successfully dispersed individuals. If intermediate personalities are selected against, the effect size of any association between personality and dispersal will be increased among the post-dispersal sample. Identifying the characteristics of pre-dispersal selection pressure would require personality measures to be taken on all juveniles before they disperse in addition to the post-dispersal measures. Unfortunately, in only one cohort of this population have personality trials been taken on juvenile red squirrels both pre- and post-dispersal (Kelley, 2014). In this cohort, less active and aggressive individuals were significantly more successful at acquiring territories (Kelley, 2014). However, since selection on red squirrel personality varies in direction and magnitude between cohorts (Taylor et al., 2014), we cannot assume that less active and aggressive individuals are consistently the most successful at acquiring territories. Thus, an important distinction in this study is that we are unable to interpret how personality is associated with all aspects of dispersal behaviour, and instead can only provide insight on the role of personality on overall dispersal outcome.

2.3. Statistical analysis

Due to the inter-correlation that results from measuring many mutually exclusive behaviours, the behaviours measured within the OF and MIS trials were not considered as unique traits. Instead, the duration and frequency of these behaviours were used collectively to represent the activity or aggression level of individuals. Following Taylor et al. (2012), a principal component analysis (PCA) was used to determine the dominant axes of behavioural variation and reduce the number of behaviours measured to two synthetic behavioural variables. Since the PCA was used to reduce dimensionality and redundancy and not as a statistical test, untransformed variables were used in the construction of the principal components (Timm, 2002). Using the trials of the 176 subjects in this study, principal component axes were calculated separately for the OF and MIS trials. The loadings produced by this dataset were found to be very similar to those in Taylor et al. (2012), which demonstrates that correlation matrices are consistent across years. Since our study could not include personality trials of individuals with unknown dispersal distances, the sample size of Taylor et al. (2012) was larger, having included trials from individuals born outside the study area. Due to the similarity in the loadings produced by both datasets, the loadings produced by the larger dataset encompassed in Taylor et al. (2012) were used in analysis. The first principal components for the OF trial (34.7% of variance explained) and the MIS trial (55.8% of variance explained) were used to calculate activity and aggression scores respectively, for each individual within this study. This methodology is consistent with Taylor et al. (2014).

We fitted a linear mixed-effects model to determine the effect of behaviour on dispersal distance. Since the distribution of dispersal distances was left-skewed, we log-transformed dispersal distances in order to meet the assumption of a normal distribution. The model contained dispersal distance as the dependent variable, and activity and aggression as fixed predictors of dispersal distance. We also fitted sex and study area as fixed effects to quantify sex-biased dispersal and to control for any differences between the two populations. As the birth year, or cohort, of study subjects ranged across 14 different years between 1998 and 2014, we added cohort to the model as a random intercept term to test if mean dispersal distance varied among years. Personality-dependent dispersal has been shown to be influenced by sex in a distinct subspecies of North American red squirrel (Merrick & Koprowski, 2017), and so we added interaction terms between sex and each personality trait separately to the model, but neither interaction was significant (sex(male) × activity: $\beta = -0.11 \pm 0.14$, df $= 162$, $t = -0.80$, $p = 0.43$; sex(male) × aggression $\beta = -0.18 \pm 0.14$, df $= 163$, $t = -1.30$, $p = 0.19$). Therefore, these interaction terms were subsequently removed from the model.

The random effect of cohort was significant in the initial model based on a log-likelihood ratio test ($\chi^2 = 7.39$, df $= 1$, $P < 0.01$). For this reason, we created two new models which fitted a random interaction between cohort and each personality trait. We used log-likelihood ratio tests again to determine whether these two random interaction effects (i.e., cohort × activity and cohort × aggression) significantly improved the fit of the model. The addition of the interaction between aggression and cohort as a random effect did not significantly improve the model ($\chi^2 = 3.33$, df $= 2, p = 0.19$), however the interaction between activity and cohort was significant ($\chi^2 = 7.50$, df $= 2$, $p = 0.02$). This result suggested that the effect of the activity trait on dispersal distance varied among cohorts, so we then sought to determine if external environmental factors that varied between cohorts were associated with this change in the effect of activity on dispersal distance. To achieve this, we fitted models including interaction terms between activity and different environmental factors individually. These variables were conspecific population density in the year of birth, cone index in the year of birth, and cone index in the year prior to birth. The conspecific population density of each study area in a given year was calculated as the number of individuals known to be alive per hectare within each study area, as observed during a two-week census period each spring. The cone index is a yearly estimate of white spruce cone production on each of the two study areas, measured each summer as the mean of a ln-transformed count of cones observed on a sample of trees spread across the study area (Lamontagne et al., 2005). Since white spruce cones form the bulk of red squirrels' diets (Smith, 1968), the cone index was considered a meaningful measure of food availability. The cone index in the year prior to birth is a measure of the amount of hoarded capital across the study area at the time of the juveniles' birth, as these cones will have been cached by red squirrels in the previous autumn. The cone index in the year of birth represents the amount of cones that will be available for subsequent hoarding in the coming autumn once the juveniles have dispersed. Both these cone indices are known to effect maternal bequeathal behaviour (Berteaux & Boutin, 2000; Lane et al., 2015), and through this effect, could potentially differentially affect juvenile dispersal propensity between cohorts.

In addition to fitting the effects of activity and aggression to overall dispersal distance as a continuous response variable, we also used a binomial generalized linear mixed-effects model in order to determine if activity and aggression levels affected the probability of an individual dispersing from their natal territory. In this model, the probability of dispersing was predicted by the red squirrel's activity, aggression, sex and study area as fixed effects, and the interaction between activity and cohort as a random effect (as above). Again, we added interactions between each personality trait and sex (as above), but these interactions were found to be non-significant (sex(male) × activity: $\beta = 0.10 \pm 0.24$, $z = 0.42$, $p = 0.68$; sex(male) × aggression: $\beta = 0.03 \pm 0.25$, $z = 0.12$, $p = 0.90$), and were subsequently removed from the final model.

We performed all analyses using R version 3.1.2 (R Core Team, 2014). Linear mixed models, and generalized linear mixed models were fitted using lme4 (Version 1.0-4; Bates et al., 2014) and the significance of fixed effects in these lmer models was assessed using the lmerTest (Version 2.0-30, Kuznetsova et al., 2016) package.

3. Results

Across the 14 cohorts, the average ± SD dispersal distance of red squirrels in this population was 102 ± 107 m ($N = 176$), with the maximum recorded distance being 566 m. Red squirrels that were categorized as philopatric, having settled between 0 and 30 m of the centre point of their natal territory, comprised 32% (56 of 176) of the total sample. Among the philopatric individuals, 19% ($N = 11$; 6% of total sample) had a natal dispersal distance of 0, having been fully bequeathed their natal territory by their mother.

In the overall model, a positive association between activity score and natal dispersal approached significance ($\beta = 0.14 \pm 0.08$, df = 171, $t =$

1.89, $p = 0.06$), while aggression was not associated with dispersal distance ($\beta = -0.01 \pm 0.07$, df = 168, $t = -0.19$, $p = 0.85$). Sex (male; $\beta = 0.10 \pm 0.22$, df = 168, $t = 0.44$, $p = 0.66$) and study area ($\beta = 0.10 \pm 0.21$, df = 169, $t = 0.46$, $p = 0.64$) were also not associated with dispersal distance in this model, and had no significant effect in any subsequent models either.

The significant improvement of the model with the inclusion of the interaction between activity and cohort (see Section 2.3, Statistical Analysis) suggested that the effect of activity on dispersal distance varied among cohorts. In order to determine what factors caused this variation in the activity-dispersal relationship between cohorts, we subsequently added interactions between several measurable external environmental factors and activity to the initial model of overall dispersal distance. Across the 14 cohorts and two study areas sampled, the population experienced large annual fluctuations in both food availability and population density. The cone index ranged over 2 orders of magnitude, with 80 individuals born during mast years (4 cohorts), and 96 individuals born during non-mast years (10 cohorts). Spring population densities ranged from 0.53 to 2.60 individuals/ha, with a median density of 1.19 individuals/ha. Despite the large differences observed in food availability among cohorts, there was no significant interaction between activity and cone index in the year of birth ($\beta = 0.06 \pm 0.05$, df = 169, $t = 1.42$, $p = 0.16$), or between activity and the cone index in the year prior to birth ($\beta = 0.06 \pm 0.09$, df = 140, $t = 0.73$, $p = 0.47$). In contrast, the interaction between activity and spring density in the year of birth was significant ($\beta = 0.35 \pm 0.17$, df = 163, $t = -2.02$, $p < 0.05$; Table 1; Figure 1), suggesting that the variable effect of activity on dispersal distance among cohorts was the result of an interaction with population density experienced during dispersal.

Population density in the year of birth affected the relationship between activity in the OF trial and natal dispersal distance. To further explore this pattern, we split the larger sample of 176 individuals into two groups — those born during a period of above median density ($N = 101$, cohorts = 4, density > 1.19 individuals/hectare), and those born during a period of below median density ($N = 75$, cohorts = 10, density < 1.19 individuals/hectare). Activity was significantly positively associated with natal dispersal distance in the low density cohorts ($\beta = 0.21 \pm 0.10$, df = 96, $t = 2.16$, $p = 0.03$; Table 2; Figure 1), but was not significant for individuals born in high-density cohorts ($\beta = 0.10 \pm 0.12$, df = 69, $t = 0.84$, $p = 0.40$; Table 2; Figure 1).

Table 1.
Fixed effects included in the modelling of natal dispersal distance of 176 red squirrels.

Fixed effect	Coefficient	df	*t*	*p*
Intercept*	3.76 ± 0.73	20	5.16	<0.001
Activity*	−0.01 ± 0.07	169	2.54	0.012
		166		
Aggression			−0.15	0.884
Sex (Male)	0.13 ± 0.23	166	0.59	0.553
Grid	0.07 ± 0.21	167	0.35	0.725
Density	0.06 ± 0.46	30	0.13	0.895
Activity × Density*	−0.35 ± 0.17	163	−2.02	0.045

The addition of the interaction between spring population density and activity score allowed the effect of activity on dispersal distance to vary dependent on the population density in the year of the individual's birth (cohort). The addition of this interaction term made activity significant in the model. Results are from a linear mixed-effects model ($N = 176$ individuals). Bolded variables are statistically significant ($p < 0.05$). Cohort ($N = 14$) was included as a random effect, with an intercept variance of 0.75 and residual variance of 1.71. A log-likelihood ratio test showed the random effect of cohort to be significant in this model ($\chi^2 = 11.30$, df = 1, $p < 0.001$).

* Significant effect ($p < 0.05$).

Aggression was not associated with dispersal distance for either low- or high-density cohorts.

The temporal fluctuation in the relationship between activity and dispersal distance was not caused by effects of activity on the propensity to disperse or remain philopatric. There was no effect of activity on the probability of dispersing ($\beta = 0.09 \pm 0.20$, $z = 0.45$, $p = 0.65$) and no interaction between activity and cohort on the propensity to disperse (likelihood ratio test: $\chi^2 = 2.16$, df = 2, $p = 0.34$). None of aggression ($\beta = 0.03 \pm 0.12$, $z = 0.22$, $p = 0.83$), sex (male; $\beta = 0.37 \pm 0.41$, $z = 0.90$, $p = 0.37$) or study area ($\beta = 0.51 \pm 0.39$, $z = 1.31$, $p = 0.19$) were significantly associated with probability of dispersal.

4. Discussion

More active red squirrels dispersed farther from their natal territory than less active red squirrels when population density was relatively low, but this relationship weakened at higher population densities. We found no evidence that the association between activity and dispersal distance was caused by

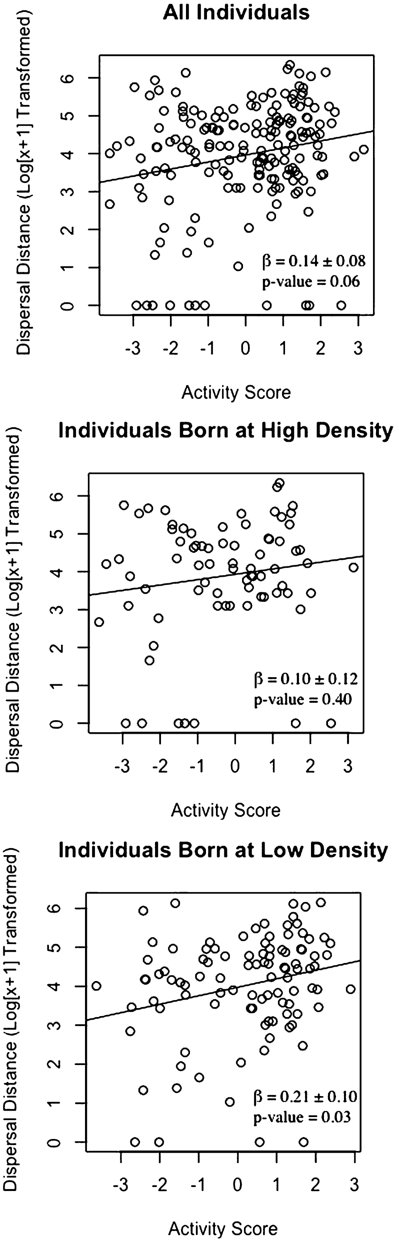

Figure 1. The effect of activity on log-transformed dispersal distance in a model containing (top panel) all individuals ($N = 176$) (centre panel) individuals born in a year of above median population density ($N = 101$) and (bottom panel) individuals born in a year of below median population density ($N = 75$).

Table 2.
Effect of activity and aggression on natal dispersal distance of red squirrels in three separate samples: all individuals (All), individuals born during a period above the median population density of 1.19 individuals/hectare (High density) and individuals born during a period below the median population density of 1.19 individuals/hectare (Low density).

Dataset	Coefficient	t	df	p
Activity				
All	0.14 ± 0.08	1.89	171	0.06
High density	0.10 ± 0.12	0.84	69	0.40
Low density	0.21 ± 0.10*	2.16	96	0.03
Aggression				
All	−0.01 ± 0.07	−0.19	168	0.85
High density	−0.12 ± 0.10	−1.20	66	0.24
Low density	0.04 ± 0.09	0.39	96	0.70

Coefficients are from linear mixed-effect models for each of the All ($N = 176$), High density ($N = 75$) and Low density ($N = 101$) datasets with dispersal distance as the dependent variable, and activity and aggression as two independent variables. Sex and study area were also included in the models and were non-significant ($p > 0.05$). Cohort was included as a random effect in all models.

* Significant value ($p < 0.05$).

an effect of activity on the probability of dispersal, indicating that higher activity is associated with longer settlement distances among non-philopatric juveniles. This finding suggests that the activity trait is positively related not only to increased locomotory behaviour in the wild, but also potentially related to exploratory behaviour through increased exploratory forays prior to dispersal, which are known to be correlated with final dispersal distances (Larsen & Boutin, 1994; Haughland & Larsen, 2004). Thus, the positive association between activity and dispersal is suggestive of a proactive-reactive behavioural syndrome (Koolhaas, 1999) in red squirrels, and increased activity is likely related to other ecologically-relevant ‘proactive’ behaviours including increased propensity to explore. Our results are consistent with most previous studies across a broad range of taxa (Cote et al., 2010) in addition to those of Merrick & Koprowski (2017), who identified a positive relationship between activity and dispersal in a mountainous subspecies of red squirrels.

In our model of natal dispersal distance, the significant interaction between activity and population density indicated that the positive effect of activity on dispersal distance was reduced as density of the surrounding population increased. When dispersal distance was modelled separately for individuals born in high-density and low-density cohorts, activity was significantly associated with dispersal distance at low density, but not high density. This difference in significance between the subsets was not just due to a difference in sample size; the effect size of activity was twice as large in low-density cohorts compared to high-density cohorts (Table 2, Figure 1). Since territorial space is limited by increasing density, and territory acquisition is necessary for overwinter survival in red squirrels (Larsen & Boutin, 1994), it is possible that increasing density forces juveniles to act less selectively in their territory choice (Larsen & Boutin, 1995), uncoupling the relationship between activity and dispersal distance at high densities. Many studies of personality-dependent dispersal in the wild focus on only one cohort for natal dispersal or one cross-section of the population for breeding dispersal. When the effects of personality on dispersal are studied within a limited temporal scope, interactions between personality and extrinsic conditions that change over time are less likely to be detected. More worrisome, if environmental conditions during the course of a study are atypical, this could result in spurious conclusions of the effects of personality on dispersal.

The second personality trait explored, aggression, was not associated with dispersal distance or dispersal propensity. This is contrary to our prediction that aggression would be negatively associated with dispersal propensity as a result of increased aggression improving a juvenile's ability to compete with siblings for philopatric territories. Although some previous studies have documented a significant association between aggression and either natal dispersal distance or propensity (Myers & Krebs, 1971; Pocock et al., 2005; Guerra & Pollack, 2010; Kelley, 2014; Aguillon & Duckworth, 2015), the direction and magnitude of the effect of aggression on dispersal distance and propensity is highly variable, dependent on the species studied (Cote et al., 2010). In red squirrels, instead of philopatric territory acquisition being dependent on a juvenile's competitive ability, as expressed through high aggression, factors extrinsic to the individual may have a greater influence. In line with this hypothesis are previous studies on maternal bequeathal of territories in red squirrels, where bequeathal events have been found to be associated most strongly with factors unrelated to the traits of the individual offspring — primarily the mother's age, resource availability in the given year, and the mother's territory quality (Berteaux & Boutin, 2000; Lane et al., 2015).

Alternatively, patterns between aggression and dispersal may have been be masked in our results if other unmeasured extrinsic factors that vary spatially within the study area have an interactive effect with aggression in influencing dispersal behaviour. The social environment is one such possible factor, and has been shown to influence dispersal in other species (Wey et al., 2015). If aggression is positively correlated to competitive ability in red squirrels, not only will an individual's own aggression impact their ability to acquire a philopatric territory, but the relative aggression of that individual's siblings will also likely have some influence. Further exploration of this theory is intriguing, and would require personality testing of complete litters in red squirrels in some future cohorts. Additionally, it's important to consider that if any changes in individual aggression from pre- to post-dispersal did occur, this would provide an alternate explanation for our inability to detect any meaningful relationship between aggression and dispersal.

The main finding of our study, that a relationship between activity and natal dispersal distance in red squirrels is mediated by population density, has important implications for our current understanding of how personality shapes dispersal more generally. It has been well established through evolutionary theory that differences in individual dispersal patterns often result from selection favouring dispersal behaviour that is conditional on external factors, as natural environments are typically heterogeneous (Johnson & Gaines, 1990). Additionally, it has been increasingly well documented in recent years that personality, as an intrinsic factor, can often have a significant effect on individual dispersal patterns as well (Clobert et al., 2009; Cote et al., 2010). Despite the apparent importance of both extrinsic environmental conditions and intrinsic personality traits in determining individual dispersal distance or propensity, the interaction between environmental factors and personality traits has rarely been empirically explored in relation to dispersal patterns (but see Myers & Krebs, 1971; Cote & Clobert, 2007; Cote et al., 2013; Aguillon & Duckworth, 2015). To our knowledge, a relationship between activity and dispersal, and an external environmental variable, in this case population density, has not previously been demonstrated.

Our study provides evidence of a naturally fluctuating environmental factor, population density, altering the effect of personality on dispersal distance. Although the natural complexity of ecological systems make it logistically impossible to account for every factor in any study of a wild population, our study highlights the importance of considering an adequate scale to study the effect of personality on dispersal. The scale of such studies should be large enough to include any reasonably regular natural fluctuations in environmental conditions, as these changes may mediate the effects of personality on dispersal, resulting in a more complex relationship between personality and dispersal than would otherwise be apparent. Longitudinal individual-based studies of wild populations are highly valuable in the study of personality-dependent dispersal because they have the power to address the complex predictors of dispersal in ecologically realistic conditions as these conditions naturally fluctuate through space and time.

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References

Aguillon, S. & Duckworth, R. (2015). Kin aggression and resource availability influence phenotype-dependent dispersal in a passerine bird. — Behav. Ecol. Sociobiol. 69: 625-633.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014). lme4: linear mixed-effects models using eigen and S4. — R package version 1.1-6. R Project for Statistical Computing, Vienna, available online at http://cran.r-project.org/package=lme4.

Bell, A.M. (2007). Future directions in behavioural syndromes research. — Proc. Roy. Soc. Lond. B: Biol. Sci. 274: 755-761.

Berteaux, D. & Boutin, S. (2000). Breeding dispersal in female North American red squirrels. — Ecology 81: 1311-1326.

Blumstein, D. & Daniel, J. (2007). Quantifying behaviour the Jwatcher Way. — Sinauer Associates, Sunderland, MA.

Bonte, D., Lens, L. & Maelfait, J. (2004). Lack of homeward orientation and increased mobility result in high emigration rates from low-quality fragments in a dune wolf spider. — J. Anim. Ecol. 73: 643-650.

Boon, A., Réale, D. & Boutin, S. (2007). The interaction between personality, offspring fitness and food abundance in North American red squirrels. — Ecol. Lett. 10: 1094-1104.

Boon, A., Réale, D. & Boutin, S. (2008). Personality, habitat use, and their consequences for survival in North American red squirrels *Tamiasciurus hudsonicus*. — Oikos 117: 1321-1328.

Boutin, S. & Price, K. (1993). Post-breeding dispersal by female red squirrels (*Tamiasciurus hudsonicus*): the effect of local vacancies. — Behav. Ecol. 4: 151-155.

Boutin, S., Krebs, C., Boonstra, R., Dale, M., Hannon, S., Martin, K., Sinclair, A., Smith, J., Turkington, R., Blower, M., Byrom, A., Doyle, F., Hik, D., Hofer, L., Hubbs, A., Karels, T., Murray, D., Nams, V., O'Donoghue, M., Rohner, C. & Schweiger, S. (1995). Population changes of the vertebrate community during a snowshoe hare cycle in Canada's boreal forest. — Oikos 74: 69-80.

Bremner-Harrison, S., Prodohl, P. & Elwood, R. (2004). Behavioural trait assessment as a release criterion: boldness predicts early death in a reintroduction programme of captive-bred Swift fox (*Vulpes velox*). — Anim. Conserv. 7: 313-320.

Careau, V., Thomas, D., Humphries, M.M. & Réale, D. (2008). Energy metabolism and animal personality. — Oikos 117: 641-653.

Clobert, J., Le Galliard, J., Cote, J., Meylan, S. & Massot, M. (2009). Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structure populations. — Ecol. Lett. 12: 197-209.

Cote, J. & Clobert, J. (2007). Social personalities influence natal dispersal in a lizard. — Proc. Roy. Soc. Lond. B: Biol. Sci. 383-390.

Cote, J., Clobert, J., Brodin, T., Fogarty, S. & Sih, A. (2010). Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structures populations. — Proc. Roy. Soc. Lond. B: Biol. Sci. 365: 4065-4076.

Cote, J., Fogarty, S., Brodin, T., Weinersmith, K. & Sih, A. (2011). Personality-dependent dispersal in the invasive mosquitofish: group composition matters. — Proc. Roy. Soc. Lond. B: Biol. Sci. 278: 1670-1678.

Cote, J., Fogarty, S., Tymen, B., Sih, A. & Brodin, T. (2013). Personality-dependent dispersal cancelled under predation risk. — Proc. Roy. Soc. Lond. B: Biol. Sci. 280: 2349-2358.

Dantzer, B., Newman, A.E.M., Bonnstra, R., Rupert, P., Boutin, S., Humphries, M.M. & McAdam, A.G. (2013). Density triggers maternal hormones that increase adaptive offspring growth in a wild mammal. — Science 340: 1215-1217.

Debeffe, L., Morellet, N., Bonnot, N., Gaillard, J., Cargnelutti, B., Vergeyden, H., Vanpe, A., Coulon, J., Clobert, R., Bon, A. & Hewison, J. (2014). The link between behavioural type and natal dispersal propensity reveals a dispersal syndrome in a large herbivore. — Proc. Roy. Soc. Lond. B: Biol. Sci. 281: 873-891.

Dingemanse, N., Both, C., Drent, P., Oers, K.V. & van Noordwijk, A. (2002). Repeatability and heritability of exploratory behaviour in great tits from the wild. — Anim. Behav. 64: 929-938.

Dingemanse, N., Both, C., van Noordwijk, A., Rutten, A. & Drent, P. (2003). Natal dispersal and personalities in Great Tits (*Parus major*). — Proc. Roy. Soc. Lond. B: Biol. Sci. 270: 741-747.

Dingemanse, N., Both, C., Drent, P. & Tinbergen, J. (2004). Fitness consequences of avian personalities in a fluctuating environment. — Proc. Roy. Soc. Lond. B: Biol. Sci. 271: 847-852.

Duckworth, R. & Badyaev, A. (2007). Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. — Proc. Natl. Acad. Sci. USA 104: 15017-15022.

Fletcher, Q.E., Boutin, S., Lane, J.E., Lamontagne, J.M., McAdam, A.G., Krebs, C.J. & Humphries, M.M. (2010). The functional response of a hoarding seed predator to mast seeding. — Ecology 91: 2673-2683.

Greenwood, P.J. (1980). Mating systems, philopatry and dispersal in birds and mammals. — Anim. Behav. 28: 1140-1162.

Guerra, P. & Pollack, G. (2010). Colonists and desperadoes: different fighting strategies in wing-dimorphic male Texas field crickets. — Anim. Behav. 79: 1087-1093.

Hadfield, J.D. (2008). Estimating evolutionary parameters when viability selection is operating. — Proc. Roy. Soc. Lond. B: Biol. Sci. 275: 723-734.

Haughland, D. & Larsen, K. (2004). Exploration correlates with settlement: red squirrel dispersal in contrasting habitats. — J. Anim. Ecol. 73: 1024-1034.

Johnson, M. & Gaines, M.L. (1990). Evolution of dispersal: theoretical models and empirical tests using birds and mammals. — Annu. Rev. Ecol. Evol. Syst. 21: 449-480.

Kelley, A. (2014). Development, stability, and consequence of personality in the juvenile red squirrel (Master's thesis). — Available online at https://era.library.ualberta.ca/files/t435gg614/Kelley_Amanda_D_201404_MSc.pdf.

Kelley, A., Humphries, M., McAdam, A. & Boutin, S. (2015). Changes in wild red squirrel personality across ontogeny: activity and aggression regress towards the mean. — Behaviour 152: 1291-1306.

Koolhaas, J.M., Korte, S.M., de Boer, S.F., van der Vegt, B.J., van Reenen, C.G., Hopster, H., de Jong, I.C., Ruis, M.A. & Blokhuis, H.J. (1999). Coping styles in animals: current status in behavior and stress-physiology. — Neurosci. Biobehav. Rev. 23: 925-935.

Kuznetsova, A., Brockhoff, P., Haubo, R. & Christensen, B. (2016). lmerTest: tests in linear mixed effects models. — R package version 2.0-30. R Project for Statistical Computing, Vienna, available online at http://cran.r-project.org/package=lmerTest.

Lamontagne, J.M. & Boutin, S. (2007). Local-scale synchrony and variability in mast seed production patterns of *Picea glauca*. — J. Ecol. 95: 991-1000.

Lamontagne, J.M., Peters, S. & Boutin, S. (2005). A visual index for estimating cone production for individual white spruce trees. — Can. J. For. Res. 35: 3020-3026.

Lamontagne, J.M., Williams, C.T., Donald, J.L., Humphries, M.M., McAdam, A.G. & Boutin, S. (2013). Linking intraspecific variation in territory size, cone supply, and survival of North American red squirrels. — J. Mammal 94: 1048-1058.

Lane, J., McAdam, A., Charmantier, A., Humphries, M., Coltman, D., Fletcher, Q., Gorrell, J. & Boutin, S. (2015). Post-weaning parental care increases fitness but is not heritable in North American red squirrels. — J. Evol. Biol. 28: 1203-1212.

Larsen, K.W. & Boutin, S. (1994). Movements, survival, and settlement of red squirrel (*Tamiasciurus hudsonicus*) offspring. — Ecology 75: 214-223.

Larsen, K.W. & Boutin, S. (1995). Exploring territory quality in the North American red squirrel through removal experiments. — Can. J. Zool. 73: 1115-1122.

Martin, J. & Réale, D. (2008). Temperament, risk assessment and habituation to novelty in eastern chipmunks, *Tamias striatus*. — Anim. Behav. 75: 309-318.

McAdam, A. & Boutin, S. (2003). Variation in viability selection among cohorts of juvenile red squirrels (*Tamiasciurus hudsonicus*). — Evolution 57: 1689-1697.

McAdam, A., Boutin, S., Skyes, A. & Humphries, M. (2007). Life histories of female red squirrels and their contributions to population growth and lifetime fitness. — Écoscience 14: 362-369.

Merrick, M.J. & Koprowski, J.L. (2017). Altered natal dispersal at the range periphery: the role of behaviour, resources, and maternal condition. — Ecol. Evol. 7: 58-72.

Myers, J. & Krebs, C. (1971). Genetic, behavioural, and reproductive attributes of dispersing field voles *Microtus pennsylvanicus* and *Microtus ochrogaster*. — Ecol. Monogr. 41: 53-78.

Pocok, M., Hauffe, H. & Searle, J. (2005). Dispersal in house mice. — Biol. J. Linn. Soc. 84: 565-583.

Price, K., Broughton, K., Boutin, S. & Sinclair, A.R.E. (1986). Territory size and ownership in red squirrels: response to removals. — Can. J. Zool. 64: 1144-1147.

R Core Team (2014). R: a language and environment for statistical computing. — R Foundation for Statistical Computing, Vienna, Austria, available online at http://www.R-project.org/.

Réale, D., Reader, S.M., Sol, D., Mcdougall, P.T. & Dingemanse, N.J. (2007). Integrating animal temperament within ecology and evolution. — Biol. Rev. 82: 291-318.

Schradin, C. & Lamprecht, J. (2002). Causes of female emigration the group living cichlid fish *Neolamprologus multifasciatus*. — Ethology 108: 237-248.

Sih, A., Cote, J., Evans, M. & Pruitt, J. (2012). Ecological implications of behavioural syndromes. — Ecol. Lett. 15: 278-289.

Smith, C.C. (1968). The adaptive nature of social organization in the genus of three squirrels *Tamiasciurus*. — Ecol. Monogr. 38: 31-64.

Smith, C.C. (1978). Structure and function of the vocalizations of tree squirrels (*Tamiasciurus*). — J. Mammal. 59: 793-808.

Spiegel, O., Leu, S.T., Bull, C.M. & Sih, A. (2017). What's your move? Movement as a link between personality and spatial dynamics in animal populations. — Ecol. Lett. 20: 3-18.

Steele, M.A. (1998). *Tamiasciurus hudsonicus*. — Mammal. Species 586: 1-9.

Stenseth, N.C. & Lidicker, W.Z. (1992). The genetic consequences of dispersal. — In: Animal dispersal: small mammals as a model (Stenseth, N.C. & Lidicker, W.Z., eds). Springer, Dordrecht, p. 37-55.

Svendsen, G. & Armitage, K. (1973). Mirror-image stimulation applied to field behavioural studies. — Ecology 54: 623-627.

Taylor, R., Boon, A., Dantzer, B., Réale, D., Humphries, M., Boutin, S., Gorrell, J.C., Coltman, D.W. & McAdam, A.G. (2012). Low heritabilities, but genetic and maternal correlations between red squirrel behaviours. — Evol. Biol. 25: 614-624.

Taylor, R., Boutin, S., Humphries, M. & McAdam, A. (2014). Selection on female behaviour fluctuates with offspring environment. — J. Evol. Biol. 27: 2308-2321.

Timm, N.H. (2002). Applied multivariate analysis. — Springer, New York, NY.

Truhlar, A. & Aldridge, D. (2015). Differences in behavioural traits between two potentially invasive amphipods, *Dikerogammarus villosus* and *Gammarus pulex*. — Biol. Invasions 17: 1569-1579.

Walsh, R.N. & Cummins, R.A. (1976). The open-field test: a critical review. — Psychol. Bull. 83: 482-504.

Wey, T.W., Spiegel, O., Montiglio, P.O. & Mabry, K.E. (2015). Natal dispersal in a social landscape: considering individual behavioral phenotypes and social environment in dispersal ecology. — Curr. Zool. 61: 543-556.

Wolf, M., van Doorn, G., Leimar, O. & Weissing, F.J. (2007). Life-history trade-offs favour the evolution of animal personalities. — Nature 447: 581-584.

Zavorka, L., Aldven, D., Naslund, J., Hojesjo, J. & Johnsson, J. (2015). Linking lab activity with growth and movement in the wild: explaining pace-of-life in a trout stream. — Behav. Ecol. 26: 877-884.