Sex- and context-specific associations between personality and a measure of fitness but no link with life history traits

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Abstract

The pace of life syndrome hypothesis posits that personality traits (i.e., consistent individual differences in behaviour) are linked to life history and fitness. Specifically, fast-paced individuals are predicted to be proactive (i.e., active and aggressive) with an earlier age at first reproduction, a shorter lifespan, and a higher fecundity than slow-paced individuals. Environmental conditions and sex differences may be important in maintaining behavioural and life history variation in populations and may influence the covariance of personality with life history or lifetime fitness. However, these effects are rarely tested together. We investigated whether the occurrence of a resource pulse (called a mast year) during adulthood altered the associations between personality and life history traits or lifetime offspring production in adult North American red squirrels (*Tamiasciurus hudsonicus*). Despite accounting for environmental context during adulthood, we found no evidence of an overall pace-of-life syndrome in this population as personality was not associated with age at first reproduction or longevity in either sex. Males and females had similar activity levels, but females were more aggressive, potentially due to the fitness benefits of protecting their offspring from predation. In all females regardless of mast experience, there was no association between activity and lifetime pup production but there was a positive association between aggression and lifetime pup production. In males that experienced a mast there was a positive association between lifetime pup production and both activity and aggression. In males that did not experience a mast, there was no association between activity and lifetime pup production but a negative association between aggression and lifetime pup production. Lifetime recruit production in either sex was not influenced by activity or aggression regardless of mast experience. Overall, our results suggest that the infrequent occurrence of mast years may contribute to maintaining variation in personality traits in red

squirrels.

Keywords: activity, aggression, behaviour, behavioural syndrome, exploration, life history, pace of life, pace of life syndrome, red squirrel, resource pulse, *Tamiasciurus hudsonicus*

Highlights

- We found no evidence of an association between personality and life history.
- Aggression was associated with higher lifetime fitness in females.
- In males the association between fitness and personality was context-specific.

Introduction

Individuals of many species exhibit consistent behavioural differences (Gosling, 2001) hereafter referred to as personality (sensu Dall, Houston, & McNamara, 2004). These behaviours frequently form syndromes of correlated traits: aggressive and bold individuals tend to be referred to as proactive, whereas shy and more passive individuals tend to be referred to as reactive (Koolhaas et al., 1999; Sih, Bell, & Johnson, 2004). Life history also varies along a continuum, with a fast life history pace being characterized as having an early age at first reproduction, short lifespan, and high fecundity and a slow life history pace being characterized as having a late age at first reproduction, a long longevity, and low fecundity. The pace-of-life syndrome hypothesis proposes that life history pace co-varies with a suite of other traits (Dammhahn, Dingemanse, Niemelä, & Réale, 2018; Réale et al., 2010; Ricklefs & Wikelski, 2002), including behavioural syndromes (Biro & Stamps, 2008), resulting in different lifetime strategies or patterns depending on where individuals rank along the fast-slow continuum. Fast-paced individuals are predicted to have a proactive behavioural syndrome as well as a faster life history: active and aggressive individuals, for example, would also have an earlier age at first reproduction and a shorter lifespan (Réale et al., 2010). Slow-paced individuals are predicted to have a reactive behavioural syndrome and a slow life history pace: less active and less aggressive individuals, for example, would have a later age at first reproduction and a longer lifespan (Réale et al., 2010).

Although personality may be linked with fitness (Biro & Stamps, 2008; Sih et al., 2004; Smith & Blumstein, 2008; Wolf & Weissing, 2010), empirical studies have demonstrated that the magnitude and direction of the link between annual reproduction or survival and measures of personality can vary depending on environmental conditions (Dingemanse & Réale, 2005; Santicchia et al., 2018; Smith & Blumstein, 2008; Taylor, Boutin, Humphries, & McAdam, 2014). For example, the relationship between fitness and personality can be affected by fluctuations in resource availability (Boon, Réale, & Boutin, 2007; Dingemanse, Both, Drent, & Tinbergen, 2004; Dingemanse & Réale, 2005; Taylor et al., 2014) or predation risk (Réale & Festa-Bianchet, 2003). Thus, the lifetime fitness consequences of a personality trait may depend on the environment that an individual encounters during its lifetime. This context-specific variation in fitness outcomes may be one reason that there is mixed evidence of the pace of life syndrome in empirical studies (Dammhahn et al., 2018; Réale et al., 2010; Royauté, Berdal, Garrison, & Dochtermann, 2018) and highlights the need to incorporate environmental conditions with major influences on life history and fitness in studies of personality.

Life history pace may also differ between the sexes (Bonduriansky, Maklakov, Zajitschek, & Brooks, 2008; Promislow, 2003). In species lacking paternal care, males typically achieve higher fitness through securing more mating opportunities whereas female success is driven by higher investment in fewer offspring. Consequently, males are predicted to have a higher wear-and-tear life history strategy and a faster pace of life than females (Bonduriansky et al., 2008; Promislow, 2003). This pattern may vary due to the mating system, sexual conflict, or other sex-specific selection pressures on life history or behaviour that may select for an alternate strategy or for traits that diverge from the optimal life history strategy for each sex (Bonduriansky et al., 2008; Hämäläinen, Immonen, Tarka, & Schuett, 2018; Promislow, 2003; Schuett, Tregenza, & Dall, 2010). The sexes may also respond differently to environmental conditions (Dingemanse & Réale, 2005; Schuett et al., 2010), resulting in sex differences in lifetime fitness under some conditions. Thus, both sex and the environmental context may alter the effect of personality on life history or lifetime fitness (Biro & Stamps, 2008; Hämäläinen et al., 2018; Smith & Blumstein, 2008; Wolf, van Doorn, Leimar, & Weissing, 2007).

We tested for sex- and environmental context-specific links between personality and life history or fitness in adult North American red squirrels (*Tamiasciurus hudsonicus*; hereafter 'red squirrels') in the Yukon, Canada. Red squirrels have consistent, repeatable, individual differences in activity within a novel test arena, herein referred to as activity, and aggressive behavioural responses to a mirror image, herein referred to as aggression (Boon et al., 2007; Taylor et al., 2012). These personality traits are linked to annual reproductive success and offspring survival (Boon et al., 2007; Taylor et al., 2014). Activity and aggression are also positively correlated (Boon et al., 2007; Taylor et al., 2012), suggestive of a proactive-reactive behavioural syndrome (Boon et al., 2007). There is also some evidence of a life history pace, as females with an earlier age at first reproduction also have a shorter lifespan (Descamps, Boutin, Berteaux, & Gaillard, 2006; McAdam, Boutin, Sykes, & Humphries, 2007).

Red squirrels in our study areas feed primarily on the seeds of white spruce (*Picea glauca*) cones (Fletcher et al., 2013) which are intermittently abundant when trees occasionally produce large seed crops, called mast years, every four to seven years (Haines et al., 2018; Krebs, Lamontagne, Kenney, & Boutin, 2012; Lamontagne & Boutin, 2007). Given this frequency of resource pulses, some individuals may not experience a mast in their lifetime. Mast cycles represent a major selective force in this system (McAdam & Boutin, 2003): cones mature in the fall but females anticipate an upcoming mast and increase their reproductive effort in the preceding spring (Boutin, McAdam, & Humphries, 2013; Boutin et al., 2006). There is also higher pup survival and recruitment during a mast year compared with other years (Humphries & Boutin, 2000; Williams, Lane, Humphries, McAdam, & Boutin, 2014), resulting in higher densities in the breeding population the following spring (Dantzer et al., 2013). Females who exhibit their maximal pup production in a mast year have higher lifetime fitness compared with females who do not (Hämäläinen et al., 2017). Male red squirrel mating behaviour is also altered by the occurrence of mast years, with males increasing their mating opportunities by committing infanticide and causing females to re-nest during a mast year (Haines et al., 2018). Annual fluctuations in the link between female personality and offspring survival are associated with these changes in food availability and corresponding changes in juvenile recruitment (Boon et al., 2007; Taylor et al., 2014). A mast year experienced after sexual maturity is thus likely a major influence on the interactive effects of behavioural phenotype and environment on fitness or life history. Although personality also influences juvenile survival in red squirrels (Boon et al., 2007; Cooper et al., 2017; Taylor et al., 2014) and dispersal distance in some cohorts (Cooper et al., 2017), here we focus on adult red squirrels and their response to whether they experience a mast during adulthood.

We first tested whether there were sex differences in activity or aggression. We then investigated whether sex and a fluctuating environment, in this case due to the infrequent occurrence of mast years, altered the direction or strength of association between personality and life history traits or lifetime reproductive success. We summarized our predictions based on existing literature in Table 1.

Predictions for sex differences in personality

Red squirrels have a promiscuous, scramble competition mating system with a male-biased daily operational sex ratio (Lane, Boutin, Gunn, & Coltman, 2009; Lane, Boutin, Gunn, Slate, & Coltman, 2008). As well, males have an earlier onset of senescence than females (Haines et al. *in prep*). This is suggestive of a faster life history pace in males than in females (Bonduriansky et al., 2008; Promislow, 2003). Thus, we expected that male red squirrels would have more proactive (i.e., more active and aggressive) personalities than females.

Predictions for associations between personality and life history traits

Female red squirrels with an early age at first reproduction have a short lifespan (Descamps et al., 2006; McAdam et al., 2007). Previous work also provides partial support for an association between life history and personality: active (but not aggressive) females have lower overwinter survival (Boon, Réale, & Boutin, 2008). Thus, we predicted that proactive males and females would have a faster pace of life (i.e., an earlier age at first reproduction and a shorter lifespan) than reactive squirrels as has been suggested by the pace of life syndrome hypothesis

(Réale et al., 2010), and that this association would be unaffected by experiencing a mast during adulthood.

Predictions for associations between personality and lifetime fitness

Previous work on annual reproductive success has shown that there is fluctuating annual selection on female personality (Boon et al., 2007; Taylor et al., 2014). Specifically, maternal activity was associated with higher annual overwinter survival of their offspring in years with low juvenile competition (Taylor et al., 2014), such as in mast years when recruitment is high; the pattern was the opposite in years with high juvenile competition, such as the years following masts when density is elevated (Taylor et al., 2014). In contrast, maternal aggression was associated with higher annual overwinter survival of their offspring in years with high juvenile competition (Taylor et al., 2014), such as in non-mast years when recruitment is low; the opposite pattern was found in mast years (Taylor et al., 2014). Female activity and aggression were not associated with litter size even when considered in fluctuating food conditions with the corresponding changes in juvenile competition (Boon et al., 2007; Taylor et al., 2014). Overwinter adult survival was higher in active, but not aggressive, females (Boon et al., 2008).

As activity does not influence litter size but is associated with lower annual maternal survival (Boon et al., 2007, 2008; Taylor et al., 2014), we predicted that active females would have lower lifetime pup production (measured by summing litter size across the entire lifetime for each female). As aggression neither influences litter size nor annual survival (Boon et al., 2007, 2008; Taylor et al., 2014), we predicted that there would be no effect of aggression on lifetime pup production in females. Based on previous findings (Taylor et al., 2014) we predicted that active females who experienced a mast during adulthood would have higher lifetime recruit production (measured by summing the total number of offspring that recruit into the population by the next breeding season for each female) but that active females who do not experience a mast during adulthood would have lower lifetime recruit production. We predicted that aggressive females who experienced a mast would have lower lifetime recruit production, but that aggressive females would have higher lifetime recruit production when they do not experience a mast year.

Males achieve higher reproductive success by traveling large areas to access more females during the breeding season (Lane et al., 2009), which suggests a potential link between activity and reproductive success. Thus, we predicted that more active males would have higher siring success regardless of mast experience, resulting in higher lifetime pup and recruit production for more active males. This pattern may suggest that there is directional selection and should result in reduced variation in this trait. However, variation could be maintained due to genetic correlation with aggression (Taylor et al., 2012) or due to genetic correlation with activity in females creating sexual conflict on this trait (Poissant, Wilson, & Coltman, 2010).

Males may achieve increased mating opportunities during mast years by committing infanticide (Haines et al., 2018), suggesting a potential role of aggressiveness in achieving reproductive success in these years. However, committing infanticide requires off-territory excursions to search for offspring to kill (Haines et al., 2018). This is similar behaviour to off-territory excursions undertaken during the mating season in order to search for receptive females (Lane et al., 2009). Searching for receptive females during the mating season is energetically costly (Lane, Boutin, Speakman, & Humphries, 2010), suggesting that aggression may be less beneficial during non-mast years due to its potential energetic costs. In addition, males are unlikely to obtain paternity benefits from infanticide during non-mast years as females typically only re-breed following litter mortality during mast years (Haines et al., 2018). We thus predicted a positive association between lifetime pup and recruit production when males do experience a mast year, but no association when they do not experience a mast year.

Variable	Behaviour	Predictions			Justification
		Females	Males	Sex Differences	
Longevity	Activity	-	-	N	- Both sexes: pace of life syndrome predicts that active and aggressive individuals will have an earlier age at first reproduction and a shorter lifespan.[1]
	Aggression	-	-	N	
AFR	Activity	-	-	N	
	Aggression	-	-	N	
Pup Production	Activity	-	+	Y	- Females: active females have lower overwinter survival.[2] - Females: no association between litter size and activity.[3, 4] - Males: males achieve higher reproductive success by searching larger areas[5]; this may be associated with activity.
	Aggression	n.s.	mast: + no mast: n.s.	Y	- Females: no association between overwinter survival and aggression.[2] - Females: no association between litter size and aggression.[3, 4] - Males: during mast years, males gain more mating opportunities through committing infanticide[6]; this may be associated with aggression. - Males: search effort is energetically demanding,[7] suggesting that aggression could be costly and that it should not be beneficial during non-mast years.
Recruit Production	Activity	mast: + no mast: -	+	Y	- Females: offspring of active females have higher overwinter survival during mast years, but lower overwinter survival during other years.[4] - Males: males achieve higher reproductive success by searching larger areas[5]; this may be associated with activity.
	Aggression	mast: - no mast: +	mast: + no mast: n.s.	Y	- Females: offspring of aggressive females have lower overwinter survival during mast years, but higher overwinter survival during other years.[4] - Males: during mast years, males gain more mating opportunities through committing infanticide[6]; this may be associated with aggression.

					- <u>Males</u>: search effort is energetically demanding,[7] suggesting that aggression could be costly and that it should not be beneficial during non-mast years.
1. Réale et al., 2010; 2. Boon et al., 2008; 3. Boon et al., 2007; 4. Taylor et al. 2014; 5. Lane et al., 2009; 6. Haines et al. 2018; 7. Lane et al., 2010					

Table 1. A summary of predictions regarding the associations between activity or aggression and longevity, age at first reproduction (AFR), lifetime pup production (Pup Production), or lifetime recruit production (Recruit Production) depending on mast experience (mast or no mast). For each combination, we indicated the justification for our prediction and included the citation as a footnote. We indicated whether we expected a positive effect (+), a negative effect (-), or no effect (not significant: n.s.). We have also indicated where we predicted a sex difference as well as where we expect differences between mast and no mast experience.

Methods

Monitoring Reproductive Success

We monitored all red squirrels in two 40 ha study areas, Kloo (KL) and Sulphur (SU), near Kluane Lake, Yukon (61°N, 138°W). We monitored female reproductive status from 1999-2014 and male reproductive success from 2003-2014. We marked squirrels individually with metal ear tags (Monel #1; 5 digits) and unique combinations of one or two coloured wires wrapped around their ear tags. We monitored all individuals throughout their lives using behavioural observations and live trapping. Further details on the population monitoring can be found elsewhere (McAdam et al., 2007).

We captured squirrels using Tomahawk live traps baited with peanut butter during the breeding season from March to August, although in some years our trapping started earlier than March or ended later than August. We targeted individual squirrels with traps set within their territories in order to monitor their survival and reproduction and to reduce the chances of catching non-target individuals. We handled individuals targeted for monitoring as described below, while non-target individuals were released without handling. We closed our traps once the target individual was captured. We did not trap in heavy rain or in extreme cold. We checked traps every 1-2 hours.

Upon capture, we transferred the squirrel from the trap into a handling bag. Some females start breeding as yearlings while others delay until a later age (see results), so when females were not breeding we captured them approximately once a month to monitor survival and to ensure they remained non-reproductive. Approximately once a month we trapped males or observed them using the coloured wires in their ears to confirm their survival. We captured reproductive (i.e., pregnant) females more frequently, typically every one to three weeks depending on their estimated parturition date. We weighed reproductive females upon capture (body mass in grams, 600-g Pesola spring scale, Pesola AG, Baar, Switzerland) and palpated their abdomen; this allowed us to detect increases in weight associated with pregnancy and to detect embryos within their abdomen to estimate their approximate parturition date based on embryo development. We determined parturition had occurred based on weight losses and by examining nipples for lactation. We monitored lactating females in order to tag their pups (described below), and then females were monitored only once a month unless they became pregnant with a second litter.

Once parturition was detected, we fitted females with a 4g radio collar (model PD-2C, 4 g, Holohil Systems Limited, Carp, Ontario, Canada), which represent 1.7% of the average body mass of 240g of a female red squirrel at parturition in this population (Humphries & Boutin, 1996). We attached radio collars with a zip tie wrapped in shrink wrap so that the collar size could be adjusted for each squirrel. We located females in their nests during the day in order to briefly remove newborn offspring from their nest, we then measured litter size and took ear tissue samples (see description below). We then removed the radio collar from the female. We captured the female once pups were estimated to be 25 days old, and if she was still lactating (i.e., if the pups had survived) we again attached a radio collar to locate her nest. We briefly removed pups from the nest to tag them so we could identify them once they had emerged from the nest. Juveniles disperse over short distances (Berteaux & Boutin, 2000; Cooper et al., 2017), so we tracked offspring with behavioural observations and live trapping to determine which individuals survived until the following spring (i.e., recruited into the breeding population).

As female red squirrels mate multiply and produce litters with multiple sires (Lane et al., 2009, 2008), we determined male reproductive success with genetic analyses. We collected ear tissue samples from all adults and juveniles, either through trapping or when juveniles were handled in the nest. We took a small ear tissue sample using sterilized scissors for newborn pups or a sterilized biopsy punch from older animals. Ear tissue was stored in 70% ethanol in the field and in a -20C freezer once the sample was taken to the lab. We extracted DNA using Qiagen DNeasy Tissue extraction kits and amplified 16 microsatellite loci using PCR. We scored genotypes with GENEMAPPER software 4.0 (Applied Biosystems) and assigned paternity at 99% confidence with CERVUS 3.0. We genotyped loci at a proportion of 0.95 on average. We determined maternity based on our field observations during nest location by telemetry and based on known mother-offspring relationships the genotyping error rate was < 1 %. Further details on paternity assignments are provided elsewhere (Gunn et al., 2005; Lane et al., 2008).

Life History Traits and Lifetime Reproductive Success

We used longitudinal monitoring to estimate two life history traits (longevity and age at first reproduction) and two components of lifetime reproductive success (sum of all pups and recruits produced, see below). For each individual, we calculated their birth year based on their first capture date; for juveniles this is the year they were born and for individuals first captured as adults we assigned them a birth year corresponding to the year before their first capture (e.g., Lane et al., 2009). Yearly detection probability is estimated to be one (Descamps, Boutin, McAdam, Berteaux, & Gaillard, 2009) and adults rarely disperse once they have established a territory (Berteaux & Boutin, 2000; Boutin, Tooze, & Price, 1993; Lane et al., 2015), so we assumed when an individual disappeared that it had died (McAdam et al., 2007; Stuart-Smith & Boutin, 1995). Longevity was therefore calculated as age at disappearance (in years). We calculated the age at first reproduction as the age (in years) at which individuals first produced a litter (females) or first sired pups (males); however, few had an age at first reproduction of greater than two (4% and 2% of males had an age at first reproduction of three or four years, respectively and 4% of females had an age at first reproduction of three years). Thus, age at first reproduction was assigned as binary: yearling (0) or older (1). We calculated two measures of lifetime reproductive success. First, we calculated the sum of all pups produced or sired (lifetime pup production). We then used the population monitoring to determine if a pup had survived through its first winter and, thus, successfully recruited into the population the following spring; we call these individuals recruits. We summed the total number of recruits (lifetime recruit production) as a second measure of lifetime reproductive success.

Defining the Occurrence of a Mast Year

We monitored white spruce cone production annually during late summer, which is when cones are visible but are not mature and thus have not yet been harvested by red squirrels. We assessed cone production by counting cones on one side in the top three metres of marked trees located systematically throughout the study areas and used this as an index of total cone production (Lamontagne, Peters, & Boutin, 2005) which can be used to distinguish mast years from non-mast years (Krebs et al., 2012). Mast years occurred in 1998, 2005, 2010, and 2014 (Haines et al., 2018; Krebs et al., 2012; Lamontagne & Boutin, 2007). We then determined whether squirrels encountered (Y) or did not encounter (N) a mast year during adulthood (i.e., at one year of age or older), which we refer to as mast experience. Although we recognize that the early life environment can be important for life history and personality development, we here focus on adult environment given that this is the life stage at which reproductive decisions are made.

Personality Trials

We measured aggression and activity using a standardized test in a novel environment as has been done previously in this system (Boon et al., 2007; Taylor et al., 2012) and in other studies of animal personality (e.g., Dammhahn, 2012; Martin & Réale, 2008). Individuals were released from a trap into a testing arena, a white plastic box (60 x 50 x 80 cm) with four false holes at the bottom, and the trials were recorded with a video camera through a clear lid. The first trial was an open field (OF) trial to measure activity in a novel environment (Cummins & Walsh, 1976; Martin & Réale, 2008). The OF trial ran for 7.5 minutes and also functioned as the habituation period for the mirror-image stimulation (MIS) trial that immediately followed it.

During the MIS trial, a mirror (35 x 40 cm) was uncovered in the side of the box; the trial began once the squirrel looked at its reflection and was ended after five minutes. The MIS trial is widely used as a measure of aggression towards conspecifics (Svendsen & Armitage, 1973), including previous studies in this system (Boon et al., 2007; Taylor et al., 2012). We have not yet used a quantitative analysis of the behaviours expressed in the MIS trials, qualitatively they resemble the behaviours we have observed during agonistic interactions in the field. Thus, we think it is unlikely that their behaviour is influenced by self-recognition, although we cannot conclusively rule this out as we do not have data to support if they do or do not recognize their own reflection. In addition, African cichlid fish (*Astatotilapia burtoni*) shown their own reflections react with behaviour and physiology that is similar to their reaction to a visible conspecific, but gene expression in their brains do differ (Desjardins & Fernald, 2010). Other research has shown that the hormonal response to a mirror image may differ from the response to a conspecific interaction (Hirschenhauser, Wittek, Johnston, & Möstl, 2008; Oliveira, Carneiro, & Canário, 2005). Thus, although reaction to a mirror has previously been interpreted as aggression, this assumption is currently under investigation. In this paper we interpret the MIS trial behaviour as a correlate of conspecific aggression, although we recognize that further work is needed to test this assumption.

Both the OF and MIS trials have previously been shown to be repeatable in red squirrels (Boon et al., 2007; Taylor et al., 2012). Behaviours during the OF and MIS trials were scored using a protocol previously established when quantifying behaviour in red squirrels (Boon et al., 2007; Taylor et al., 2012); see Supplementary Materials (Tables S1) for descriptions of the behaviours quantified in these trials.

Data Selection

We selected individuals with complete life history and personality data from our long-term data, only including in the analyses adults that survived to at least one year of age. We excluded individuals with incomplete lifetime data: first, because we only assessed male reproductive success from 2003 to 2014, we excluded males that were born prior to 2002; and second, because we only included data on female reproduction up to 2014, we excluded males and females that were still alive in 2015. We only included individuals for which we had data on lifetime reproductive success, life history traits, and personality (n = 137 females and 135 males). Some individuals did not breed successfully in their lifetime, so the sample sizes were smaller for analyses with age at first reproduction (n = 127 females and 101 males). Our dataset included females born from 1998 to 2012 and males born from 2002 to 2013. Personality trials were conducted on females from 2005 to 2012 and on males from 2005 to 2014. Squirrels were either tested as adults (n = 110 females and n = 114 males) or juveniles (i.e., less than one year old, n = 27 females and n = 21 males). Many individuals were tested multiple times in their life, but personality measures are repeatable (Boon et al., 2007; Taylor et al., 2012) and in our analyses we focus on lifetime measures (i.e., life history and lifetime reproductive success) with only one measure per squirrel. Additionally, squirrels habituate to some aspects of the personality trials if measured repeatedly (Taylor et al., 2012). Thus, we included only the measure from the first personality trial in our analysis.

Statistical Analyses

Quantifying activity and aggression

As we did not expect the behaviours recorded during the OF and MIS to be independent, we used principal component analyses (PCA) to create composite measures of behavioural traits. Specifically, the first axis of the unrotated principal component analysis from the OF trial was interpreted as activity in a novel environment (hereafter known as our measure of activity) and the first axis of the principal component from the MIS trial as aggression toward conspecifics (hereafter known as our measure of aggression), as has been done previously in other species (e.g., Martin & Réale, 2008) and in red squirrels (Boon et al., 2007, 2008; Cooper et al., 2017; Kelley, Humphries, Mcadam, & Boutin, 2015; Taylor et al., 2012, 2014). To generate activity and aggression scores that are comparable between the sexes, for each of the OF and MIS behavioural measures we combined data from the sexes. Previous work showed that multiple years have similar loadings (Taylor et al., 2012), indicating that years do not need to be considered separately. Using the prcomp function in R version 3.4.4 (R Core Team, 2018), we centred the data on zero and scaled it to have unit variance before generating the PCA axes.

In the OF trial, the first axis of the principal component analysis explained 31.4% of the variation in behaviour in the arena. Positive values described active individuals that spent more time walking, hanging, chewing, those that jumped and inspected holes more frequently, and that spent less time grooming or sitting still. The first axis of the principal components analysis of the MIS trial explained 56.5 % of the variation in behaviours, and negative values indicated squirrels that spent more time at the front of the arena near the mirror, spent less time at the back of the arena away from the mirror, attacked the mirror more frequently, and approached and attacked the mirror more quickly. We multiplied this variable by -1 so that positive values represented more aggressive individuals. More details of the principal components loadings are supplied in Supplementary Materials (Tables S2-S3).

Effects of activity or aggression on life history traits and fitness

We used R version 3.4.4 (R Core Team, 2018) for all statistical analyses. We tested for a correlation between aggression and activity using Pearson's correlation. We then used generalized linear mixed models (GLMM) computed with the R-package *lme4* version 1.1-15 (Bates, Maechler, Bolker, & Walker, 2015) to test whether sex influenced this association by including activity as the dependent variable, an interaction between aggression and sex as the independent variable, and a covariate of study area to account for site effects. We then tested whether there were sex differences in personality traits by including either activity or aggression as the dependent variable (including each personality score in a separate model), sex as the independent variable, and study area as a covariate. We then tested whether mast experience was associated with certain personality traits as this could influence the outcome of our analyses. We included activity or aggression as the dependent variable with mast experience in adulthood and study area as fixed effects. For all models, we included cohort year as a random effect because cohort effects have been shown to affect female reproduction (Descamps, Boutin, Berteaux, &

Gaillard, 2008) and to account for any potential bias resulting from incomplete sampling in later cohorts (i.e., the exclusion of animals still alive in 2015 and later; see Data Selection).

We then tested whether activity and aggression scores had an effect on sex-specific life history traits or fitness, including separate models each with dependent variables of: age at first reproduction, longevity, lifetime pup production, and lifetime recruit production. For each model, we included personality score (activity or aggression), mast experience, the two-way interaction between them, and study area as fixed effects. As there are methodological differences in calculating reproductive success for each sex, we separated the sexes in analyses focused on life history and fitness. We concluded there were sex differences when the separate models generated different conclusions (see Table 2 for a comparison of the results between the sexes). We also modelled each personality score (activity or aggression) and each life history or fitness measure separately. We included cohort year as a random effect for all models. We only included age at first reproduction as a dependent variable because including it as a covariate excluded individuals that did not successfully breed in their lifetime; we wished to include these individuals when considering other measures of life history and fitness and excluding them would have also reduced our sample size (see sample sizes in footnotes of Tables 3-5). When we found a significant interaction, we split the data by mast experience in order to run separate models for squirrels who experienced a mast compared with those who did not (see Tables S7). We also plotted the predictions generated separately for data from squirrels with and without mast experience in Figure 1.

We used linear mixed effects models and generalized linear mixed effects models implemented in the R package *lme4* version 1.1-15 (Bates et al., 2015) and generated p-values with the package *lmerTest* version 2.0-36 (Kuznetsova, Brockhoff, & Christensen, 2017). We used backward stepwise selection to drop variables with $p > 0.05$. Models resulting from this backward stepwise selection are shown in Results, but the full original models with all variables included can be found in Supplementary Materials. We used a normal distribution with a linear mixed effects model for models including activity or aggression scores as the dependent variable. We used a binomial generalized mixed effects model with logit-link for models with age at first reproduction as the dependent variable, and a Poisson generalized mixed effects model with log-link for models with longevity, lifetime pup production, or lifetime recruit production as the dependent variable. We used the cor.test function to generate confidence intervals for the Pearson correlation coefficients.

Animal Welfare Note

This study was conducted with approval from the University of Alberta Animal Care and Use Committee for Biosciences (animal care protocol number AUP00000028) in accordance with the Canadian Council on Animal Care Guidelines and Policies. This research was conducted under the following Government of Yukon permits: Scientists and Explorers Act License (Scientists and Explorers License number 15-07 S&E) and Yukon Wildlife Research Permit (permit number WRP 0140). This research followed the ASAB/ABS Guidelines for the Use of Animals in Research.

We took several measures to reduce our impact on the red squirrels we studied. We used Tomahawk live traps set within the territory of target squirrels in order to reduce the chances of capturing non-target individuals, and we closed traps once the target individual was captured. We captured and handled individuals only as frequently as was needed for monitoring, and non-target individuals were released without handling. Traps were checked frequently (typically every one to two hours) and trapping was not done during heavy rain or extreme cold. Each individual squirrel in our study area was tagged with metal tags in their ears, but we also used coloured wires to identify individuals from a distance. Where possible we used behaviour observations instead of trapping to collect data, thus further reducing how frequently they were handled.

Monitoring reproduction required additional trapping and handling, but again we took steps to reduce our impact on the females in our population. We determined pregnancy status by weighing females and palpating their abdomen to feel for embryos. Non-reproductive females could then be monitored less frequently. To accurately estimate reproductive success, we needed to estimate litter size close to birth as pups may not survive to an older age. Thus, we fitted females with 4g radio collars (which represents approximately 1.7% of their body mass) which were adjustable to properly fit each squirrel. We removed these collars from a female as soon as her nest was located. As we monitor survival and recruitment of pups, we needed to handle them again at 25 days of age: at this age pups are developed enough to tag but have not yet left their nest. We thus captured females when pups were estimated to be 25 days old, first determined if they were still lactating (i.e., confirmed that the pups had survived), before then attaching the radio collar. We quickly captured the female after her nest was located and removed the radio collar. Each time that a nest was entered, we returned pups to the nest as quickly as possible to minimize the time spent away from their mother. Once emerged from the nest, juveniles were monitored through behaviour observations (where possible) and trapping (when necessary) to determine if they survived and recruited into the breeding population. Females were captured less frequently once their pups had been tagged. To determine paternity to assess male reproductive success, we used sterilized scissors or sterilized biopsy punches to remove a small piece of tissue from the edge of their ear.

Personality measures were taken using a lightweight testing arena that could be folded up and transported. This set-up allowed us to measure personality in the field: when a target squirrel was captured, the arena was taken to the location of the target squirrel to avoid additional stress of being transported. The test was video-taped to be analyzed later, and the squirrel was released at upon completion of the trial. The release occurred at the same location where the squirrel was captured.

Results

Most females in our sample (82 individuals, 60%) bred as a yearling, 45 individuals (33%) did not breed until two years or older, and ten individuals (7%) never bred. Males were roughly equally successful at first siring pups as yearlings (48 individuals, 36%) or at two years of age and older (53 individuals, 39%), though 34 individuals (25%) were never successful at siring pups. Females and males lived until an average of 3.2 (95% confidence interval: 2.9-3.5, mode = 3, range 1-7) and 3.0 (95% confidence interval: 2.8-3.2, mode = 3, range = 1-7) years of age, respectively. Females in our sample produced an average of 8.9 pups during their lifetime (mode: 3, 95% confidence interval: 7.8-10, range = 0-32) and an average of 1.9 recruits during their lifetime (mode: 0, 95% confidence interval: 1.5-2.3, range = 0-11). Males in our sample sired an average of 5.4 pups during their lifetime (mode: 0, 95% confidence interval: 4.4-6.4, range = 0-29) and an average of 1.2 recruits (mode: 0, 95% confidence interval: 0.9-1.5, range 0-12). Eighty-three females (61%) and 83 males (61%) experienced a mast year during adulthood.

Sex differences in personality

Aggression and activity scores were positively correlated overall (Pearson's product-moment correlation = 0.42, 95% confidence interval = 0.32-0.51, t = 7.570, df = 270, $p < 0.001$), confirming a previously described behavioural syndrome along a reactive-proactive axis in this species (Boon et al., 2007; Taylor et al., 2012). This association between aggression and activity was not influenced by sex (Table 3): there was no statistically significant effect of an interaction between aggression and sex on activity ($\beta = 0.027$, SE = 0.094, p = 0.778, Table S4). When comparing the personality scores between the sexes, females were more aggressive than males (mean aggression score ± standard error (SE) in females = 0.206 ± 0.142, mean score ± SE in males = -0.209 ± 0.144; sex effect: $\beta = -0.409$, SE = 0.198, p = 0.040, Table 3). There was no sex difference in activity (mean activity scores ± SE in females = 0.040 ± 0.128, mean score ± SE in males = -0.040 ± 0.127; $\beta = -0.126$, SE = 0.177, p = 0.478, Table 3, Table S4). In both sexes we found that activity or aggression scores were not influenced by whether they experienced a mast during adulthood (effect of mast experience on activity in females: $\beta = -0.252$, SE = 0.263, p = 0.341; activity in males: $\beta = -0.171$, SE = 0.312, p = 0.585; aggression in females: $\beta = 0.291$, SE = 0.326, p = 0.376; aggression in males: $\beta = 0.320$, SE = 0.353, p = 0.367; Table 3, Table S4).

Associations between personality and life history traits

All predictions and outcomes derived from the following results on the associations between personality, life history, and lifetime reproductive success are summarized in Table 2.

There was no association between longevity and activity in either sex regardless of mast experience. The interaction between mast experience and activity scores had no effect on longevity in either females (β = -0.078, SE = 0.076, p = 0.304, Table S5) or males (β = 0.107, SE = 0.079, p = 0.178, Table S5). There was also no effect of activity scores on longevity in either sex (females: β = 0.027, SE = 0.063, p = 0.665, Table S5; males: β = -0.048, SE = 0.067, p = 0.474, Table S5). Mast experience was the only variable significantly associated with longevity in both sexes, as squirrels who lived longer tended to encounter a mast year during adulthood (females: β = 0.725, SE = 0.134, $p < 0.001$; males: β = 0.481, SE = 0.152, p = 0.002; Table 4).

There was no association between aggression scores and longevity regardless of sex or mast experience. The interaction between mast experience and aggression scores was not significant in either sex (females: β = -0.024, SE = 0.063, p = 0.705; males: β = 0.065, SE = 0.067, p = 0.331; Table S5). There was also no association between longevity and aggression (females: β = 0.029, SE = 0.051, p = 0.571; males: β = -0.059, SE = 0.056, p = 0.293; Table S5), As a result, the final model was the same as when we tested for an association between activity and longevity: mast experience was the only variable significantly associated with longevity (Table 4).

Whether a squirrel experienced a mast during adulthood or not, we found no association between activity and age at first reproduction regardless of sex (Table 4). In females when considering the full model with all variables included, we found that age at first reproduction was associated with a significant interaction between mast experience and activity (β = -0.668, SE = 0.332, p = 0.044, Table S5). However, when we removed variables that were not statistically significant, the interaction was no longer significant. There was no association between activity and age at first reproduction in the final model (Table 4). In males, the interaction between mast experience and activity scores was not significant (β = 0.254, SE = 0.394, p = 0.519, Table S5).

Age at first reproduction was also not associated with activity scores (β = -0.105, SE = 0.339, p = 0.756, Table S5).

In both sexes, we found no association between age at first reproduction and aggression regardless of mast experience (Table 4). In females, an interaction between mast experience and aggression score had no effect on age at first reproduction (β = -0.377, SE = 0.250, p = 0.132, Table S5). We also found that aggression score did not affect age at first reproduction (β = 0.142, SE = 0.179, p = 0.428, Table S5). In males the aggression score x mast experience interaction was not significant (β = -0.036, SE = 0.274, p = 0.896, Table S5). There was also no association between age at first reproduction and aggression (β = -0.116, SE = 0.221, p = 0.601, Table S5).

Associations between personality and lifetime fitness

In females, activity did not affect lifetime pup production: an interaction between activity and mast experience was not significant (β = -0.071, SE = 0.049, p = 0.146, Figure 1, Table S6) and activity was also not significant (β = 0.035, SE = 0.041, p = 0.391, Table S6). Mast experience affected lifetime pup production: females who experienced a mast had higher lifetime pup production than those who did not (β = 1.141, SE = 0.089, p < 0.001, Table 5). Study area also affected lifetime pup production as females on the study area SU had lower lifetime pup production than KL (β = -0.243, SE = 0.068, p < 0.001, Table 5).

In males, activity was associated with lifetime pup production but the relationship depended on mast experience (activity x mast experience interaction: β = 0.145, SE = 0.063, p = 0.020; Table 5), so we explored this significant interaction by splitting the data for males that experienced masts and those that did not. We found a positive association between lifetime pup production and activity in males that experienced a mast during adulthood (β = 0.090, SE =

0.034, $p = 0.008$, Table S7, Figure 1). We found no association between lifetime pup production and activity in males that did not experience a mast year ($\beta = -0.072$, SE = 0.053, $p = 0.175$, Table S7, Figure 1).

There was a positive association between female aggression and lifetime pup production ($\beta = 0.064$, SE = 0.020, $p = 0.001$; Table 5, Figure 1), but this was not influenced by mast experience (aggression score x mast experience interaction not significant: $\beta = 0.027$, SE = 0.040, $p = 0.511$, Table S7). Male lifetime pup production was explained by an interaction between aggression score and mast experience ($\beta = 0.383$, SE = 0.058, $p < 0.001$, Table 5), so we separated males that experienced a mast from those that did not. We found a positive association between lifetime pup production and aggression scores in males who experienced a mast year ($\beta = 0.093$, SE = 0.028, $p = 0.001$; Table S7, Figure 1). We found a negative association between lifetime pup production and aggression scores in males who did not experience a mast ($\beta = -0.285$, SE = 0.055, $p < 0.001$; Figure 1, Table S7).

Lifetime recruit production was not influenced by activity or aggression in either sex (Table 5). Lifetime recruit production was not influenced by an interaction between mast experience and activity (females: $\beta = 0.006$, SE = 0.110, $p = 0.955$; males: $\beta = 0.013$, SE = 0.155, $p = 0.934$; Table S6) or by activity (females: $\beta = -0.033$, SE = 0.096, $p = 0.732$; males: $\beta = -0.013$, SE = 0.140, $p = 0.928$; Table S6). Lifetime recruit production was not influenced by an interaction between aggression and mast experience (females: $\beta = -0.100$, SE = 0.091, $p = 0.273$; males: $\beta = 0.189$, SE = 0.130, $p = 0.147$; Table S6) or by aggression (females: $\beta = 0.103$, SE = 0.079, $p = 0.192$; males: $\beta = -0.085$, SE = 0.119, $p = 0.474$; Table S6). In females we found that only mast experience (females who experienced a mast year had higher recruit production: $\beta = 1.424$, SE = 0.200, $p < 0.001$, Table 5) and study area (females on the study area SU had lower recruit production than females on KL: β = -0.324, SE = 0.141, p = 0.021, Table 5) significantly affected lifetime recruit production. In males we found that only mast experience significantly affected lifetime recruit production: males who experienced a mast year had higher recruit production than those who did not (β = 1.065, SE = 0.249, p < 0.001, Table 5).

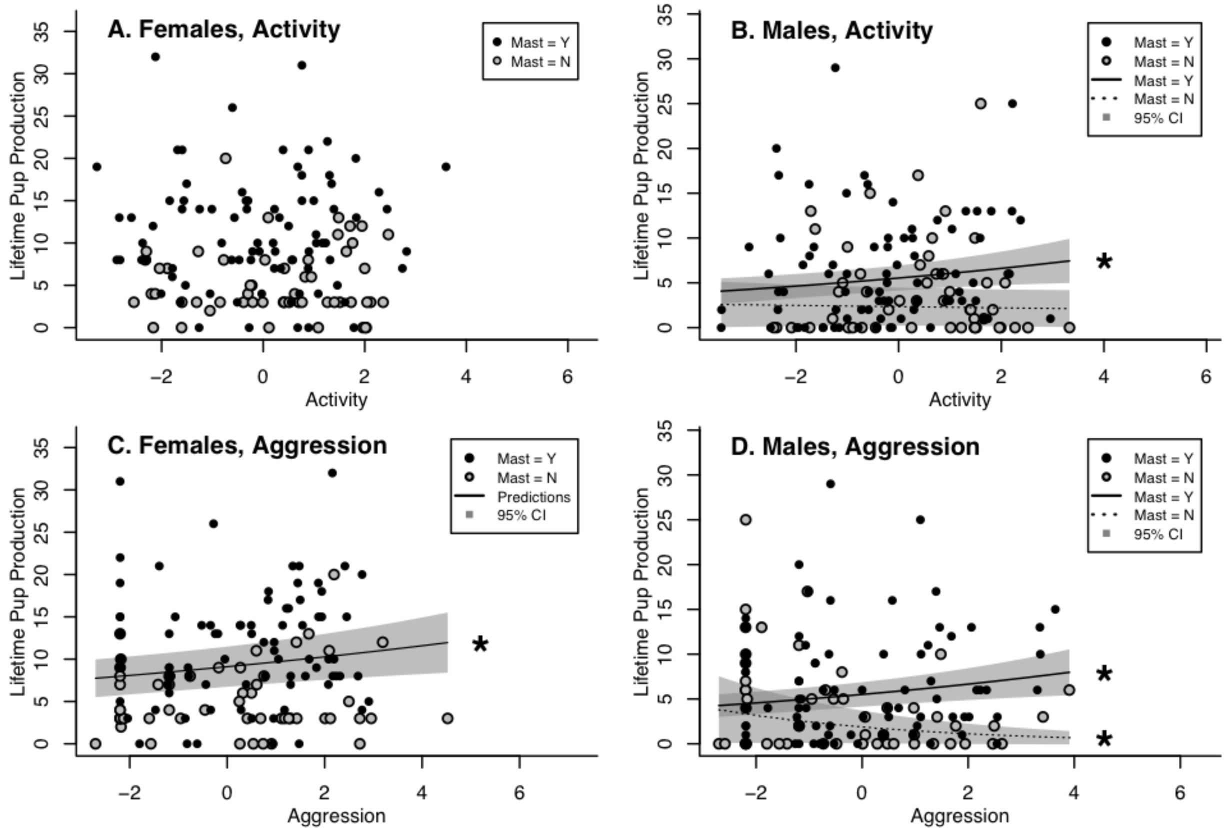

Figure 1. Relationship between lifetime pup production and activity (A and B) in females (A) and males (B), as well as the relationship between lifetime pup production and aggression (C and D) in females (C) and males (D). Points indicated whether squirrels experienced a mast year. Where there was a significant association between activity or aggression and lifetime pups production, we split the data according to whether squirrels experienced a mast or not and generated model predictions separately for each group; these were back-transformed to the

original scale and indicated by lines along with their confidence intervals (CI, indicated by grey shading). Where there was a significant effect of personality score but not a significant interaction with mast experience, model predictions and CI’s were generated without separating by mast experience. Where study area was significant (see Table 5) this was set as KL and the random effect of cohort was set to zero (i.e. the mean). Only some models were statistically significant (see Tables 5 and S7) and these were indicated by a * next to the prediction line.

Variable	Behaviour	Females		Males		Sex Difference	
		Prediction	Results	Prediction	Results	Prediction	Results
Longevity	Activity	-	n.s.	-	n.s.	N	N
	Aggression	-	n.s.	-	n.s.	N	N
AFR	Activity	-	n.s.	-	n.s.	N	N
	Aggression	-	n.s.	-	n.s.	N	N
Pup Production	Activity	-	n.s.	+	mast: + no mast: n.s.	Y	Y
	Aggression	n.s.	+	mast: + no mast: n.s.	mast: + no mast: -	Y	Y
Recruit Production	Activity	mast: + no mast: -	n.s.	+	n.s.	Y	N
	Aggression	mast: - no mast: +	n.s.	mast: + no mast: n.s.	n.s.	Y	N

Table 2. Associations between activity or aggression and longevity, age at first reproduction (AFR), lifetime pup production (Pup Production), and lifetime recruit production (Recruit Production). For each relationship, we indicated our predicted patterns (Prediction) and the outcome (Results) based on statistical tests. We indicated whether we expected or found a positive effect (+), a negative effect (-), or no effect (not significant: n.s.). We have also indicated where we predicted or found a sex difference as well as where we expected or found an effect of mast experience (indicated by mast or no mast).

Dependent	Sex	Variable	# squirrels	# cohorts	β	SE	df	t	p	cohort variance	residual variance
Activity	Both	**Intercept**	272	15	-0.086	0.169	9.562	-0.510	0.621	0.282	1.617
		Aggression			0.369	0.048	267.78	7.638	< 0.001		
		Sex							n.s.		
		Study area							n.s.		
		Aggression*Sex							n.s.		
Activity	Both	**Intercept**	272	15	-0.090	0.190	10.292	-0.474	0.646	0.336	1.957
		Sex							n.s.		
		Study area							n.s.		
Activity	Females	**Intercept**	137	14	0.016	0.160	5.648	0.102	0.922	0.097	2.157
		Mast experience							n.s.		
		Study area							n.s.		
Activity	Males	**Intercept**	135	12	-0.101	0.240	9.411	-0.422	0.683	0.437	1.837
		Mast experience							n.s.		
		Study area							n.s.		
Aggression	Both	**Intercept**	272	15	0.187	0.196	22.266	0.954	0.35	0.225	2.556
		Sex			-0.409	0.198	269.34	-2.063	0.040		
		Study Area							n.s.		
Aggression	Females	**Intercept**	137	14	0.226	0.190	11.941	1.187	0.258	0.183	2.588
		Mast experience							n.s.		
		Study area							n.s.		
Aggression	Males	**Intercept**	135	12	-0.230	0.215	11.127	-1.068	0.308	0.242	2.585
		Mast experience							n.s.		
		Study area							n.s.		

Table 3. The relationship between activity or aggression and sex or mast experience, showing only the final models (i.e., with non-significant variables removed using backward stepwise selection and indicated as n.s.). We included estimate (β), standard error (SE), degrees of freedom (df), t values (t), and p-values (p) of fixed effects, variance of the random effect of cohort (cohort variance and residual variance), and sample size (# cohorts and # squirrels). Significant variables are shown in bold. The reference category for sex, mast, and study area were females, no mast experience, and KL, respectively. The full original models prior to backward stepwise regression are included in Supplementary Materials (Table S4).

Behaviour	Sex	Dependent	Variable	# squirrels	# cohorts	β	SE	z	p	cohort variance
Activity	Females	Longevity	**Intercept**	137	14	0.653	0.140	4.673	<0.001	0.071
			Activity						n.s.	
			Mast			0.725	0.134	5.419	<0.001	
			Study Area						n.s.	
			Activity*Mast						n.s.	
	Males	Longevity	**Intercept**	135	12	0.752	0.140	5.390	<0.001	0.017
			Activity						n.s.	
			Mast			0.481	0.152	3.169	0.002	
			Study Area						n.s.	
			Activity*Mast						n.s.	
	Females	AFR	**Intercept**	127	14	-0.563	0.401	-1.406	0.160	1.336
			Activity						n.s.	
			Mast						n.s.	
			Study Area						n.s.	
			Activity*Mast						n.s.	
	Males	AFR	**Intercept**	101	12	0.219	0.319	0.686	0.492	0.448
			Activity						n.s.	
			Mast						n.s.	
			Study Area						n.s.	
			Activity*Mast						n.s.	
Aggression	Females	Longevity	**Intercept**	137	14	0.653	0.140	4.673	<0.001	0.071
			Aggression						n.s.	
			Mast			0.725	0.134	5.419	<0.001	
			Study Area						n.s.	
			Aggression*Mast						n.s.	
	Males	Longevity	**Intercept**	135	12	0.752	0.140	5.390	<0.001	0.017
			Aggression						n.s.	

		Mast			0.481	0.152	3.169	0.002	
		Study Area						n.s.	
		Aggression*Mast						n.s.	
Females	AFR	**Intercept**	127	14	-0.563	0.401	-1.406	0.160	1.336
		Aggression						n.s.	
		Mast						n.s.	
		Study Area						n.s.	
		Aggression*Mast						n.s.	
Males	AFR	**Intercept**	101	12	0.219	0.319	0.686	0.492	0.448
		Aggression						n.s.	
		Mast						n.s.	
		Study Area						n.s.	
		Aggression*Mast						n.s.	

Table 4. Final models (i.e., with non-significant variables removed using backward stepwise selection and shown as n.s.) showing the relationship between activity or aggression and life history traits: longevity and age at first reproduction (AFR). We included estimate (β), standard error (SE), z-score (z), and p-values (p) of fixed effects, variance of the random effect of cohort (cohort variance), and sample size (# cohorts and # squirrels). Significant variables are in bold. The reference category for mast and study area were no mast experience and KL, respectively. The full original models prior to backward stepwise regression are included in Supplementary Materials (Table S5).

Behaviour	Sex	Dependent	Variable	# squirrels	# cohorts	β	SE	z	p	cohort variance
Activity	Females	Pups	**Intercept**	137	14	1.376	0.136	10.083	<0.001	0.155
			Activity						n.s.	
			Mast			1.141	0.089	12.848	<0.001	
			Study Area			-0.243	0.068	-3.557	<0.001	
			Activity*Mast						n.s.	
	Males	Pups	**Intercept**	135	12	1.244	0.168	7.398	<0.001	0.205
			Activity			-0.050	0.052	-0.958	0.338	
			Mast			0.519	0.110	4.706	<0.001	
			Study Area						n.s.	
			Activity*Mast			0.145	0.063	2.319	0.020	
	Females	Recruits	**Intercept**	137	14	-0.369	0.222	-1.664	0.096	0.144
			Activity						n.s.	
			Mast			1.424	0.200	7.114	<0.001	
			Study Area			-0.324	0.141	-2.300	0.021	
			Activity*Mast						n.s.	
	Males	Recruits	**Intercept**	135	12	-0.688	0.255	-2.698	0.007	0.136
			Activity						n.s.	
			Mast			1.065	0.249	4.281	<0.001	
			Study Area						n.s.	
			Activity*Mast						n.s.	
			Study Area						n.s.	
Aggression	Females	Pups	**Intercept**	137	14	1.321	0.140	9.444	<0.001	0.160
			Aggression			0.064	0.020	3.190	0.001	
			Mast			1.162	0.091	12.784	<0.001	
			Study Area			-0.215	0.068	-3.149	0.002	
			Aggression*Mast						n.s.	
	Males	Pups	**Intercept**	135	12	1.057	0.181	5.851	<0.001	0.230

		Aggression			-0.289	0.052	-5.608	<0.001	
		Mast			0.683	0.120	5.683	<0.001	
		Study Area						n.s.	
		Aggression*Mast			0.383	0.058	6.587	<0.001	
Females	Recruits	**Intercept**	137	14	-0.369	0.222	-1.664	0.096	0.144
		Aggression						n.s.	
		Mast			1.424	0.200	7.114	<0.001	
		Study Area			-0.324	0.141	-2.300	0.021	
		Aggression*Mast						n.s.	
Males	Recruits	**Intercept**	135	12	-0.688	0.255	-2.698	0.007	0.136
		Aggression						n.s.	
		Mast			1.065	0.249	4.281	<0.001	
		Study Area						n.s.	
		Aggression*Mast						n.s.	

Table 5. Final models (i.e., with non-significant variables removed using backward stepwise selection) showing the relationship between activity or aggression and lifetime pup production (Pups) or lifetime recruit production (Recruits). We included estimate (β), standard error (SE), z-score (z), and p-values (p) of fixed effects, variance of the random effect of cohort (cohort variance), and sample size (# cohorts and # squirrels). Significant variables are in bold. The reference category for mast and study area were no mast experience and KL, respectively. The full original models prior to backward stepwise regression are included in Supplementary Materials (Table S6).

Discussion

While aggression and activity form a behavioural syndrome in red squirrels (this study; Boon et al., 2007; Taylor et al., 2012), we found no support for the hypothesis of a correlation between the pace of life history and aggression towards a mirror, which we interpret as a correlate of conspecific aggression, or activity in a novel environment (Biro & Stamps, 2008; Wolf et al., 2007). Specifically, we found no association between personality and either age at first reproduction or longevity, regardless of sex or mast experience. We did, however, find evidence of sex differences and environmental modulation of the association between personality and lifetime pup production (but not recruit production).

Sex differences but no association between personality and life history

Following the predictions of the pace-of-life syndrome hypothesis (Réale et al., 2010; Ricklefs & Wikelski, 2002), we predicted that more proactive (i.e., more active and more aggressive) individuals would also have a faster pace of life history; specifically, that they would have an earlier age at first reproduction and a shorter lifespan. However, counter to these predictions, we found no evidence of a link between personality and life history traits in either sex, regardless of mast experience. Failing to account for environmental conditions may be one reason that many studies do not find evidence of a pace-of-life syndrome (Royauté et al., 2018), as environmental conditions are expected to alter pace-of-life syndromes (Dammhahn et al., 2018; Montiglio, Dammhahn, Dubuc Messier, & Réale, 2018; Réale et al., 2010). We accounted for an influential component of the adult environment (mast experience) and this did not alter our conclusions. This adds to a handful of studies that have examined behaviour-life history associations under different environmental conditions (e.g., Bergeron et al., 2013; Charmantier, Demeyrier, Lambrechts, Perret, & Grégoire, 2017; Cote, Fogarty, Tymen, Sih, & Brodin, 2013; Debecker, Sanmartín-Villar, de Guinea-Luengo, Cordero-Rivera, & Stoks, 2016; Goulet, Ingley, Scharf, & Pruitt, 2016; Le Galliard, Paquet, & Mugabo, 2015; Montiglio, Garant, Bergeron, Messier, & Réale, 2014). Some studies have found an effect of the environment on pace of life syndrome expression (Cote et al., 2013; Goulet et al., 2016), while others have not (Bergeron et al., 2013). Given the rarity of studies, the specific reasons for these discrepancies are currently unclear.

Juvenile red squirrels experience annual changes in competition for vacant fall territories, in part due to the occurrence of mast events. These fluctuations in juvenile competition resulted in positive selection on maternal activity and negative selection for maternal aggression in some years, but the opposite patterns in other years (Taylor et al., 2014). This was found even though activity and aggression are phenotypically and genetically correlated (Boon et al., 2007; Taylor et al., 2012). Fluctuations in spruce cone availability also influence female red squirrel life history traits; for example, a greater proportion of yearling females breed in the spring preceding a mast than in years with low cone availability (Boutin et al., 2006). A stochastic environment can favour a range of reproductive tactics depending on the prevailing conditions, potentially resulting in decreased selection for any given phenotype (Hämäläinen et al., 2018). This can decouple the association between behaviour and life history leading to no overall association between life history and behaviour (Hämäläinen et al., 2018), as we found in our study.

Our results also suggest that there are sex differences in behaviour. Generally, males in species that lack paternal care are predicted to have a faster pace of life and more proactive behaviour than females (Hämäläinen et al., 2018) largely due to higher selection for males to increase encounter rates with potential mates or to compete with other males for mates.

However, in our study the sexes did not differ in activity and females were more aggressive than males. Thus, counter to theoretical predictions and some empirical evidence (Bonduriansky et al., 2008; Promislow, 2003; Réale et al., 2010), female red squirrels exhibit a more proactive phenotype than males in at least one trait. Aggressiveness may have higher fitness benefits for females than males such as through defending pups from predation (Studd, Boutin, Mcadam, Krebs, & Humphries, 2015; Westrick et al., 2019; Wolff & Peterson, 1998).

Sex- and context-specific fitness consequences of personality

We found that personality was associated with lifetime pup production but that the effect was sex- and context-specific. In males, we found a positive association between aggression and lifetime pup production when males experienced a mast year, supporting our initial prediction. Male red squirrels commit infanticide during mast years, likely to increase their mating opportunities (Haines et al., 2018), and we would expect an association between aggression and lifetime pup production if aggressive males are more successful at committing infanticide and gaining paternity benefits from it. In females, we had predicted that there would be no association between aggression and lifetime pup production as previous work found that aggression did not influence litter size or adult female overwinter survival (Boon et al., 2007, 2008; Taylor et al., 2014). Contrary to our predictions, we found a positive and significant association between lifetime pup production and aggression. Aggressive females may be better able to defend resources or protect their offspring (Sinn, While, & Wapstra, 2008; Studd et al., 2015; Wolff & Peterson, 1998). For example, aggressive female red squirrels may be better able to protect their offspring from infanticide, although this is contradicted by the lack of association between aggression and lifetime recruit production.

We had predicted that active males would have higher lifetime pup production as males achieve reproductive success by traveling large areas to access multiple females (Lane et al., 2009), but we only found support for this pattern in males that experienced a mast year. Proactive individuals are predicted to have higher metabolic rates and energy expenditure (Réale et al., 2010) and this has been supported by some empirical research in other species (e.g., Careau, Bininda-Emonds, Thomas, Réale, & Humphries, 2009; Careau, Réale, Humphries, & Thomas, 2010; Careau et al., 2011; Holtmann, Lagisz, & Nakagawa, 2017). Environmental influences may alter the association between personality and metabolism (Salzman, McLaughlin, Westneat, & Crowley, 2018). Although personality and metabolism in different contexts has not been tested in red squirrels, the association between energy expenditure and mating behaviour has been tested. Male red squirrels searching for females have high energy expenditure, but males searching the same area for females expend more energy during mast years compared with non-mast years (Lane et al., 2010). Thus, if proactive red squirrels also have higher metabolic rates, then active males may be better able to increase their mating effort and take advantage of the increased mating opportunities during mast years.

In both sexes, under some environmental conditions we found evidence that an active or aggressive phenotype was negatively associated or was not at all associated with lifetime pup production. Specifically, in all females we found no significant effect of activity on lifetime pup production, while in males who did not experience a mast year we found no association between activity and lifetime pup production, but a negative association between aggression and lifetime pup production. Negative associations or no associations may occur due to the energetic costs of being proactive (Holtmann et al., 2017; Réale et al., 2010) resulting in selection against these behaviours under some environmental conditions. Our results also suggest that there is fluctuating selection on personality due to fluctuating environmental conditions as has been found previously in red squirrels (Boon et al., 2007; Taylor et al., 2014) and in other species (Dingemanse et al., 2004; Dingemanse & Réale, 2005; Réale & Festa-Bianchet, 2003; Smith & Blumstein, 2008). However, we also found no association between personality and the number of recruits produced regardless of sex and mast experience. Thus, the higher total number of pups produced did not translate to an association between personality and offspring recruitment. This finding contrasts with previous work that demonstrated an association between maternal personality and annual offspring survival in red squirrels and also no association between litter size and maternal personality (Boon et al., 2007; Taylor et al., 2014). However, offspring quantity may trade off with offspring quality (Stearns, 1989) and this potential trade-off was not captured in our analysis. Thus, it is possible that although there is a link between personality and the number of pups produced over an individual's lifetime, there is a trade-off between red squirrel pup quality and quantity that warrants further consideration. Overall, this study adds to the accumulating evidence that ecological conditions play a significant role in determining the expression and fitness consequences of personality-life history associations. This research also adds to the series of studies that have failed to provide empirical support for the pace of life syndrome hypothesis.

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