Development, Stability, and Consequences of Personality in the Juvenile Red Squirrel

By

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ABSTRACT

Animal personality – defined as consistent differences in behaviour among individuals – is a growing field in behavioural ecology due to its demonstrated effects on fitness. However, the ontogeny of personality under natural conditions remains relatively unexplored. In this thesis, I examine the development, stability, and consequences of juvenile personality in the North American red squirrel (*Tamiasciurus hudsonicus*). I demonstrate that 1) conditions in early life – particularly sibling relations – influence juvenile personality, 2) both aggression and activity change from juvenile to yearling stages, but activity maintains rank stability, 3) juveniles that gain territories early in the season do not experience a decrease in syndrome deviation, and 4) both dispersal activity and territory acquisition are influenced by juvenile aggression. These results suggest that environmental effects are important in shaping juvenile personality, and personality in turn influences a juvenile's ability to meet the challenges associated with natal dispersal.

PREFACE

Some of the research conducted for this thesis forms part of a research collaboration (The Kluane Red Squirrel Project), led by Stan Boutin at the University of Alberta, Andrew McAdam at the University of Guelph, and Murray Humphries at McGill University. Data from 2005 used in Chapter 4 were collected by Mark Andruskiuw and Adi Boon as part of their individual research projects. All analyses, literature review, and writing in all chapters are my original work.

The research project, of which this thesis is a part, received research ethics approval from the Animal Care and Use Committee: BIOSCIENCES for the University of Alberta, in accordance with the Canadian Council on Animal Care Guidelines and Policies (“effects of resource variation on behavioural and life history characteristics of red squirrels”, 679/03/13).

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CHAPTER 1: GENERAL INTRODUCTION

By its simplest definition, personality refers to differences in behaviours among individuals that are consistent over time or contexts (Reale et al. 2010). In humans, personality has been studied for at least a century, and it remains one of the most widely studied topics in psychology (Nettle and Penke 2010). The study of personality in animals, however, began much more recently: the first studies, in the field of comparative psychology, were conducted under controlled laboratory settings (Careau and Garland 2012), and within the last two decades, ecologists began to test for the prevalence and relevance of personality in wild populations (Sih et al. 2004a, Sih et al. 2004b, Dingemanse and Reale 2005, Reale et al. 2007). The delay in studying animal personality can be attributed to both a fear of anthropomorphism (Briffa and Weiss 2010, Trillmich and Hudson 2011), as well as differences in how questions are framed across disciplines (Nettle and Penke 2010). It is readily apparent that humans differ from each other, and we assume that these differences are important; in contrast, within-population variations in behaviour were traditionally considered by ecologists to be only nonadaptive noise around the mean (Dall et al. 2004, Wilson 1998, Nettle and Penke 2010). However, both laboratory and field studies have shown that animal personality has important consequences, at both the individual and population levels.

In wild populations, personality has been shown to have important fitness consequences (Smith and Blumstein 2007), and the heritability of personality has been a major driver in the surge of popularity of the field. However, direct genetic effects may only account for a small proportion of the variance in personality (Bell 2005, Taylor et al. 2012). Indeed, the range of phenotypic maternal influences on offspring behaviour suggests that genetic influences merit less emphasis than they are currently given (Groothuis and Maestripieri 2013). Because heritability estimates can vary across populations (Bell 2005), contexts (Sinn et al. 2006, Bell and Sih 2007), and ontogeny (Krueger et al. 2008, Haworth et al. 2010), there is a need to study what factors influence personality, and how it may change over time.

The maternal environment, which encompasses both dam-offspring interactions and sibling interactions, can have strong, long-lasting effects on offspring (Mousseau and Fox 1998, Lindstrom 1999), and may intuitively influence the development of personality. Juveniles are an important age class to study because if personality is not stable across ontogeny, the influences of early life variables may not be detectable. Additionally, juveniles may not inhabit the same social or ecological niche as adults; as such, they may need to exhibit different behaviours in order to navigate the unique challenges of juvenile life (Groothuis and Trillmich 2011). To date, most studies of the ontogeny of personality have been conducted in laboratories, where these challenges are lessened, making it difficult to infer ecological validity (Groothuis and Maestripieri 2013). Monitoring individuals throughout ontogeny in their natural environment is the only way to be certain of the effects of early life on personality, how personality changes as individuals mature, and importantly, the real-life consequences of personality. In this study, I use the North American red squirrel (*Tamiasciurus hudsonicus*) to investigate these questions.

The North American red squirrel (Tamiasciurus hudsonicus)

Red squirrels are small, asocial, semi-arboreal mammals (Gurnell 1984). Adults maintain permanent territories centered on a food cache (midden), and for most of the year, spend little time off of their territories (Gurnell 1984, McAdam et al. 2007, Rusch and Reeder 1978). Females are promiscuous, and are the sole care-takers of young. They give birth in the spring (March-May) and juveniles emerge from the nest once they are ~50 days old (Larsen and Boutin 1994, Stuart-Smith and Boutin 1995). Juveniles continue to nurse for up to three more weeks, and during this time, make forays into the surrounding habitat in search of a territory (Larsen and Boutin 1994). Juveniles typically disperse less than 100m from their natal territory (Berteaux and Boutin 2000); however, mortality is high, with on average less than 30% of juveniles surviving to the following spring (McAdam et al. 2007). Those that do not secure a midden before winter are unlikely to survive (Larsen and Boutin 1994).

The life history characteristics of the red squirrel make it an ideal animal for studying the ontogeny of personality under natural conditions. Reproductive females are easily to locate, and young may be removed from the nest for short periods with no risk of the mother abandoning them. Once emerged, juveniles often remain within the study area, making them relatively easy to trap and submit to personality trials. Additionally, the differences in environments experienced by juveniles and adults raise an interesting question with respect to the stability of personality across ontogeny. Juveniles must interact with their siblings and mother, gain familiarity with the landscape around them, and successfully locate and secure territory, which may require a different set of behaviours than that required for adult life.

Lastly, personality has been confirmed in this species; activity and aggression are repeatable and form a behavioural syndrome in adults (Boon et al. 2007, 2008, Taylor et al. 2012). Heritability of personality is low in red squirrels (0.08-0.12), and there is evidence that maternal effects may be influential (Taylor et al. 2012). Additionally, a mother's activity is correlated with her offspring's growth, and her aggression is correlated with their survival (Boon et al. 2007). However, personality in juveniles themselves has not been studied.

Thesis overview

In this thesis I investigate the ontogeny of personality in the red squirrel. In Chapter 2, I explore how both the shared and individual environments in the nest influence juvenile personality. In Chapter 3, I test how personality changes as juveniles mature and gain territories, which can shed light on how selection pressures vary across ontogeny. In Chapter 4, I examine the potential for how personality influences dispersal, survival, and territory acquisition. Finally, in Chapter 5, I provide general conclusions on my research, and suggest avenues for further work.

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CHAPTER 2: THE EFFECTS OF EARLY LIFE ON JUVENILE PERSONALITY

INTRODUCTION

Animal personality is defined as behavioural differences among individuals that are consistent over time or contexts (Reale et al. 2012, Wolf and Weissing 2012). Commonly studied personality traits include boldness, aggression, and activity/exploration; however, personality traits may also correlate with each other to form behavioural syndromes (Sih et al. 2004a). For example, bold individuals also tend to be more aggressive and active (Sih et al. 2004a). The fitness consequences of personality have been well documented (Smith and Blumstein 2007); however, how differences in personality arise is a relatively new area of study (Groothuis and Trillmich 2011).

Like human personality (Krueger et al. 2008), animal personality is influenced by both genes and the environment (Carere and Eens 2005, Groothuis and Carere 2005). Although the environment may influence personality at any point in ontogeny, early life experiences tend to have more pronounced effects (Curley and Branchi 2013). These variations in experience – from conception to weaning – may result in personality variation both within and across litters (Carere et al. 2005, Hudson et al. 2011). Within a litter, environmental influences can be divided into those that are shared, or common to all individuals in the litter – for example, litter size and birth date – and those that are individual, or unique to each offspring in the litter, such as relationships among siblings (Sulloway 2007, 2010). For example, among mammals, a mother influences the absolute amount of food her litter receives, but competition among siblings for milk and warm central positions in the huddle may influence growth rates relative to each other (Rodel et al. 2008a). These early differences in growth and development may be particularly influential on activity and aggression later in life.

Activity, though frequently used in personality research, is difficult to interpret; it may reflect an individual's nervousness, fear, or exploration tendency (Walsh and Cummins 1976, Hughes 1997, Stanford 2007). When paired with stress response, activity can be considered as part of a coping style (Koolhaas et al. 1999). Coping styles are categorized along a proactive-reactive axis, where proactive individuals exhibit a fight-or-flight response and reactive individuals exhibit a freezing response (Koolhaas et al. 1999). There is an indication that activity may be influenced by both shared and individual environmental effects in early life. More active individuals have been associated with smaller litter size (Dimitsantos et al. 2007), compromised immunity in early life (Butler et al. 2012), female-biased sex ratios (Naguib et al. 2011), and lower weights relative to siblings (Bautista et al. 2010).

Development of aggression may also be influenced by a range of shared and individual effects. In some species, high aggression is correlated with greater provisioning in early life (Carere et al. 2005, Andersson and Hoglund 2012) and earlier parturition dates (Rodel and von Holst 2009). An association with litter size has also been found, though results are inconsistent (D'Eath and Lawrence 2004, Rodel and von Holst 2009). Additionally, both stress hormones and pre-natal androgens may masculinize offspring and increase aggression (Ryan and Vandenbergh 2002, Uller 2006, Groothuis and Maestripieri 2013). One way to detect masculinization in mammals is to measure the anogenital distance (AGD); in rodents, masculinization results in a larger AGD (Ryan and Vandenbergh 2002, Monclus and Blumstein 2012). AGD has been connected to behaviour in adult life (Monclus et al. 2012), and ultimately, fitness (Monclus and Blumstein 2012).

Previous studies on shared and individual effects on personality have been carried out under laboratory (Hudson et al. 2011, Rodel and Meyer 2011) and semi-natural conditions (Carere et al. 2005, Rodel and von Holst 2009, Rodel and Monclus 2011). Although these studies are useful for illuminating the detailed mechanisms of personality development (Curley and Branchi 2013), field studies are necessary (Hudson et al. 2011) due to the effects that artificial selection may have on personality in captive animals. Additionally, *ad libitum* feeding and consistently warm conditions may significantly alter sibling interactions by reducing competition. Currently, little work has been done on juvenile personality in wild animals (but see Dingemanse et al. 2003, Cote and Clobert 2007), and development of personality under natural conditions remains largely unexplored (but see Petelle et al. 2013).

In this study, I tested for the presence of shared and individual effects on juvenile aggression and activity in the red squirrel (*Tamiasciurus hudsonicus*). Specifically, I studied the effects of the shared and individual environment on juvenile activity and aggression. I developed seven predictions based on studies conducted under both laboratory and semi-natural conditions. They are that higher aggression and activity would be correlated with 1) higher aggression and activity in the mother, 2) larger litter size, 3) increased proportion of male siblings, 4) earlier parturition date, 5) higher rate of motor development, 6) higher growth rate, and 7) larger anogenital distance. Predictions 1-4 involve only the shared maternal environment, whereas predictions 5-7 may follow from both shared and individual effects.

METHODS

Study population

This study was conducted in 2012 and 2013 as part of a long-term study on a wild population of red squirrels in the southwestern Yukon, Canada (61°N, 138°W). I trapped on two 40 hectare grids (KL and SU). A detailed description of the study and general methods can be found in McAdam et al. (2007).

Finding and marking litters

Females were trapped regularly to monitor reproductive status. Abdominal palpations and changes in mass were used to estimate parturition dates. Once females gave birth, they were trapped and fitted with radio collars to assist in nest location. Shortly after birth, pups were briefly removed from the nest to count, sex, and weigh them. Their ears were also notched so they could be identified at the second nest check. At Day 25, pups were again removed, re-weighed, and marked with permanent numbered ear tags. Anogenital distance (AGD) (Monclus and Blumstein 2012) and latency to falling in a hanging test (see below and Hilber and Caston 2001) were also measured.

Juvenile trapping

Squirrels were trapped with tomahawk traps in order to submit them to the personality trials. General trapping methods may be found in McAdam et al. (2007). In brief, we pre-baited natal middens with peanut butter several days prior to the predicted emergence date of juveniles from the nest. We predicted emergence date as 50 days after the pups were born. We began trapping on the predicted emergence date and continued to trap intensively (every 1-3 days) until either all emerged juveniles had been captured, or we failed to observe any juveniles on the territory for >3 days.

Open field (OF) and Mirror Image Stimulation (MIS) trials

Following Boon et al. (2007), I conducted two trials to measure personality. The first, an open-field (OF) trial, was used to measure activity in response to a novel environment (Hall 1936, Martin and Réale 2008). The second, a mirror-image stimulation (MIS) trial, was used to assess aggression towards conspecifics (Svendsen and Armitage 1973). The testing arena was a 60 x 50 x 80cm box made of white corrugated plastic with a clear acrylic lid through which the behaviours were recorded with a digital camcorder (Canon Legria FS306). Four blind holes in the floor allowed the subject further opportunity to explore. A 35 x 40cm mirror on one side of the arena was exposed during the MIS trial.

I conducted both trials in the same session and in the same arena, with the OF trial also serving as a habituation period for the MIS trial (Svendsen and Armitage 1973). Subjects were placed in the arena directly from the handling bag, and the OF trial began as soon as the door to the arena was closed. After 7.5 minutes, a mirror was exposed, and the 5 minute MIS trial began once the subject first saw its reflection. After the session, the squirrel was released, the number of feces in the arena were counted, and the arena was cleaned with unscented disinfectant wipes (Wet Ones). Methods are also described by Boon et al. (2007) and Taylor et al. (2012).

Although multiple assays in quick succession may increase habituation (Dingemanse et al. 2012), I chose to use a minimum trial interval of two days in an effort to obtain multiple trials per individual. There is only a small window for obtaining repeat measurements, as juvenile red squirrels experience high mortality (Boutin and Larsen 1993, Steele 1998, McAdam et al. 2007), usually remain on midden for only 3 weeks post-emergence (Stuart-Smith and Boutin 1995), and are not habituated to traps, making them more difficult to capture (ADK, personal observation). Mothers were submitted to the same trials as juveniles. Each mother was tested once, and all personality measures on mothers were taken after their pups were 25 days old.

Synthesis of aggression and activity variables

I scored all videos using Cowlog software (Hanninen and Pastell 2009). I only included behaviours with high inter-observer repeatability (Taylor et al. 2012, Table 2.1). I then used principal components analysis to reduce the number of dependent variables for each personality trait. For all statistical analyses, I used only the first principal component.

For juvenile personality scores, I used linear mixed models (LMM) to take into account non-target influences on personality, as well as generate a single OF and MIS score for each individual (Martin and Réale 2008). I also included (Age|ID) as a random term (Martin et al. 2011), which did not result in significantly different estimates from simple LMMs (r=0.98). However, I retained it in the model, as it could help explain additional variance in personality. Following Nakagawa and Schielzeth (2010), I retained individuals with single measures in the model. The fixed effects in the initial model included age, trial date, trial time, trial number, time between trials, parturition date, and study site. Fixed effects were removed by backwards AIC selection; forward selection yielded the same results. The final model for activity included (Age|ID) as a random effect and time between trials as a fixed effect. The final model for aggression included only the (Age|ID) effect. From the pruned models, I used the ranef() function to obtain single OF and MIS scores for each individual. All statistical analyses were performed in R version 3.0.2 with the lme4 package (Bates et al. 2012).

I calculated within-year repeatability as the proportion of the model variance explained by the individual term (Lessells and Boag 1987) and followed Nakagawa and Shielzeth (2010) to calculate repeatability confidence intervals.

Shared environment

I used linear mixed models to test the influence of shared effects on juvenile activity and aggression. I used separate models for activity and aggression; each included the mother's activity and aggression, parturition date, sex ratio, litter size, sex, and grid as fixed effects, and litter ID as a random effect. I removed non-significant terms using backwards selection with a p value cutoff of 0.25. I also tested for the influence of the mother's personality on parturition date, sex ratio, and litter size using linear regression. I included both linear and quadratic forms of the mother's OF and MIS in each model. In all linear mixed models, the significance of parameters was estimated by comparisons to a probability distribution obtained by 10 000 Markov Chain Monte Carlo simulations using pvals.fnc() from the R package LanguageR (Baayen et al. 2008).

Motor development and growth

I quantified motor development using a hanging test (e.g. Hilber and Caston 2001). For the test, pups were held near a 30cm length of 4mm doweling suspended ~30cm above soft fabric. Pups instinctively reached out, and once they had gripped the doweling with their forepaws, they were released and the observer measured latency to falling. I used 60 seconds as a cutoff, based on earlier tests. I rationalized that this test of muscular strength would indicate relative development and ability of pups to gain preferred positions in the litter huddle (Hudson et al. 2011).

I calculated growth in body weight (hereafter referred to as growth) as the difference between weights at parturition and Day 25 (measured as grams per day). As not all nest checks were completed at the same time, I limited the data to offspring with an initial mass <50g, a final mass <100g, and more than 5 days between the two measures, following McAdam et al. (2003a).

To compare maternal (shared) and sibling (individual) effects on both motor development and growth rate, I used a linear regression model that included only the litter mean and individual deviations from the mean. I use the term absolute growth to refer to untransformed individual growth, and the term relative growth to refer to individual growth rate minus the average growth rate for the litter. The latter provides a measure of growth and development relative to siblings only. Although there are no differences in absolute growth rate between the sexes (t_{155}= 0.71, p=0.48), females grow more slowly than their male siblings (t_{153}=2.15, p=0.033); as such, I tested growth rates in males and females separately. There were no sex differences in either absolute ($t_{149.02}$=0.59, p=0.56) or relative ($t_{149.22}$=0.54, p=0.59) hanging times, so I pooled sexes in all analyses.

Anogenital Distance

Anogenital distance was measured with calipers as the distance between the anus and genital papilla. To assess the strength of AGD as a measure of masculinization, I first ran a linear mixed effects model with proportion of male siblings, parturition date, and the mother's aggression as fixed effects, and litter as a random effect. I also included weight as a fixed effect to account for the influence of body size on AGD (Ryan and Vandenbergh 2002). Since the effects of masculinization may differ between the sexes, I separated the sexes for all analyses. I used backwards selection to fit the best model. To test the effects of AGD on juvenile OF and MIS, I used simple linear regressions with weight as an additional fixed effect to control for confounding effects of size on AGD.

RESULTS

I monitored 224 pups from 73 litters. Partial litter mortality was observed in 40% of litters (29), and in 33% of litters (24) no pups were observed to have emerged, indicating complete litter loss. I was able to capture 72% of emerged juveniles (69/96). Although age at first capture was highly variable (50-114 days old), almost half were first caught within ten days of emergence (39/69). In total, I tested personality in 44 mothers and 67 post-emergence juveniles. I had the full complement of data for 44 juveniles.

Principal Component Analysis

The first principal components explained 35% of the variation in activity and 53% of the variation in aggression (Table 2.2). Both components were bipolar; that is, they included coefficients with negative and positive signs (Martin and Réale 2008). For activity, walking and jumping were opposed by remaining still, whereas for aggression, time spent in the third of the arena closest to the mirror was opposed by time spent in the farthest third, latency to approach, and latency to attack. Individuals tended to either immediately attempt escape (walking, jumping), or initially remain still, and then slowly explore the arena (descriptive statistics: Table 2.3). This type of response is consistent with proactive-reactive coping styles (Koolhaas et al. 1999, Koolhaas et al. 2010), and is similar to PCA results from adults in this population (Boon et al. 2007). Both aggression and activity displayed moderate within-season repeatability (MIS: 0.37 (95% CI: 0.36-0.38), OF: 0.55 (95% CI: 0.39-0.71)), which is consistent with repeatability estimates from other studies (Bell et al. 2009).

Strictly shared effects

There was little evidence for a strong connection between elements of the shared environment and juvenile personality. Of the other shared effects I tested – the mother's activity and aggression, parturition date, sex ratio, and litter size – only the latter influenced juvenile activity (coef: -0.49, p=0.0008), and no shared effects significantly influenced juvenile aggression (Table 2.4). Testing the effects of the mother's personality on the shared environment also yielded few connections. Less active mothers give birth earlier in the season (coef: -2.85, p=0.020); however, there was no influence of a mother's personality on either the sex ratio or size of her litter (all *p*>>0.05).

Motor development and growth

The final mixed model used to explain hanging time included grid, age, parturition date, and litter size, and all but the latter variable were significant (Table 2.5). Pups from the SU grid were able to hang on 41% longer than pups on the KL grid (SU: 29.9 ± 1.97, KL: 17.5 ± 3.25). Additionally, pups that were older at the time of the test and those that were born later in the season had longer hanging times. However, there was no direct relationship between mass and latency to falling in the hanging test (r_τ=0.043, p=0.43).

Neither absolute nor relative hanging times were correlated with activity post-emergence ($F_{1,53}$=2.96, p=0.091; Table 2.6). Growth rates were linked to activity, but not aggression (Table 2.7); in females only, both absolute and relative growth rates were positively correlated with activity.

Anogenital distance

I found no link between male AGD and exposure to any of the potential sources of prenatal androgens (Table 2.8). However, in females, AGD was significantly affected by parturition date: females born earlier in the season had larger AGDs (coef: -0.0012, p = 0.0071; Table 2.8). And counter-intuitively, females in litters with a smaller proportion of males also had larger AGDs (coef: -0.071, p = 0.027). AGD was not correlated with aggression in either sex (F: r=-0.058, p=0.75; M: r=0.25, p=0.29). In females only, activity was marginally negatively correlated with AGD (F: r=-0.34, p=0.055; M: r=0.18, p=0.46).

DISCUSSION

Shared environment effects

Animal personality research has placed a great deal of emphasis on the genetic component of personality and parent-offspring resemblance (Sih et al. 2004a, Sih et al. 2004b). Even if heritability is low, as is the case with the red squirrel (Taylor et al. 2012), offspring may develop a phenotypic resemblance to their parent(s). For example, in zebra finches (*Taeniopygia guttata*), offspring have similar exploration rates to their foster parents' offspring (Schuett et al. 2013). However, I found no correlations between mother and offspring personality. One explanation is that juveniles may yet come to resemble their parents. Personality is not fixed in juvenile red squirrels (Chapter 2), and as juveniles mature, they may become better able to select or construct environments that favor their personalities (Stamps and Groothuis 2010a, Stamps and Groothuis 2010b, Groothuis and Trillmich 2011). These genotype-environment effects (Scarr and McCartney 1983) may thus result in increased heritability estimates over the course of ontogeny (Krueger et al. 2008). Alternately, personality in this species may be influenced to a larger extent by environmental effects rather than genetic ones.

Although there were no apparent similarities between mother and offspring personality, the mother's personality does influence her offspring via parturition date: more active mothers gave birth later in the season. Red squirrels born earlier in the season grow faster (McAdam et al. 2002) and are more likely to survive (McAdam and Boutin 2003b, Reale et al. 2003), so a mother's low activity may benefit offspring indirectly. However, this relationship may not be consistent over time: Boon et al. (2007), studying the same red squirrel population, found that the mother's activity was correlated with offspring growth and her aggressiveness was correlated with offspring survival, but that the sign and the magnitude of the relationships varied across years. Additionally, Boon et al. (2007) found no relationship between a female's parturition date and her personality, supporting the idea that the nature of personality relationships may fluctuate along with resource availability in this system.

Aside from the indirect influences of the mother's personality, the only other significant shared environmental effect was litter size: offspring from smaller litters were more active post-emergence. Because pups from smaller litters grow faster (McAdam et al. 2002), the relationship between activity and litter size may be an indirect result of increased food resources. One explanation for the apparent lack of influence of the shared environment is that its effects are partially masked by the unique environment each individual experiences in relation to its siblings (Bergmuller and Taborsky 2010, Sulloway 2010). Sulloway (2010) has suggested that siblings develop behavioural niches within a litter similar to how Darwin's finches evolved to fill an array of ecological niches: nests, like small islands, are highly competitive environments that favor a diversification of strategies. High intra-litter variance in behavioural strategies has been shown in several non-human mammals (Hudson et al. 2011); however, I was unable to test this in red squirrels due to the small number of litters for which I had all personality measures.

Shared and individual environment effects

Motor development

The inclusion of pup age, litter size, and parturition date in the best model for latency to falling supports that it is a biologically relevant measure and a valid test of motor development. As expected, older pups displayed a longer latency to falling in the hanging test: as they grow older, they become better able to grasp and cling to the doweling. And though litter size was not a significant term, the sign of the relationship is consistent with previous studies: pups from larger litters should have enhanced motor development as a result of jostling with siblings (Nicolas et al. 2011). However, I can only speculate as to why parturition date and study area would influence motor development. Perhaps those born later in the season develop faster to compensate for the shortened growth period, or timing and location of birth influence pace of life, and hence, behavioural strategies (Guenther and Trillmich 2012).

Surprisingly, latency to falling was not correlated with growth rates or weight. Although growth can be correlated with increased motor development (Altman et al. 1971, Mucino et al. 2009), growth in body weight is not synonymous with physical maturation. In human infants, for example, growth in body mass and motor development are independent of each other, except in cases of severe malnutrition (Onis 2006). And eye opening in red squirrels pups – though rare in 25 day olds – does not occur exclusively in heavier individuals (personal observation). Additionally, litter size may disrupt the relationship between growth and motor development: siblings in larger litters jostle with each other more, but they also gain weight more slowly (Rodel et al. 2008b). As such, there may be a trade-off between maturation and growth in size (Billerbeck et al. 2001).

In terms of personality, siblings that had greater motor skills in the nest were more aggressive post-emergence; however, there was no effect of absolute development, indicating that this relationship may be solely a result of sibling dynamics. It is important to note that the relationship between motor development and personality is only correlative: faster development may increase aggression through the positive reinforcement of winning conflicts (the winner effect, Dugatkin 1997), or aggression in the nest may increase competitive ability and allow pups to develop more quickly.

Growth

Although there were no sex differences in absolute growth rates, females did grow slower than their male siblings, and in females only, growth rates were positively correlated with activity. Perhaps the correlation between growth and activity is generated by the stronger competitive pressures experienced by slower growing females. If the relatively large size of males gives them a significant advantage in gaining milk (Bautista et al. 2013), the relationship may be non-significant, or too weak to detect.

The association between growth and activity is not surprising; increased growth rates have been associated with risky behaviours – such as activity, exploration, and boldness – in a variety of wild species (Biro and Stamps 2008). Additionally, manipulations of growth rate in some domestic species have led to an increase in risk-taking behaviour (Johnsson et al. 1996, Tymchuk et al. 2006). It has been suggested that these behaviours may represent a growth-mortality tradeoff (Mangel and Stamps 2001, Biro et al. 2006, Stamps 2007). Active, bold individuals that exhibit greater risk-taking may be able to forage more successfully and grow faster, but are also more likely to be predated. And conversely, low-activity, shy individuals have greater survival at the cost of slower growth. These alternate strategies may be maintained in a population if food resources or predation pressure fluctuate over time.

In the red squirrel system, offspring do grow faster when conspecific density – or perceived density – increases (Dantzer et al. 2013). Although faster growth rates in and of themselves may decrease time spent in the nest, and hence, give juveniles an earlier start in searching for a territory, active personality types associated with growth could conceivably provide an additional advantage through increasing exploration. Additionally, fluctuations in food density and territory availability result in varying rewards for risky behaviour. However, activity in the juvenile red squirrel has not been validated as a measure of risk (Chapter 4).

Although both absolute and relative growth rates were correlated with activity in females, growth relative to siblings was more highly significant. Siblings may benefit from development of a within-litter hierarchy while in the nest because it reduces conflict and energy expenditure (Bergmuller and Taborsky 2010). A dominance system could thus generate alternate growth strategies. But as is the case with aggression and motor development, we cannot infer causality between growth and activity: individuals with inherently higher growth rates may become more active in order to support their higher energetic demands, or alternately, active individuals may be able to achieve faster growth rates (Mangel and Stamps 2001).

Anogenital distance

AGD was only linked to masculinizing sources in females. Presumably, females are more sensitive to masculinizing agents, and indeed, Dela Cruz and Pereira (2012) manipulated prenatal testosterone exposure and found no effect on male AGD. However, presumed masculinization influenced female AGD in a counter-intuitive manner, in that females with larger AGDs had a smaller proportion of male siblings. Possibly this is due to the interaction with a third unknown variable. For example, Eccard and Rodel (2011) found that in European rabbits (*Oryctolagus cuniculus*), high aggression is associated with small litters, and small litters are born earlier in the season. Stewart (2012) also found that female mice born earlier in the season had larger AGDs, indicating that seasonal influences may be more important than exposure to male siblings. However, my data set was not powerful enough to detect such complex interactions.

Another counter-intuitive finding is that AGD was correlated with activity but not aggression. AGD may be more strongly correlated with activity than aggression in juveniles because juvenile aggression undergoes larger changes across ontogeny (Chapter 3). Alternately, I may have had insufficient power to detect a relationship between AGD and aggression; although activity and aggression were correlated in this subset, sample sizes were small. However, the sign of the relationship was also opposite to what I expected to find given the behavioural syndrome: less active females has larger AGDs. D'eath et al. (2004) also found the same relationship in female piglets, and suggested that prepubescent animals may respond differently to exposure to sex steroids. To conclude, there may be a connection between female AGD and personality, but the exact nature of the relationship is far from clear.

Conclusion

Some early life experiences do influence juvenile personality, but counter-intuitively, shared experiences provided by the mother are less prevalent than sibling effects. It is remarkable that sibling effects are significant, as within-litter variations in growth and development are small compared to those across litters. However, the high nestling mortality rates may make even small differences in relative development and growth highly consequential. These results suggest that laboratory studies with relaxed food competition may underestimate the importance of sibling effects.

The significance of strong sibling effects raises the question of how learned positions benefit individuals once they leave the nest, particularly in asocial species such as the red squirrel. One hypothesis is that once emerged, differences in personality may have equivalent fitness benefits, given the fluctuations in food and predation, as well as imperfect knowledge of future environments (Stamps 2007, Wolf and Weissing 2010). Alternately, variation in personality may represent a form of bet-hedging on the part of the mother (Wolf and Weissing 2010). Further research into the effects of sibling competition on personality in natural populations will help to address how these early influences on behaviour translate across life stages.

Table 2.1. Ethogram for scoring activity (open field trial; OF) and aggression (mirror-image stimulation trial; MIS) in North American red squirrels. F = frequency, D = cumulative duration, L = latency.

Trial	Behaviour	Description	Category
OF	Hole	Sniffs or puts head inside one of the four blind holes.	F
	Jump	Jumps.	F
	Chew	Chews or scratches the arena.	D
	Still	Remains stationary for more than two seconds, not including non-significant movements, such as twitching.	D
	Hang	Hangs from the top of the arena. Chewing and scratching may be performed while hanging.	D
	Groom	Cleaning the body with paws or mouth.	D
	Walk	Moving in the arena. May be walking or running.	D
MIS	Front	Time spent in the third of the arena closest to the mirror.	D
	Back	Time spent in the third of the arena farthest from the mirror.	D
	Approach latency	Latency to moving in the direction of the mirror.	L
	Attack latency	Latency to attack the mirror.	L
	Attack	Aggressively contacts the mirror (i.e., bats the mirror with paws). Multiple attacks are separated by non-contact with the mirror.	F

Table 2.2. First principal component loadings in Principal Component Analysis for behaviours of juvenile North American red squirrels in the open field trial (activity) and the mirror image stimulation trial (aggression). D=Duration, F=Frequency, L=Latency. Durations were measured as a percentage of time. Major contributing coefficients (>0.40) are shown in bold.

Activity		Aggression	
Behaviour	Component 1	Behaviour	Component 1
Walk (D)	**0.50**	Front (D)	**0.48**
Jump (F)	**0.42**	Attack (F)	0.37
Pellets (F)	0.31	Back (D)	**-0.41**
Hang (D)	0.28	Attack (L)	**-0.48**
Hole (F)	0.25	Approach (L)	**-0.48**
Chew (D)	0.23		
Groom (D)	-0.19		
Still (D)	**-0.51**		
Std. deviation	1.66	Std. deviation	1.63
Prop. of variance	0.35	Prop. of variance	0.53

Table 2.3. Descriptive statistics on individual behaviours displayed by juvenile North American red squirrels in an open field arena during a 450 second open field (OF) trial and a 300 second mirror-image stimulation (MIS) trials. D = duration, shown as a proportion of the total time spent engaging in the behaviour. F = frequency, shown as total number of times a behaviour was displayed. L = latency, shown as the latency to display a behaviour.

Trial	Behaviour	Minimum	Maximum	Mean	Variance	Category
OF	Walk	0.00	0.81	0.33	0.03	D
	Jump	0.00	132.00	33.00	808.50	F
	Hole	0.00	15.00	2.11	5.98	F
	Hang	0.00	1.00	0.25	0.05	D
	Chew	0.00	0.60	0.10	0.02	D
	Groom	0.00	0.50	0.06	0.00	D
	Still	0.00	0.90	0.18	0.06	D
MIS	Front	0.00	1.00	0.39	0.13	D
	Back	0.00	1.00	0.46	0.15	D
	Attack latency	0.00	300.00	212.76	14242.31	L
	Approach latency	0.52	300.00	117.17	17550.74	L
	Attack	0.00	98.00	5.61	252.85	F

Table 2.4. Final linear mixed effects model examining the influence of shared environment on juvenile North American red squirrels' activity in an open field trial. The model was reduced by using backwards selection to remove all terms with p>0.25. The model included litter as a random effect. Grid = study area.

Effect	Parameter estimate [95% CI]	*p*MCMC
Intercept	1.51 [0.60, 2.49]	0.0042
Grid	-0.31 [-0.71, 0.020]	0.074
Litter size	-0.49 [-0.72, -0.21]	**0.0008**
Proportion of male siblings	0.56 [-0.17, 1.24]	0.13

Table 2.5. Final linear mixed effect model examining the influence of shared environment on latency to falling in nestling (~25 days old) North American red squirrels. The model was reduced by using backwards selection to remove all terms with p>0.25. The model included litter as a random effect. Parturition data = birth data, age = age at testing, grid = study area.

Effect	Parameter Estimate [95% CI]	*p*MCMC
Intercept	-74.1 [-129, -14.09]	0.013
Litter size	5.31 [-0.52, 9.09]	0.08
Parturition date	0.19 [0.015, 0.42]	**0.035**
Age	2.7 [0.56, 4.91]	**0.014**
Grid	13.93 [5.56, 19.98]	**0.0014**

Table 2.6. Linear models examining the effects of shared (maternal) and individual (relative to sibling) contributions to nestling (~25 days old) hanging time on juvenile aggression and activity in North American red squirrels. Shared effects = litter mean, individual effects = individual deviation from the litter mean.

Trait	Effect	Estimate (s.e.)	*p*-value
Aggression	shared	0.0043 (0.0061)	0.49
	individual	0.017 (0.0075)	**0.024**
Activity	shared	0.0072 (0.0054)	0.19
	individual	0.0070 (0.0066)	0.29

Table 2.7. Linear models examining the effects of shared (maternal) and individual (relative to sibling) contributions to growth rate on juvenile aggression and activity in North American red squirrels. Shared contribution = litter mean, individual contribution = individual deviation from the litter mean.

Trait	Sex	Effect	Estimate (s.e.)	*p*-value
Aggression	M	shared	-0.68 (0.75)	0.37
		individual	-0.42 (1.32)	0.76
	F	shared	-0.013 (0.52)	0.98
		individual	-0.27 (1.63)	0.87
Activity	M	shared	0.37 (0.78)	0.64
		individual	-1.37 (1.36)	0.33
	F	shared	0.81 (0.39)	**0.045**
		individual	3.47 (1.18)	**0.0065**

Table 2.8. Fixed effects in a liner mixed effects model examining the effects of potential androgen sources on anogenital distance (AGD) in North American red squirrels. The model included litter as a random effect and weight as a constant fixed effect to control for the influence of body size on AGD.

	Females		Males	
Effect	Estimate (s.e.)	*p*MCMC	Estimate (s.e.)	*p*MCMC
Intercept	0.41 (0.046)	<0.0001	1.47 (0.21)	<0.0001
Weight	0.0014 (0.00081)	0.097	0.0094 (0.0033)	0.0064
Mother’s aggression	-0.0075 (0.0043)	0.088	0.009 (0.016)	0.57
Proportion of male siblings	-0.071 (0.031)	**0.027**	-0.12 (0.16)	0.44
Parturition date	-0.0012 (0.00043)	**0.0071**	-0.0023 (0.002)	0.25

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CHAPTER 3: STABILITY ACROSS ONTOGENY

INTRODUCTION

In many taxa, juveniles experience a very different physical and social environment from adults, so one might expect juveniles to change their behaviours as they mature. In a variety of species, adults (Dall et al. 2004, Sih et al. 2004a, Sih et al. 2004b), and more recently, juveniles (Kanda et al. 2012, Wilson and Krause 2012, Carlson and Langkilde 2013, Castanheira et al. 2013) have been shown to display personality; that is, consistent differences in behaviour across time and/or contexts (Dall et al. 2004). However, behavioural differences need not be consistent across *all* time and *all* contexts (Groothuis and Trillmich 2011). Indeed, studies have found that while repeatability may be high within a particular context, it may change with season (Kluen and Brommer 2013), food availability, or predation risk (Quinn et al. 2012). Though some have found linkages between early life and adult personality (Dimitsantos et al. 2007, Gracceva et al. 2011, Butler et al. 2012, Schuett et al. 2013), if personality undergoes ontogenetic changes, these relationships may be more complex than initially thought (Rodel and von Holst 2009). Additionally, knowing whether personality traits remain stable across ontogeny is important for studying the evolution of these traits, as selection may act differently on juvenile and adult traits (Groothuis and Trillmich 2011).

The concept of behavioural stability (also referred to as consistency) can be studied on several scales. Correlations across time and contexts can be calculated among individuals (differential stability), within individuals (individual stability), or between traits (structural stability) (Stamps and Groothuis 2010). Differential stability (Emmerich 1968), which considers only relative scores (often as ranks), is one of the most frequent measures. By this definition, personality is considered stable over time even if an individual’s absolute score changes, as long as its rank position remains consistent (Stamps and Groothuis 2010). For example, more aggressively ranked male tree swallows (*Tachycineta bicolor*) have higher reproductive success (Betini and Norris 2012). Individual stability (also known as absolute or ipsative stability), focuses on changes within an individual; that is, absolute changes in trait values over time. At the population level, these can be expressed as mean-level consistency. Where more than one personality trait is measured, the stability of correlations among traits (structural stability) may also be considered. These suites of behaviours – known as behavioural syndomes (Sih et al. 2004b) – have been shown to be affected by predation risk (Bell and Sih 2007) and conspecific density (Niemelä et al. 2012), suggesting that there may be low stability in behavioural syndromes across ontogeny.

Few studies have been conducted on the ontogeny of personality, and to my knowledge, only one other has assessed these changes in a wild, free-living population (*Marmota flaviventri*, Petelle et al. 2013, Table 3.1). Even within the primates – the most intensively studied group in animal personality research – only 9% of studies have been conducted on wild populations (Freeman and Gosling 2010). Studying personality in wild animals is important, as growing up in a stable captive environment – usually with relaxed predation pressures and open access to food – may have a profound influence on behavioral development (Archard and Braithwaite 2010). Additionally, it has been established that gene by environment interactions play a role in personality development (Dingemanse et al. 2009), and there may be costs to behavioural flexibility (DeWitt et al. 1998, Dall et al. 2004). Therefore, captive populations may display higher stability across ontogeny. Although laboratory studies provide valuable information, studies in natural systems are required to determine how juveniles change in response to growing up in an uncertain and dangerous environment.

In the present study, I used open field trials to measure aggression and activity in the North American red squirrel (*Tamiasciurus hudsonicus*) at both juvenile and yearling ages. Testing multiple times during early life and reassessing personality at maturity allowed me to test for individual, mean-level, differential, and structural stability. Individual and mean-level stability often change across ontogeny (Edenbrow and Croft 2011, Hedrick and Kortet 2011, Kanda et al. 2012), and I expect to observe the same in the red squirrel, especially due to the unstable natural conditions in this system. Previous research has shown that aggression and activity are measurable personality traits in the red squirrel (Boon et al. 2007, 2008, Taylor et al. 2012), and that dam personality affects offspring survival (Boon et al. 2007); however, personalities of the juveniles themselves have not yet been studied.

METHODS

Testing for stability

For within-season repeatability calculation methods, see Chapter 2. To test for differential effects – effects that result in a relationship between an individual's initial score and the change in score over time – I used spearman's correlations, then corrected for the statistical effect of regression to the mean following Kelly and Price (2005).

To test for sex differences in behavioural syndromes, I used an ANCOVA with sex as a covariate to test the correlation between aggression and activity, followed by the Levene's test for homogeneity of variance across groups. Sex was not significant as a covariate (ANCOVA: $F_{1,63}$=0.16, p=0.70), so I pooled sexes in all analyses. I used a Fisher's Z transformation to test differences in correlation coefficients between juvenile and yearling stages (Zar 1999).

I calculated syndrome deviation (SYD) as the absolute value of aggression rank minus activity rank (Herczeg and Garamszegi 2011). Changes in syndrome deviation were calculated as yearling SYD minus juvenile SYD, expressed as ranks (Spearman's rho correlation).

Due to small sample sizes, I could not effectively apply transformations to non-normal data; in these situations, I chose the test in which the fewest assumptions would be violated (in all cases, the t-test for unequal variances (Ruxton 2006). I calculated Chi-square values for small n values according to Campbell (2007). For all correlations, I used Spearman's rho, or in cases with tied ranks, Kendall's tau-B. All statistical analyses were performed in R version 3.0.2 with the lme4 package (Bates et al. 2012).

RESULTS

I measured personality traits in 68 juveniles and 20 yearlings (Table 3.2); 16 individuals were tested at both ages. Juveniles were tested an average of twice (range: 1-10), whereas yearlings were only tested once. In May 2013, I was able to capture all yearlings living on grid. Because the average natal dispersal distance of red squirrels is <100m (Larsen and Boutin 1994, Berteaux and Boutin 2000), I can assume that most survivors remained within our study area (two 40ha grids). Timing of territory acquisition was extremely variable in this cohort: 5 juveniles obtained territories prior to August 15, 2012 (when I left the field site), and 6 still had not gained territories by the following spring. Of those who gained territories earlier in the season (hereafter referred to as young owners), 2 were bequeathed territories from their mothers (red squirrel bequeathal: Boutin and Schweiger 1988, Price and Boutin 1993), and 3 gained the territories of recently deceased neighbors.

Individual, mean-level, and differential stability

In juveniles, both aggression and activity displayed moderate within-season repeatability (MIS: 0.37 (95% CI: 0.36-0.38), OF: 0.55 (95% CI: 0.39-0.71)), which is consistent with repeatability estimates from other studies (Bell et al. 2009). From juvenile to yearling stages, there were significant changes in absolute personality values (MIS: $t_{14}=2.51$, $p=0.025$; OF: $t_{14}=3.32$, $p=0.0051$). Specifically, more aggressive juveniles tended to become less aggressive as they matured, whereas less aggressive juveniles tended to become more aggressive ($r_\rho=0.77$, $p=0.00056$; Figure 3.1). The same pattern occurred with activity ($r_\rho=0.84$, $p<0.0001$; Figure 3.2). At the population level (mean-level stability), juveniles became less active as they matured ($t_{15}=4.33$, $p=0.00059$), but showed no mean change in aggression (t_{15}=0.48, p=0.63). Differential stability was maintained for activity (r_τ=0.52, p=0.0032) but not aggression (r_τ =0.35, p=0.07).

Structural stability and ownership interaction

Aggression and activity were correlated in both juveniles (r_τ=0.38, n=66, p<0.0001) and yearlings (r_τ=0.60, n=20, p=0.0049). However, syndrome deviation was associated with territory acquisition: young owners tended to increase in syndrome deviation, whereas those that spent time searching for territories tended to decrease (χ^2_1=4.45, n=16, p=0.035). In the latter group, the correlation between activity and aggression became significantly stronger with age (z=2.75, n=12, p=0.006).

DISCUSSION

I examined the stability of personality across maturation in a natural population of red squirrels. Following changes in behaviour across development has rarely been attempted in wild animals due to the issues associated with personality-biased sampling (Biro and Dingemanse 2009, Garamszegi et al. 2009) and the low likelihood of recapturing juveniles as adults. However, I was able to use an intensively trapped, large population to minimize these effects and obtain a sufficient sample size to detect changes over time. My results indicate that some personality traits in this species are not consistent across ontogeny, and that development of personality may be dependent on environmental change, as well as physiological change.

Juveniles exhibited moderate within-season repeatability of both activity and aggression, and like adults in this population (Taylor et al. 2012), showed habituation only in the activity trial. As such, we can conclude that juvenile red squirrels display personality. The pattern of regression to the mean (independent of statistical artifacts) from juvenile to yearling life stages suggests that intermediate values of both activity and aggression may be preferred in this cohort of yearlings, and furthermore, that squirrels are behaviourally malleable during this life stage.

On average, juveniles decreased in activity as they matured, but showed no mean change in aggression, indicating that in this cohort, high activity levels are not beneficial to adults. The decrease in activity scores may represent an increase in anxiety, indicating that squirrels are less fearful as juveniles. While this result corroborates the current theory on risky adolescent behaviour (Lynn and Brown 2009), I must also emphasize the possibility of environmental influence. Results on lab species show varied results on the ontogeny of anxiety: anxiety levels of juveniles may be higher, lower, or the same as adults, depending on the tests and conditions (Slawecki 2005). For example, juvenile rats show increased anxiety relative to adults only when juveniles undergo stressful experiences (Slawecki 2005).

In light of this apparent flexibility, we should exercise caution in making long-term extrapolations on the nature of changes in wild populations. Natural conditions are inherently more variable than lab conditions, and so we may expect the sign and magnitude of relationships to vary as well. Examining these changes may be particularly important in resource pulse systems such as ours, where annual food supply – and hence, competition – fluctuates greatly (McAdam and Boutin 2003).

Although the mean activity level decreased with maturation, individuals maintained their activity rank; that is, most juveniles decreased with similar magnitudes. In aggression, however, some individuals decreased and others increased, significantly altering the rank order. This indicates that individuals may be more flexible in their aggression towards conspecifics. Similarly, Bell and Sih (2007) found that, in sticklebacks, aggression was more flexible than boldness. Specifically in juveniles, Guenther and Trillmich (2012) found differential stability in exploration but not boldness. The greater changes in aggression observed here may be due to the importance of territory acquisition and maintenance in this species: red squirrels are both active and territorial year-round, and depend on their food caches for winter survival (Rusch and Reeder 1978).

Juveniles and yearlings both exhibit behavioural syndromes, and in one group – those that did not gain territories relatively early – the correlational strength increased with maturity. That is, high activity became more closely associated with high aggression, and low activity with low aggression. Behavioural syndromes can be thought of as alternative coping strategies (Sih et al. 2004a). They do not take into account the magnitude of differences among individuals, nor even the traits themselves: the correlations themselves are adaptive (Herczeg and Garamszegi 2011). The development of these coping strategies may be dependent on environmental cues and the stress response (Sachser et al. 2011, Sih 2011). For example, Bell and Sih (2007) have demonstrated experimentally that predation pressure can create a correlation between boldness and aggression. In my study, perhaps dispersal stressors function in a similar fashion.

If behavioural syndromes are adaptive, why then should the group of individuals that obtained territories early ('young owners') not undergo an increase in matching between activity and aggression? Possibly, the relatively lower stress environment negated the need for change. Young owners probably did not spend as much time making dispersal forays, and settled on sites that were at least somewhat familiar, both of which present less risk. (Predation risk increases once juvenile red squirrels leave the natal territory (Larsen and Boutin 1994), and there is some indication that familiarity is important to juvenile dispersers (Haughland and Larsen 2004).) Of the young owners, only one individual did not settle on or immediately adjacent to its natal territory (this individual originated in poor quality habitat where territories are spread apart), and as vacant territories are claimed within hours (Boutin et al. 1993), juveniles – or their mothers – must have been able to quickly detect and seize the vacancies. This association between ownership timing and a behavioural syndrome indicates that the act of dispersal is an important event in shaping future behaviour, and backs previous research indicating an interaction between territoriality and personality (Dingemanse 2004).

Though the results of this study suggest that personality is not static, and changes may be related to territory ownership, it is important to note that both the juvenile and yearling samples are biased. Firstly, juveniles that survived longer were more likely to be trapped and sampled, which may make survival consequences more difficult to detect. Additionally, some regularly observed individuals proved impossible to trap, despite intensive trapping efforts: I estimate that I captured 72% of the juveniles that were observed on grid (69/96) (see Chapter 2 for details). Differences in trapability may be due to differences in neophobia (Stuber et al. 2013) or exploration (Garamszegi et al. 2009); as such, I am likely missing the least active and aggressive individuals. However, this likely only leads to an underestimate of effect sizes (Carter et al. 2012).

To summarize, this study demonstrates – in a wild animal – that personality undergoes changes as individuals mature. While juveniles displayed individual differences in activity and aggression, not all forms of stability were maintained across ontogeny: individual-level aggression and activity, mean-level activity, and aggression rank changed significantly as squirrels matured. Additionally, there is some indication that the social and physical changes that accompany maturation – in this case, territory acquisition – can influence personality changes, irrespective of aging.

Table 3.1. Current research on the stability of personality traits across ontogeny in non-primates. I=Individual, D=Differential, M=Mean-level, S=Structural. Natural individuals were observed under natural conditions. Semi-natural individuals experienced relaxed predation or food supplementation. Wild-caught individuals were caught in the wild as juveniles and reared in the lab. Captive individuals were born and reared in the lab.

Species	Source	Behaviour	Stability				Reference
			I	D	M	S	
Cavia aperea	Captive	Exploration	-	Y	-	-	Guenther and Trillmich 2012
(cavie)		Boldness	-	N	-	-	
		Boldness-exploration	-	-	-	N	
Gasterosterus aculeatus	Wild-caught	Activity	-	Y	-	-	Bell and Stamps 2004
(three-spined stickleback)		Aggression	-	N	-	-	
		Boldness	-	Y	-	-	
		Boldness-aggression	-	-	-	Y	
		Activity-aggression	-	-	-	Y	
		Boldness-activity	-	-	-	Y	
Gryllus integer	Wild-caught	Boldness ♀	Y	-	N	-	Hedrick and Kortet 2011
(field cricket)		Boldness ♂	N	-	N	-	
Kryptolebias marmoratus	Captive	Boldness	-	N	N	-	Edenbrow and Croft 2011
(killifish)		Exploration	-	N	N	-	
		Boldness-exploration	-	-	-	N	
Lacerta vivipara	Semi-natural	Social tolerance	-	Y	-	-	Cote and Clobert 2007
(common lizard)							
Lestes congener	Wild-caught	Boldness	-	Y	-	Y	Brodin 2008
(damselfly)		Activity	-	Y	-	Y	
Marmota flaviventris	Natural	Boldness	N	-	-	-	Petrelle et al. 2013
(yellow-bellied marmot)		Docility	Y	-	-	-	
Oryctolagus cuniculus	Semi-natural	Aggression	-	Y	-	-	Eccard and Rodel 2011
(European rabbit)							
Parus major	Captive	Exploration	-	-	N	-	Carere et al. 2005
(great tit)							
Phodopus sungorus	Captive	Activity	-	-	N	-	Kanda et al. 2012
(Siberian dwarf hamster)		Boldness	-	-	N	-	
		Boldness-activity	-	-	-	Y	
		Activity-reactivity	-	-	-	N	
Pyrrhocoris apterus		Boldness	Y	Y	N	-	Gyuris et al. 2012
(firebug)		Exploration	Y	Y	N	-	
		Activity	Y	Y	N	-	
		Boldness-exploration	-	-	-	Y	
		Boldness-activity	-	-	-	Y	
		Activity-exploration	-	-	-	Y	
Rana ridibunda	Wild-caught	Activity/exploration	-	Y	-	-	Wilson and Krause 2012
(lake frog)		Anti-predator response	-	N	-	-	
Rattus norvegicus	Captive	Exploration	-	-	N	-	Lynn and Brown 2009, 2010
(brown rat)		Anxiety	-	-	N	-	

Rattus norvegicus	Captive	Boldness	N	-	-	-	Rodel and Meyer 2011
(brown rat)		Exploration	N	-	-	-	
Taeniopygia guttata	Captive	Exploration	Y	-	-	-	David et al. 2012
(Zebra finch)		Struggle rate	N	-	-	-	

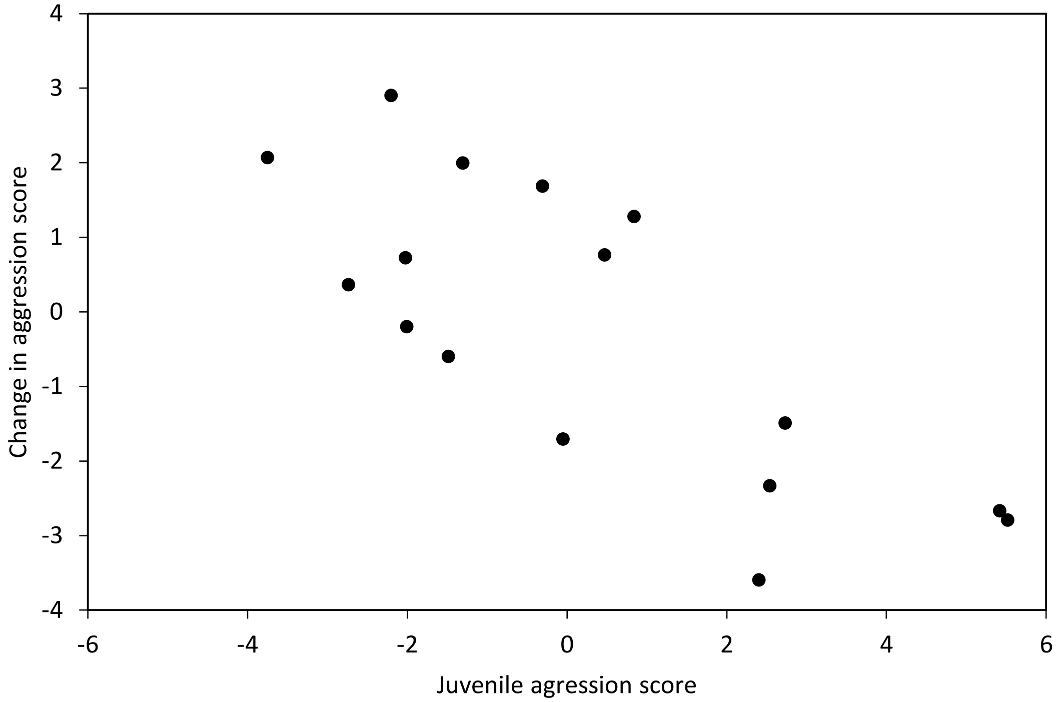

Figure 3.1. The correlation between aggression scores in juvenile North American red squirrels and the amount that aggression scores changed from juvenile to yearling stages. Change in score was calculated as the yearling score minus the juvenile score; therefore, positive values denote an increase in aggression and negative values denote a decrease in aggression. The correlation was calculated using Spearman's ranks; actual values are used here for illustrative purposes only.

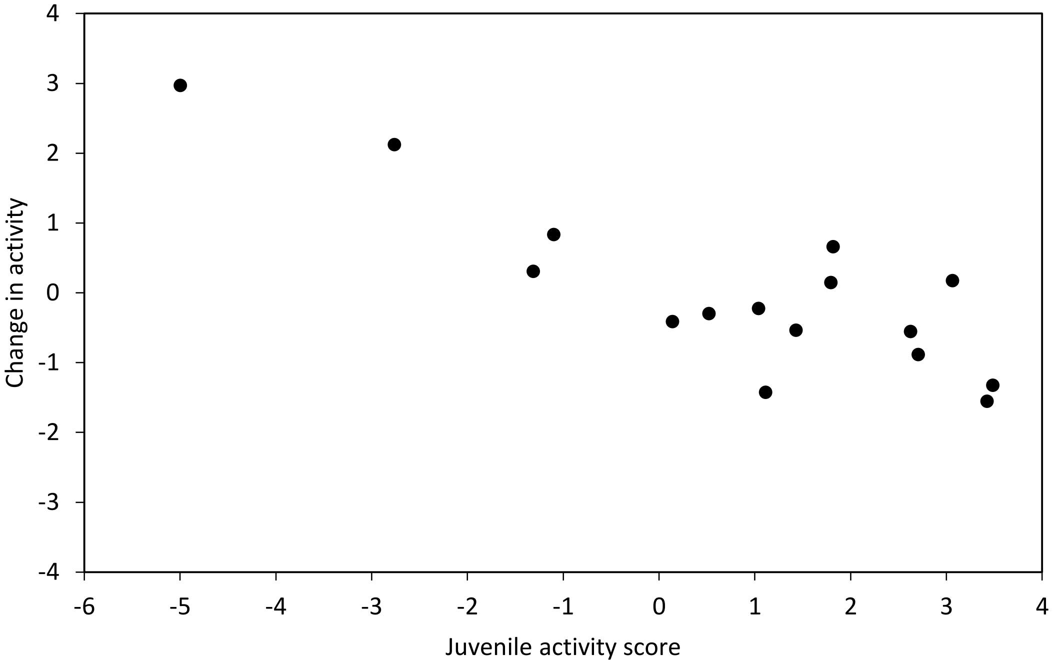

Figure 3.2. The correlation between activity scores in juvenile North American red squirrels and the amount that activity scores changed from juvenile to yearling stages. Change in score was calculated as the yearling score minus the juvenile score; therefore, positive values denote an increase in activity and negative values denote a decrease in activity. The correlation was calculated using Spearman's ranks; actual values are used here for illustrative purposes only.

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CHAPTER 4: CONSEQUENCES OF JUVENILE PERSONALITY

INTRODUCTION

Natal dispersal is an important life history characteristic on a population level, influencing gene flow and species distributions (Clobert et al. 2001, Bowler and Benton 2005). On an individual level, dispersal is a way in which animals can respond to their environments in order to increase their fitness (Bowler and Benton 2005). Juveniles often experience high mortality and must make critical decisions with little experience; as such, differences in behaviour may be particularly important. Indeed, dispersers are often phenotypically different from non-dispersers (Murren et al. 2001), and there is growing evidence that animal personality is an important determinant of dispersal behaviour (Cote and Clobert 2007, Cote et al. 2010, Cote et al. 2011, Chapple et al. 2012, Rasmussen 2012). For example, immigrant great tits (*Parus major*) are more explorative than residents (Dingemanse et al. 2003), and invasive populations of crayfish (*Pacifastacus leniusculus*) are more aggressive than those within their native distribution (Pintor et al. 2008). Studies of personality-dependent dispersal have the potential to inform both spatial ecology, via the influence of personality on animal movement, and behavioural ecology, via the distribution of personality types across landscapes (Martin and Reale 2008, Rasmussen 2012).

In this chapter, I examine the consequences of juvenile activity and aggression on natal dispersal forays, overwinter survival, territory acquisition, and trapability in the red squirrel. The dispersal process is relatively easy to study in the red squirrel because it is highly philopatric: most individuals disperse within 100 meters of their natal territory (Berteaux and Boutin 2000). However, it is unclear which personality type should make longer distance dispersal forays. If there is a positive association between proactive personality types (high aggression, activity, boldness) and dispersal distance, as has been demonstrated in several species (e.g., Fraser et al. 2001, Dingemanse et al. 2003, Cote et al. 2010, Quinn et al. 2011, van Overveld et al. 2014), I predict that proactivity and dispersal forays will be positively correlated. However, an alternate hypothesis is that highly active and aggressive juveniles may be better able to secure nearby vacancies first or compete with other dispersers, resulting in a negative relationship between proactivity and dispersal distance. In terms of survival, I expect that highly active and aggressive individuals will experience greater mortality due to an increase in risky behaviours (Smith and Blumstein 2007, Le Galliard et al. 2013).

Although trappability is not a central question in my research as it does not directly relate to real life consequences, I address it here because it provides a metric for testing the ecological validity of open-field trials (Reale et al. 2007); that is, I can compare behaviour under experimental and natural conditions. Although aggression in the mirror-image stimulation (MIS) trial is straightforward in its biological meaning, activity in the open-field (OF) trial can have several interpretations (Chapter 1), and therefore different biological consequences. Previous work on adults in this population suggests that activity is positively associated with risk-taking, as measured by trappability (Boon et al. 2008). I predict that if activity indeed represents a true measure of risk-taking or exploration in juveniles, more active individuals will have higher trappability.

METHODS

Dispersal forays

Because there were few surviving yearlings in the spring of 2013, I was unable to test for dispersal differences within my own data set. However, I was able to use movement data from 2005, collected by former Kluane Red Squirrel Project student Mark Andruskiw, and pair this with personality scores collected by Adi Boon in the same year. Boon's methods were similar to my own (see Chapter 2); detailed descriptions can be found elsewhere (Boon et al. 2007). Juvenile movements were monitored using radio telemetry. In brief, juveniles were fitted with radio collars just prior to emergence (~40 days of age), and were located an average of 2.8 times per day, from emergence until settlement or death. Two siblings per litter were followed, except in litters with less than three offspring, in which case only one offspring was followed. While within experimental areas, observers recorded locations according to the XY grid stakes, while off-grid locations were recorded using a GPS. All locations were then converted to XY coordinates.

I analyzed dispersal forays in two ways. Firstly, I compared individual maximum distances travelled to both activity and aggression using Kendall's Tau correlations, as data were non-normal and included ties. However, a single long-distance movement may not be representative, so I further grouped individuals into one of three categories based on foray activity: 1) low exploration juveniles that did not travel > 100m from their natal territory, 2) medium exploration individuals that made multiple forays > 100m from their natal territory but remained anchored to their natal midden at the end of the observation period, and 3) high exploration juveniles that made multiple long distance forays and remained >100m from their natal territory. The 100m cutoff is based on the average documented dispersal distance for red squirrels (Berteaux and Boutin 2000); since foray distances are a good predictor of settlement distances (Haughland and Larsen 2004), these groupings should reflect average to long distance dispersal activity. I tested for differences among groups using a nonparametric ANOVA

(Kruskal-Wallis) and used post-hoc Mann-Whitney U tests to determine where the significant differences were within each ANOVA.

Overwinter Survival and Territory Ownership

Survival and territory ownership were determined through a site census conducted in May 2013. In brief, territory ownership was based on trapping, behavioural observations, and territorial calls. Juveniles that were not trapped during the first two months of the field season (March-April) were considered to have perished. To test for the effects of juvenile and mother personality on survival, I used a linear mixed regression model with juvenile OF and MIS, mother OF and MIS, parturition date, sex, and grid as fixed effects, and litter ID as a random effect.

Since the average natal dispersal in the red squirrel is 96 meters (Berteaux and Boutin 2000), the majority of dispersing juveniles remain within the study area. However, I also searched the perimeters of both study areas for dispersed yearlings, and found none. In fact, most of the study area edges are determined by natural breaks in the coniferous forest, including marshlands, open grassed areas, and aspen copses. Red squirrels have been observed to avoid moving through such areas (Bakker and Van Vuren 2004), and they may be a natural hindrance to safe dispersal. Using grid stakes as a rough unit of measure, I estimate that 92% (2100/2280 meters) of the SU perimeter and 85% (2085/2060 meters) of the KL perimeter were adjacent to poor quality habitat that would not be conducive to easy dispersal.

I divided territory ownership into two categories: those that owned a territory by themselves (‘owners’) and those that shared with their mother or a sibling, or did not live on a midden (‘non-owners’). I used t-tests to compare activity and aggression between owners and non-owners.

Trappability

Juveniles were target trapped on natal middens (specific methods: Chapter 1). I calculated trappability as the total number of captures/hours trapped*the number of traps, using last date observed (seen or trapped) as the cutoff for each individual. Since I never reached trap saturation, I did not incorporate the number of squirrels living on each midden. I used Kendall’s tau correlations to compare trappability to personality scores.

RESULTS

Dispersal forays

I used movement and personality data of 42 juveniles from 2005 (20 females and 22 males). Individuals were followed for an average of 53.6 days (range: 23-127), and the average number of fixes per squirrel was 98.4 (range: 22-187). In 2005, males were both more active ($t_{38.27}$=-2.30, p=0.027) and aggressive than females ($t_{38.12}$=-2.36, p=0.023); however, there were no sex differences in maximum foray distance ($t_{22.41}$=-1.66, p=0.11). Maximum foray distance was positively correlated with aggression ($r\tau$= 0.26, p=0.014), but not activity ($r\tau$= 0.20, p=0.063); however, the difference between correlation coefficients was not significant (z=0.28, n=42, p=0.78). When juveniles were categorized according to exploration, there was a significant positive influence of aggression on exploration (Kruskal-Wallis: χ^2_2 = 7.62, p=0.022; Figure 4.1), and a marginally significant influence of activity on exploration (Kruskal-Wallis: χ^2_2 = 5.90, p=0.052; Figure 4.2).

Overwinter survival and territory ownership

Of the 96 juveniles that emerged from the nest in 2012, only 21% (20) survived until the following spring. Overwinter survival was not influenced by juvenile personality (Table 4.1), nor were any of the variables in the best fit model significant (parturition date: χ^2_1= 3.52, p=0.061; sex: χ^2_1= 3.00, p=0.084). Owners were less active than non-owners, both as juveniles ($t_{12.33}$=3.30, p=0.0061) and as yearlings ($t_{15.19}$=3.52, p=0.0031; Figure 4.3). Owners were also less aggressive as yearlings ($t_{17.99}$=3.60, p=0.0021), but not as juveniles ($t_{7.02}$=1.04, p=0.33).

Trappability

Trappable juveniles were less aggressive (r_τ=-0.30, p=0.0048), but not less active (r_τ=-0.14, p=0.19).

DISCUSSION

Dispersal forays

The methods I used to gauge foray activity (maximum dispersal distance and low-medium-high foray strategies) were coarse grained; however, they both indicate a positive relationship between proactive personality types (high aggression and activity) and exploratory behaviours during natal dispersal. This is consistent with findings in other species, and refutes the species-based prediction that proactive juveniles would be better able to gain nearby vacant territories. One explanation is that there may have been too few local vacancies – all becoming available at random times throughout the season – to allow proactive juveniles a true advantage in seizing them first. If so, the personality-based differences in foray activity begin to make more sense, as proactive personalities are more explorative (Reale et al. 2010), and may be better suited for novel habitats. For example, Duckworth (2008) found that aggressive male bluebirds were more likely to colonize new habitats, and furthermore, that aggressive individuals were more successful in new habitats, whereas non-aggressive individuals were more successful in mature habitats. Personality differences – and accompanying behavioural trade-offs – may thus be maintained by spatial or temporal heterogeneity (Sih et al. 2012). In our system in particular, large inter-annual fluctuations in spruce cone availability are already known to have a major influence on many aspects of red squirrel life (Berteaux and Boutin 2000, Humphries and Boutin 2000, McAdam and Boutin 2003a, Boon et al. 2007).

Overwinter survival

I was unable to detect any relationship between juvenile personality and survival. However, the odds of survival are stacked heavily against all juveniles (Larsen and Boutin 1994), regardless of what benefits or detriments personality may confer, so it is likely extremely difficult to detect individual effects on survival. Additionally, juvenile survival is dependent on a variety of factors, including parturition date, food availability, juvenile weight, and territory bequeathal (Berteaux and Boutin 2000, McAdam and Boutin 2003b, Reale et al. 2003, Kerr et al. 2007, Larivée et al. 2010), and so it may be impossible to detect the effects of personality on survival without larger sample sizes. Similarly, Bergeron et al. (2013) found no influence of selection on juvenile exploration, though they were able to detect a relationship between exploration and survival in adults.

Territory ownership

Yearlings that owned territories in the spring were less active and less aggressive than non-owners. And importantly, yearling owners were also less active as juveniles, indicating that reactive personality types (low aggression and low activity) may have helped juveniles to gain territories. This is counter to my expectations, as aggressive juveniles should be better able to compete for territories. However, dominance is influenced by situation (Verbeek et al. 1999), as well as personality (Dingemanse et al. 2004), so proactive types are not always dominant. For example, in great tits, territory ownership influences the relationship between exploration and dominance: when territorial, high exploration birds are dominant, but when non-territorial, low exploration birds are dominant (Dingemanse 2004). These less explorative individuals (which are also less aggressive) may be dominant because they are better able to cope with defeat: fast explorers display high aggression at first, but if they lose, they are more likely to relocate, rather than stay and fight (Verbeek 1998, Verbeek et al. 1999, Carere et al. 2001, Carere et al. 2003). Juvenile red squirrels repeatedly encounter their siblings, and likely other juveniles, so confrontations may result in proactive squirrels losing vacant territories.

In addition to the environmental context experienced by dispersing juveniles, the testing context may also influence relative scores. In our study, juveniles were tested on aggression towards a reflection; hence, it was possible to lose, but not win. This may affect how squirrels respond to the confrontation. For example, fast-exploring great tits are dominant in experimental pairwise confrontations (Verbeek et al. 1996), but slow-exploring tits are dominant in stable group hierarches (Verbeek et al. 1999). Although I can only speculate on why juvenile owners were less aggressive and active, it appears that personality does influence territory acquisition, an important step in the long term success of an individual.

Trappability

Counter to current literature, I observed no relationship between trappability and activity. In previous studies – including one on adult red squirrels – trappability has been positively correlated with activity (Boon et al. 2008, Garamszegi et al. 2009, Boyer et al. 2010, Carter et al. 2012b). Activity is often interpreted as a measure of boldness, exploration, or willingness to take risks (Sih et al. 2004, Reale et al. 2007), all of which intuitively apply to trappability. Indeed, some studies have even used trappability as a direct measure of boldness (Wilson et al. 1993, Reale et al. 2000, Garamszegi et al. 2009). However, it is difficult to accurately interpret the motivations behind locomotor activity (Hughes 1997), and as such, I can only speculate as to why I have not detected a relationship between activity and trappability. Because I used extremely targeted on-midden trapping methods, which included securing traps into nest trees and pre-baiting around the trap, trappability may not accurately reflect exploration or risk-taking. Alternately, activity in a forced open-field trial may not be equivalent to voluntarily approaching a novel object. For example, Burns et al. (2008) compared several commonly used measures of boldness in guppies (*Poecilia reticulata*) and found that there was no significant correlation between the responses in novel object and open field tests, indicating that each test measured a different trait. That said, trappability was influenced by aggression, which is itself correlated with activity.

Although aggression did influence trappability, it was in an unexpected direction. The negative correlation between aggression and trappability is difficult to explain, as low aggression is often correlated with low risking-taking and exploration, and risk-averse individuals tend to be less trappable (Wilson 1998, Mills and Faure 2000, Garamszegi et al. 2009). One explanation is that low aggression, reactive individuals spent more time investigating the traps, and were hence more likely to enter them. It is well known in psychology that less anxious humans focus away from stimuli, whereas more anxious ones focus on it (MacLeod et al. 1986, MacLeod and Mathews 1988, Bar-Haim et al. 2007). If reactive animals inspect novel objects longer (Carter et al. 2012c), they may be more likely to overcome their fear in favor of obtaining the bait. In my study, some juvenile squirrels did seem to show signs of approach-avoidance conflict when encountering traps: they were attracted to the peanut butter, but hesitant to enter the trap.

Conclusion

My findings support the growing evidence that personality plays an important role in the lives of juveniles, in terms of both natal dispersal and territory acquisition. My work also helps to support how variation in personality may be maintained. Heterogeneous selection (due to temporal, spatial, or social variations) is common in behavioural traits (Dingemanse and Reale 2013). However, life history trade-offs may also be responsible for the maintenance of variation in personality (Reale et al. 2010, Dammhahn 2012). Yearling territory holders were less aggressive than yearling floaters, indicating that their personality may have given them an advantage in territory acquisition. However, it should be emphasized that all squirrels that survived their first winter are successful relative to their entire cohort, as 79% of emerged juveniles perished during that period. So while nonaggressive juveniles are better at gaining territories, aggressive juveniles may be suited to living in the gaps until a territory becomes available. Indeed, the lack of relationship between personality and survival may be due to the combination of reactive juveniles succeeding in gaining territories and proactive juveniles surviving without them.

Trappability is linked to juvenile personality, though in an unexpected way. This adds to the growing evidence that the behaviours in open-field trials and under laboratory conditions cannot always be easily transferred to behaviours in the wild (Carter et al. 2012a, Carter et al. 2012c). The link between personality and trappability also indicates that there is sampling bias in target trapping; however, it leads to underestimates of effect sizes, rather than overestimates (Carter et al. 2012b). If the consequences of personality for juvenile success are stronger than I am able to detect here, further research is certainly warranted.

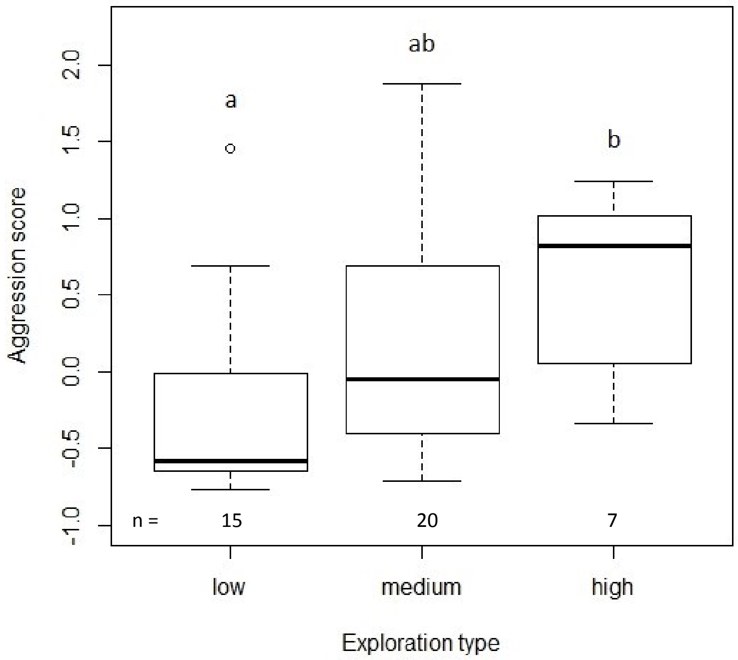

Figure 4.1. Relationship between aggression score in a mirror-image stimulation trial and exploration category (based on radio-telemetry) for juvenile North American red squirrels. Low = did not travel > 100m from the natal territory, medium = made multiple forays > 100m from the natal territory but remained anchored to their natal midden at the end of the observation period, high = made multiple long distance forays and remained >100m from their natal territory. Letters represent the results of post-hoc Mann-Whitney U comparisons of group medians, in conjunction with K-W tests.

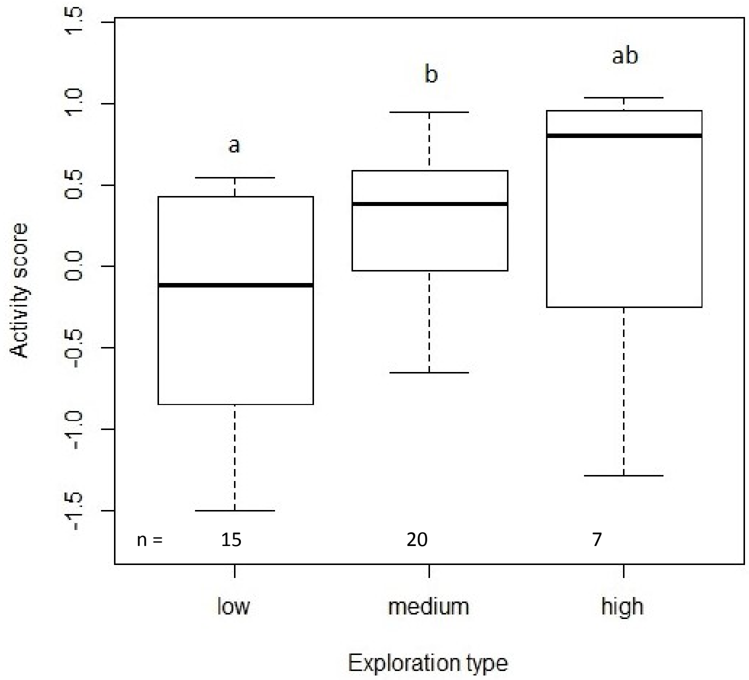

Figure 4.2. Relationship between activity score in an open field trial and exploration category (based on radio-telemetry) for juvenile North American red squirrels. Low = did not travel > 100m from the natal territory, medium = made multiple forays > 100m from the natal territory but remained anchored to their natal midden at the end of the observation period, high = made multiple long distance forays and remained >100m from their natal territory. Letters represent the results of post-hoc Mann-Whitney U comparisons of group medians, in conjunction with K-W tests.

Table 4.1. Linear mixed effects model testing the effects of mother and juvenile personality on juvenile survival in North American red squirrels. Birth date (Part), sex, the mother's activity score (MOF), the mother's aggression score (MMIS), juvenile activity score (OF), juvenile aggression score (MIS), and study area (Grid) were included as fixed effects, and litter was included as a random effect. Both juvenile aggression and activity were absent in the top models.

Fixed Effects	AIC
Part + Sex	60.03
Part + Sex + MOF	60.93
Part + Sex + MOF + MMIS	61.88
Part + Sex + MOF + MMIS + MIS	63.02
Part + Sex + MOF + MMIS + MIS + Grid	64.47
Part + Sex + MOF + MMIS + MIS + Grid + OF	66.47

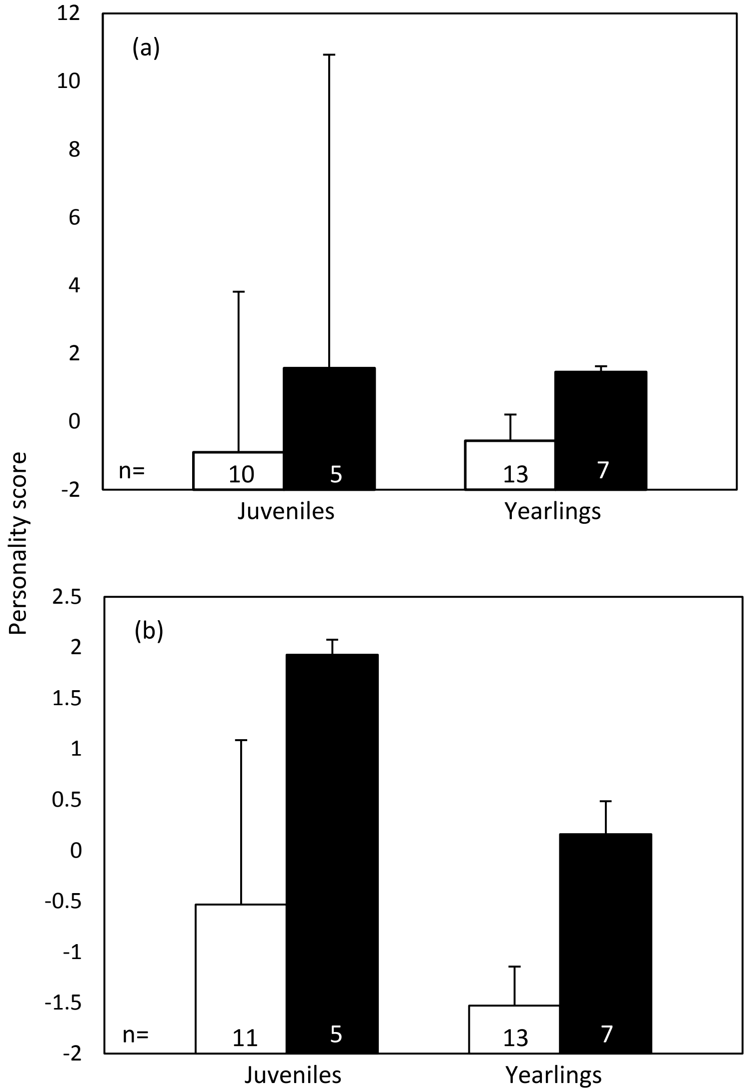

Figure 4.3. Mean aggression (a) and activity (b) scores (+ s.e.m.) and yearling territory ownership status (open bars: owners, filled bars: non-owners) when North American red squirrels were juveniles (prior to gaining territories) and yearlings. Ownership status was based on trapping and behavioural observations. Low personality scores indicate low activity/aggression.

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CHAPTER 5: GENERAL CONCLUSIONS

In this thesis, I investigated the development, stability and consequences of personality in free-living juvenile red squirrels. In Chapter 2, I examined the influence of both the shared and individual environments on juvenile personality, and found that differences among siblings in growth and development were predictors of juvenile personality. Surprisingly, I found little support that the shared environment significantly influenced juvenile personality. These results suggest that environmental effects have a strong influence on juvenile personality and highlight the need to look further into genotype-environment correlations and changes in heritability across ontogeny. In Chapter 3, I compared juvenile and yearling personality measures within the same set of individuals. I discovered that personality scores tended to regress towards the mean, and rank order was only maintained for activity, illustrating that personality does undergo significant changes as squirrels mature. Additionally, I found evidence that territory acquisition may influence personality change, as the activity-aggression behavioural syndrome strengthened only for juveniles that did not gain territories early in the season. Lastly, in Chapter 4, I investigated the consequences of juvenile personality, and found that yearling territory owners were less aggressive than non-owners, and dispersal activity was positive correlated with aggression. These results support my hypothesis that personality is important for dispersing juveniles.

Although I have found support for the importance of early life on personality, it is unclear that these relationships remain consistent over time. Environmental heterogeneity – temporal and spatial – is theorized to be one mechanism for maintaining variation in personality (Dingemanse and Reale 2013), and previous work in the red squirrel system has suggested that fluctuations in food availability may influence selection on personality (Boon et al. 2007). As such, it is likely that the relationships I observed in 2012 are not consistent across years. Even a lack of relationship may be due to year effects. For example, Cote et al. (2013) experimentally demonstrated that predation pressure disrupts personality dependent dispersal in the mosquitofish (*Gambusia affinis*). Future work on the red squirrel system and other natural systems should focus on how environmental heterogeneity influences the development and stability of personality across ontogeny. Additionally, other life stages and transitions should be considered. In the red squirrel, for example, yearlings are often smaller and usually do not breed, so while they are sexually mature, they may still be undergoing changes in personality. These next steps should broaden the understanding of the ontogeny of personality.

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