Habitat-dependent effects of personality on survival and reproduction in red squirrels

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1   **Title:** Habitat-dependent effects of personality on survival and reproduction in red squirrels

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Abstract

Variation in intrinsic (body mass, reproductive condition) and extrinsic factors (habitat quality, spatio-temporal variation in food availability) can affect the costs and benefits of personality traits. Relationships between personality and fitness components can vary with changes in population density and/or habitat quality. Here, using capture-mark-recapture data of individually marked Eurasian red squirrels (*Sciurus vulgaris*), we explored whether indices of boldness and exploration are correlated with local survival in either of the sexes and with a measure of reproductive success in females, under different conditions of food availability. PCA scores derived from the number of captures (trappability) and number of different traps where an individual was captured (trap diversity), in the first one or two years of presence, were used as indices of personality (boldness and pure exploration). The relationships between boldness and local survival differed between habitats in both sexes. Bold squirrels survived better than shy ones in Norway spruce forest, while in the other two study areas (Scots pine, or mixed spruce-fir forest) survival was lower for bolder squirrels. Pure exploration behavior was negatively correlated with local survival in all habitats and in both sexes. Female reproductive success increased with body mass and decreased with the tendency to explore, a relationship consistent across habitat types. Bolder females did not have a reproductive advantage in years of poor food availability. We suggest that costs and benefits of boldness vary with spatio-temporal differences in availability of high-quality food resources which may help to maintain variation in personality in red squirrels in heterogeneous landscapes.

Significance statement

Differences in personality among individuals can affect their survival or reproductive success. We investigated the relationship between personality traits and fitness components in Eurasian red squirrels under different food availability. We scored boldness and exploration using indices derived from capture-

mark-recapture data. Bold red squirrels survived longer than shy ones in spruce forest where food availability varied strongly between years. Instead, in mixed forests with more stable food supplies shy individuals survived longer. Heavy females produced more litters in their lifetime than those with lower body mass. Explorative squirrels were more likely to die young and to produce no or few litters, independent of the habitat they lived in. Our results suggest that variation in personality traits within populations of Eurasian red squirrels was maintained by changing fitness benefits in relation to habitat type in pulsed resource systems.

Introduction

According to evolutionary theory, the way an individual behaves under local conditions should be adaptive because of natural selection favoring animals whose behavior increases fitness, given that this behavior is heritable. Variation in behaviors is maintained because of spatio-temporal changes in intrinsic and/or extrinsic environmental conditions causing variation in selective pressures (Carter et al. 2013; Weiss and Adams 2013). However, from the perspective of adaptive behavior, the fact that animals display variation in individual behaviors that are consistent over time (within or across generations) and/or under different contexts is more difficult to explain (Dall et al. 2004; Réale et al. 2007; Biro and Stamps 2008). Animal personality refers to between-individual differences in behavior that persist through time (Biro and Stamps 2008; Carter et al. 2013). These differences in individual personality, also called temperament or 'coping style' (Bergmüller and Taborsky 2010), are often measured through traits such as reaction to potential risks or handling novelty, aggressiveness and sociability (e.g. Réale et al. 2007). If differences in personality are adaptive, they may affect how populations respond to environmental change and how species are able to persist (Dall et al. 2004; Le Coeur et al. 2015).

An individual's willingness to take risks, referred to as boldness, has been investigated in many wild populations showing that this personality trait is related to several ecological aspects, such as propensity to explore and acquire information about the environment, dispersal distance and/or speed (Fraser et al. 2001; Korsten et al. 2010; Minderman et al. 2010; van Overveld et al. 2015). Although recent studies have shown

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that personality can affect several components of fitness (Dingemanse and Réale 2005; Patterson and Shulte-Hostedde 2011; Mutzel et al. 2013; Zhao et al. 2016), it remains unclear whether bold phenotypes have a fitness advantage over shy ones. Several studies on birds and mammals found that bold and/or fast exploring individuals are often the most dominant ones during intraspecific encounters (Dingemanse and de Goede 2004; Rödel et al. 2015). For example, fast-exploring males of the great tit (*Parus major*) occupied better quality territories and fast-fast pairs produced offspring in better condition than slow-exploring pairs (Both et al. 2005). In Norway rats (*Rattus norvegicus*) explorative individuals survived longer than less explorative ones (Cavigelli and McClintock 2003).

However, in a taxonomically broad meta-analysis Smith and Blumstein (2008), exploring the effects of exploration and boldness on fitness components (survival and/or reproductive success), reported contrasting findings. Some studies showed that bolder animals encounter more risks due to their exploring tendency, which resulted in higher susceptibility to predation and higher mortality risk (e.g. Bremner-Harrison et al. 2004; Carter et al. 2010; Hall et al. 2015). In the European rabbit (*Oryctolagus cuniculus*), explorers had significant survival costs during the juvenile life-stage (Rödel et al. 2015). Still a different pattern was revealed in Eastern chipmunks (*Tamias striatus*) where animals with average exploration levels suffered higher mortality than extreme phenotypes (Bergeron et al. 2013).

Variation in personality may be maintained by fitness trade-offs. For example, bold (active and aggressive) female North American red squirrels (*Tamiasciurus hudsonicus*) were more likely to bequeath their territory, which resulted in higher reproductive success through increased overwinter survival of their offspring. However, bold females had higher winter mortality than shy ones (Boon et al. 2008). In addition, spatio-temporal variation in ecological selection pressures can play a role in maintaining animal personalities in populations in heterogeneous environments, both in short- and long-lived species (Réale et al. 2000; Le Coeur et al. 2015; Vetter et al. 2016).

So far, most studies on personality-fitness relationships have been carried out in a single population and we know only a few studies on mammals that have investigated effects of personality on fitness in different habitats (e.g. Boon et al. 2007; Martin and Réale 2008; Monestier et al. 2015).

103   Here we measured personality traits in the Eurasian red squirrel (*Sciurus vulgaris*) in three different

104   habitats and investigated to what extent boldness and exploration tendency of adults were correlated with

105   phenotypic traits (body size and body mass) and with fitness components. The red squirrel is a good model

106   species to investigate relationships between personality and fitness components under different habitat

107   conditions for several reasons: 1) previous studies on other tree squirrels have shown that personality traits

108   can affect habitat and/or space use, survival and reproductive success (e.g. Boon et al. 2008; Boyer et al.

109   2010; Le Coeur et al. 2015); 2) reliable methods and indices to study personality have already been developed

110   for other sciurids (Boon et al. 2008; Boyer et al. 2010); 3) long-term capture-mark-recapture data of

111   individually-marked squirrels combined with radio-tracking show high capture probabilities for the majority

112   of resident adults and provide detailed information of phenotype, local survival, and reproductive success

113   (of females) (Wauters et al. 2004, 2007, 2008).

114   Our main hypothesis is that costs and benefits of personality types vary according to environmental

115   conditions. Hence, we predict that in different habitats (with spatio-temporal variation in food availability)

116   different personality types will perform better; in other words, bold squirrels may perform better than shy

117   ones in one habitat type, but not in other habitat(s). To test this hypothesis we first checked for correlations

118   between personality indices and body size and body mass. Since in this species heavier males tend to be

119   more aggressive and have higher mating success (Wauters and Dhondt 1989, 1992; Wauters et al. 1990),

120   while in females body mass positively affects the probability to enter estrus and lifetime reproductive success

121   (Wauters and Dhondt 1989, 1995). Next, we explored potential advantages or disadvantages of being bold

122   by studying whether our indices of boldness and exploration were correlated with local survival in both sexes

123   and with a measure of reproductive success in females, and whether these relationships varied among

124   habitats. Finally, we also tested the hypothesis that being bold might be advantageous for reproduction only

125   in years of poor food availability. We used capture-mark-recapture data of individually marked squirrels to

126   obtain data of sex, body size and body mass, and estimates of local survival and female reproductive success.

127   The total number of captures (trappability) and number of different traps where an individual was captured

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128 (trap diversity), over a maximum of two years, were used as indices of the personality traits boldness and

129 exploration, respectively (Boon et al. 2008; see methods for details).

130

131 **Materials and methods**

132 *Study species*

133   Eurasian red squirrels have overlapping home ranges, with intensively used core- areas, whose size

134 differs between the sexes, and in relation to season and habitat quality (e.g. Wauters and Dhondt 1992; Lurz

135 et al. 2000; Wauters et al. 2001, 2005). The mating system is promiscuous, although most females only mate

136 with a dominant male of high body mass (Wauters et al. 1990). Reproduction is seasonal, with 1 to 2 litters

137 per year, and is strongly affected by the female's body condition, food abundance and, in the mountains,

138 elevation (Wauters and Dhondt 1995; Wauters et al. 2008; Rodrigues et al. 2010). In our study areas, females

139 can be lactating between April and October and may produce one or two litters/year (Boutin et al. 2006;

140 Wauters et al. 2008). Most animals disperse as juveniles and subadults (from 4 to 10 months old, Wauters

141 and Dhondt 1993; Wauters et al. 1993, 2010). Once settled, adult squirrels tend to have a high site-fidelity.

142 There is no sexual size dimorphism (Wauters et al. 2007).

143

144 *Study areas and food availability*

145   We studied red squirrels in three study areas in the Italian Alps, two in Lombardy and one in Valle

146 d'Aosta, N. Italy. Cedrasco (CED, 46°07' N, 9°48' E, elevation 1100 – 1600 m a.s.l.) is a mixed montane conifer

147 forests on the northern slope of the Orobic Alps, N. Italy. The study area extends over 76 ha of mature

148 secondary forest (mean tree density ± SD = 449 ± 163 trees ha^{-1}), with large areas of even-age stands

149 dominated by silver fir (*Abies alba*, tree cover 56%) and Norway spruce (*Picea abies*, 25%), with sparse Scots

150 pine (*Pinus sylvestris*, 5%), larch (*Larix decidua,* 3%) and dead trees (5%). Spruce and fir were interspersed at

151 a fine-grained level and not clumped. At lower elevations, spruce and fir were mixed with some beech (*Fagus*

152 *sylvatica*, 7% tree cover). The second study area, Oga (OGA, 46º28´N, 10º22´E, elevation from 1280 m to

153 1450 m a.s.l.), is part of a mature mixed montane conifer forest (47 ha, mean tree density ± SD = 765 ± 251

154 trees ha^{-1}), dominated by Scots pine (*Pinus sylvestris*, 88.7% tree cover) with some Norway spruce (*Picea*

155 *abies,* 8.8%) and larch (*Larix decidua,* 2.5%). The third study area, in Val di Rhêmes (RHE, 45°39'N, 7°12'E,

156 elevation 1740 – 1890 m a.s.l.) is a mature Norway spruce forest (85%) with some mixed patches of larch

157 (11%) and spruce (69 ha, mean tree density ± SD = 773 ± 333 trees ha^{-1}). Snags (dead trees) are common

158 (4%), occurring throughout the study area. Distances between the areas are CED-OGA 58 km, CED-RHE 217

159 km, OGA-RHE 271 km (Trizio et al. 2005).

160   Each year between 26 July – 9 August, the new (current year) maturing cones were counted in the

161 canopy of sample trees of all conifer species to estimate food availability. Methods are described in detail

162 elsewhere (Salmaso et al. 2009; Di Pierro et al. 2011). Based on species-specific energy values per cone

163 (kJ/cone) and data on tree species composition and density (Salmaso et al. 2009), these counts allowed us to

164 estimate the average yearly tree seed-energy production in each study area (Table 1).

165   The three populations had similar sex ratio's and age structure (Wauters et al. 2007, 2008). There

166 were no differences in allelic richness between areas, but squirrels at RHE had slightly lower observed

167 heterozygosity than at CED and OGA (10 microsatellites, Trizio et al. 2005). All had goshawk, red fox and

168 marten as potential squirrel predators.

169

170 *Trapping and handling*

171   Trapping was carried out in three periods per year (April-May, June-July, September-October)

172 between April 2000 and October 2006 in OGA and between April 2000 and April 2009 in CED and RHE (Table

173 1). A trapping session involved the use of 25 (CED), 23 (OGA) or 30 (RHE) ground-placed Tomahawk "squirrel"

174 traps (models 201 and 202, Tomahawk Live Trap, WI, USA). Steep slopes and mountain orography made it

175 impossible to set traps in a perfect grid, hence traps were more or less homogeneously distributed over the

176 study area, with distances of 100-130 m between traps and average trap density of 0.7-0.8 traps ha^{-1}.

177   In CED and RHE the forest continued beyond the boundaries of the study area. In contrast, the study

178 area of OGA was entirely surrounded by hard edges (road and parking area, meadows, river). Traps were pre-

179   baited with sunflower seeds and hazelnuts 4 to 6 times over a 30 day period, then baited and set for 6-10

180   days, until no new, unmarked squirrels were trapped for at least 2 consecutive days (Wauters et al. 2008).

181   Traps were checked two-three times per day.

182   Each trapped squirrel was flushed into a light cotton handling bag with a zipper or a wire-mesh

183   "handling cone" to minimize stress during handling, and individually marked using numbered metal ear-tags

184   (type 1003 S, National Band and Tag, Newport, KY, USA). It was weighed to the nearest 5 g using a spring-

185   balance (Pesola AG, Baar, Switzerland) and the length of right hind foot (without nail) was measured (0.5

186   mm) with a thin ruler. Foot length is a measure of structural size and remains fixed once the animal has

187   reached adult size (12-18 month old). In contrast, body mass can also vary with season, age or between years

188   with poor or high food availability (Wauters et al. 2007). Therefore, in our models (see "Effects of personality

189   on fitness components") foot length as adult and average body mass over the three trapping sessions in the

190   first year the squirrel was classified as adult (12-18 months old, see also Wauters and Dhondt 1989) were

191   used as measures of morphological parameters. For foot length, variance from repeated measures was low

192   (13% of total variance) compared to variance caused by individual differences in size (87% of total variance),

193   indicating that measurement error was small (Wauters et al. 2007). Sex and age class were determined on

194   the basis of external genitalia and body mass, with juveniles weighing less than 250 g (Wauters and Dhondt

195   1995). Female reproductive condition was determined based on external genitalia and condition of the

196   nipples: pregnant females have enlarged vulva and small nipples, lactating females have swollen nipples and

197   milk excretion can be stimulated, post-lactation females have still large nipples but no longer produce milk

198   (Wauters and Dhondt 1995). It was not possible to record data blind because our study involved capture-

199   mark-recapture in the field.

200   Capture probabilities of squirrels in the three populations were calculated using loglinear robust

201   design in package Rcapture (Rivest and Baillargeon 2014). Robust design applies a closed population model

202   for each trapping session. The Poisson regression used to fit a robust design model has one entry for each

203   possible capture history, including those that are unobserved.

204

205 *Personality: trappability and trap diversity indices*

206   For each individual we calculated two indices of personality: a trappability and trap diversity index.

207 The first is a measure of tendency to take risks (boldness), the second measures the animal's propensity to

208 explore novel environments. In sciurid rodents, these two indices have been shown to be repeatable

209 measures of personality, but they also tend to be correlated (Boon et al. 2008; Boyer et al. 2010). The indices

210 were estimated using the standardized values, per study area, of the ratio of number of captures on the

211 length of capture period (i.e. the number of capture days from the first to the last trapping session for a given

212 animal; boldness); or the ratio of the number of different traps in which an animal was captured on the

213 number of available traps (exploration). Since recent studies have shown that personality traits can change

214 over time (flexible component of personality, e.g. Dingemanse et al. 2012), we only used capture data of the

215 first two years an individual was present (using only subadults and adults). Since we only had three

216 sessions/year, using only first year data would strongly reduce the variation among individuals in trappability

217 and trap diversity. Standardization was done for each study area separately because of differences in capture

218 histories and number of available traps.

219   Since the two standardized indices were strongly and positively correlated (r = 0.76; n = 141; $P <$

220 0.0001), they could not be used together as explanatory variables in multivariate models because of lack of

221 independence when estimating their partial effects. Therefore, we used a principal component analysis (PCA)

222 to derive two new variables, the principal components PC1 and PC2 (orthogonally rotated), maximizing the

223 variance of these among individual squirrels. PC1 (loadings: 0.707 trappability index + 0.707 trap diversity

224 index, eigenvalue 1.33) explained 88% of total variance, PC2 12% (loadings -0.707 trappability index + 0.707

225 trap diversity index, eigenvalue 0.49). PC1 has a high score for those animals that are often captured and in

226 many different traps, so it can be considered as a measure of boldness which includes both risk taking and

227 exploration. PC2 has a high score for those animals that are captured few times but nearly always in a

228 different trap, hence indicating a specific exploration component of the animal's personality. The fact that

229 PC2 has an eigenvalue below 1 is inherent to a PC-analysis with two variables. The commonly used threshold

230 of PC's with eigenvalues above 1 is thus not meaningful here to decide which components to retain for further

231 analyses. On the contrary, the aim of our PC-analysis was to generate uncorrelated dimensions of personality

232 that can jointly be included in statistical analyses. We thus argue that as long as PC2 is repeatable over time,

233 it contains biologically relevant information to include in our analyses. Recent data on arena tests (open field

234 test and mirror image stimulation test) with red squirrels showed that trappability and trap diversity indices

235 of personality are confirmed by behavior in the arena test, as in other sciurids (Boon et al. 2008; Boyer et al.

236 2010; Le Coeur et al. 2015; our unpubl. data).

237 Our data could potentially contain a bias in estimates of trappability, trap diversity and survival, due

238 to a lower capture probability for individuals living at the edge of the study areas (e.g. Boyer et al. 2010).

239 However, position and size of home ranges of 91 radio-tracked squirrels (for details see Wauters et al. 2005;

240 Romeo et al. 2010; Di Pierro et al. 2011) showed that their large home range overlapped with several traps

241 (5 to 10) both at study area periphery and more central ones. Hence, to eliminate the risk of a potential bias

242 we removed from our dataset those animals only caught in edge traps. Radio-tracking data also confirmed

243 the reliability of our survival estimates, with only two (2%) radio-tagged squirrels still present (alive) after the

244 last capture event.

245

246 *Repeatability of trapping indices and PCA scores*

247 To analyse the link between trapping characteristics and individual personality we needed to verify

248 that trapping characteristics were consistent across years for the same individual (i.e. trapping characteristics

249 as an expression of personality, e.g. Boyer et al. 2010). Using a restricted sample of 49 individuals that were

250 caught in two successive years during the study period, we estimated the repeatability, also called Intra-class

251 Correlation Coefficient (ICC), in the number of captures per year and in trap diversity per year with a Linear

252 Mixed Model (LMM) (Nakagawa and Schielzeth 2010). Repeatability was estimated using the R package rptR

253 v 0.9.2 (CI= 95%, number of parametric bootstraps for interval estimation= 5000, number of permutations

254 used when calculating asymptotic p-values= 1000; Stoffel et al. 2017). In this case, number of captures was

255 log transformed (using natural logarithm) and trap diversity (number of different traps) square root

256 transformed to meet assumptions of normality (Shapiro-Wilk's test on transformed data, both $W > 0.95$) (see

257 also Boyer et al. 2010). We included sex, study area and year and second order interactions as fixed effects

258 and squirrel identity as random factor. Length of capture period was constant between the two years. We

259 also estimated repeatability of the PC1 and PC2 scores derived from these trapping indices (see below) using

260 the same LMM model structure as above.

261

262 *Effects of personality on fitness components*

263   To explore relationships between personality and fitness parameters we estimated local survival of

264 squirrels of both sexes and reproductive success of females. Length of residency was used as a proxy for local

265 survival and was estimated as the number of months between first and last capture, for those squirrels that

266 remained on the study area for at least 6 months (see also Wauters et al. 2007). To avoid potential bias in

267 survival estimates due to selective disappearance or between population differences in age structure, we

268 only used squirrels from extinct cohorts (n = 132). Reproductive success was measured as the total number

269 of litters produced per female throughout its lifetime, using only females that were trapped in at least two

270 of three sessions/year (for models on number of litters). In April-May, females could be scored as pregnant

271 or lactating if they had a spring litter. In June-July, as pregnant-lactating in case of a single intermediate litter

272 or an autumn litter or as post-lactating in case of spring litter. In September-October, as lactating or post-

273 lactating (autumn or intermediate litter, respectively). Hence, females that were trapped in at least two of

274 three sessions allowed to distinguish between production of no, a single or two litters/year. Since both

275 parameters are counts, we used them as dependent variables in GLM models with Poisson error distribution

276 and used sex, study area, body mass, foot length (as co-variate of body mass, see Wauters et al. 2007), and

277 the boldness and exploration scores (PC1 and PC2) from the PCA as fixed effects, and the second order

278 interactions of study area with PC1 and PC2 (both models) and of sex with PC1 and PC2 (survival model).

279 Although the standard deviation of PC2 was below 1 (which is inherently so when only 2 variables are

280 included in the PC-analysis), we did include it in these analyses because of its biological interpretation

281 (specific exploration) and the fact that PC2, as well as PC1, appeared repeatable over time (see below). When

282   none of these interactions were statistically significant (all partial *P* > 0.05) we presented models only with

283   main effects. In contrast, if one of the interactions was significant, further model selection was carried on a

284   subset of the data (by study area) to allow reliable estimates of fixed effects (Online Resource 1 Tables S1 –

285   S3). Since patterns of longevity were sex-biased (higher local survival in males than in females; significant sex

286   by PC2 interaction, Online Resource 1 Table S1) the models were tested for males and females separately

287   (see also Wauters et al. 2004). In both sexes, significant interactions were found between study area and

288   PC1: they always indicated a different relationship for study area RHE in comparison to study areas CED and

289   OGA (Online Resource 1 Tables S1 – S3, see also results). Therefore, in these cases separate models for (a)

290   CED and OGA, and (b) RHE were further tested using only the main effects.

291   We also tested the hypothesis that being bold might be advantageous for reproduction only in years

292   of poor food availability (e.g. Le Coeur et al. 2015). We classified seed-crops in two categories: poor vs.

293   medium-good seed crop (Table 1). In each reproductive period (spring and summer-autumn) we determined

294   if a female produced a litter or not (binary dependent variable, 190 observations of 57 different females) and

295   investigated relationships with study area, food availability (poor vs medium-good) and PC1 score along with

296   the interaction of PC1 with food availability, using a mixed effects logistic regression model which included

297   squirrel identity as a random effect. Spring litters were related to the previous year's seed-crop, summer-

298   autumn litters to the same year's seed-crop (Boutin et al. 2006; Wauters et al. 2008).

299   Distributions of data on longevity and reproductive success were skewed. Therefore, we repeated

300   the above models using a negative binomial distribution of the dependent variable. Since results were similar

301   as models with a Poisson distribution we only present results of the latter.

302   All tests of significance are two-tailed and the significance level was set at 0.05. Except for

303   repeatability, all other statistical analyses were done using SAS/STAT 9.4 software (Copyright © 2011, SAS

304   Institute Inc., Cary, NC, USA).

305

Results

Trappability and trap diversity indices

In the three study areas, the capture probabilities at population level (including only the animals used in this study) were high and stable over time (mean capture probability per year ± SE: CED 0.98 ± 0.05; OGA 0.96 ± 0.02; RHE 0.98 ± 0.01; details in Table S4).

Within a period of maximum two years (see methods), the number of captures per individual red squirrel varied between 2 and 41 times (median 7, mean ± SE = 9.4 ± 0.6 captures), and number of different traps from 1 to 13 (median 5, mean ± SE = 5.2 ± 0.2 traps). On average, males were trapped more often than females (males, n = 78, 11.2 ± 1.0 captures; females, n = 63, 7.2 ± 0.7 captures; $F_{1, 135}$ = 11.5, P = 0.0009), and in more different traps (males, n = 78, 5.8 ± 0.4 traps; females, n = 63, 4.4 ± 0.3 traps; $F_{1, 135}$ = 9.90, P = 0.002). The number of times a squirrel was captured did not differ significantly between study areas ($F_{2, 135}$ = 1.40, P = 0.25); however, on average squirrels were trapped in more different traps in OGA (n = 40, 5.3 ± 0.5 traps) and RHE (n = 56, 5.8 ± 0.4 traps) than in CED (n = 45, 4.2 ± 0.4 traps; area effect $F_{2, 135}$ = 4.59; P = 0.012; Fig. 1). These differences between areas did not influence our results since trapping indices were standardized within study areas.

We observed consistent individual variation across years in number of captures (n = 49; repeatability = 65%, 95% CI = 46 − 81%, Likelihood ratio test LRT = 25.9; df= 1; P < 0.001) and in trap diversity (repeatability = 69%, 95% CI = 52 − 83%, Likelihood ratio test LRT = 29.9; df= 1; P < 0.001). Thus, trappability and trap diversity indices are consistent through time suggesting they are reliable estimates of a red squirrel's personality. Similarly, highly significant repeatabilities were found for the PC1 and PC2 scores derived from these indices (PC1: repeatability = 78%, 95% CI = 66 − 88%, Likelihood ratio test LRT = 43.9; df= 1; P < 0.0001; PC2 repeatability = 37%, 95% CI = 14 − 63%, Likelihood ratio test LRT = 6.58; df= 1; P = 0.005). In spite of the fact that PC2 explained only 12% of the total variation, it does seem to be moderately repeatable through time and this reflect a biologically real phenomenon. This, in combination with the fact that PC2 has a straightforward biological interpretation of an aspect of squirrel personality favors its use in the statistical analyses below.

13

Phenotypic variation and personality

Neither foot length, nor body mass were correlated with the personality scores (Table 2). These patterns were consistent when analyzed by sex (Table 2).

Fitness components of males

Local survival of male red squirrels was higher in OGA (n = 21, mean ± SD = 27 ± 19 months) than in CED (n = 24, 19 ± 10 months) and RHE (n = 29, 18 ± 15 months) and relationships between PC scores and survival differed between study areas (Comparison RHE against OGA and CED, all partial $P < 0.05$). In study areas OGA and CED, local survival increased with body mass but not with body size (Table 3a). Both PC scores for personality were negatively related with longevity (Table 3a).

In study area RHE patterns were different. Larger males had a higher local survival and boldness score (PC1) was positively related to survival. The effect of body size was much stronger than of body mass. The specific exploration score (PC2) was negatively related to local survival as in the other study areas (Table 3b). In the full model, the partial effect of PC1 was not significant, but considered as a single factor there was a positive relationship between boldness score and local survival (estimate 0.13 ± 0.04, $\chi^2 = 12.9$; $P = 0.0003$).

Fitness components of females

Also among female red squirrels, local survival was higher in OGA (n = 19, mean ± SD = 20 ± 17 months) than in CED (n = 15, 14 ± 8 months) and RHE (n = 24, 15 ± 8 months) and the relationship between survival and the two PC scores differed between study areas (comparison RHE against OGA and CED, all partial $P < 0.01$). In study areas OGA and CED the GLM model gave the same results as for males: there was no significant effect of body size on female survival, while heavier females survived longer than those of lower body mass (Table 4a). Local survival was negatively related to both PC scores, but only PC2 was significant (Table 4a). In contrast, in RHE the coefficient of foot length was negative, while that of body mass positive, indicating a strong positive effect of body condition (mass rather than size) on local survival of

female red squirrels (Table 4b). As for males in this study area, the boldness score (PC1) was positively

related, and the specific exploration score (PC2) negatively related to female survival (Table 4b).

The number of litters that females weaned while present on the study area varied between 0 and 7

(n = 57, mean ± SD = 1.67 ± 1.54). Heavier females produced more litters than those of poorer body mass

(body mass parameter estimate 0.019 ± 0.005; χ^2 = 13.7; df = 1; P = 0.0002). Tendency to explore was

negatively related to the number of litters produced (partial effect PC2 score -0.86 ± 0.24; χ^2 = 12.3; df = 1; P

= 0.0005). On average, females tended to produce more litters in OGA (n = 17, mean ± SE = 2.29 ± 0.54 litters)

than in RHE (n = 23, 1.52 ± 0.23 litters) and CED (n = 17, 1.24 ± 0.31 litters; area effect χ^2 = 5.91; df = 2; P =

0.052), but pairwise differences were significant only between OGA and CED ($P < 0.05$). Partial effects of foot

length or boldness score (PC1) were not significant (both P = 0.10).

In periods of poor seed-crops (46 observations), there were 16 cases (35%) of offspring production

and 30 cases (65%) of females not reproducing. In contrast, in years of medium-good seed-crops (144

observations) females were more likely to produce offspring (81 cases, 56% against 63 cases of females not

reproducing; food availability estimate 0.96 ± 0.38; χ^2 = 6.42; df = 1; P = 0.011). Bolder females were not more

likely to produce offspring than shy ones (PC1 χ^2 = 0.10; df = 1; P = 0.75), and this did not change between

periods of poor against medium-good seed-crops (PC1 by food availability interaction χ^2 = 0.69; df = 1; P =

0.40). There was no effect of study area (χ^2 = 1.94; df = 2; P = 0.38).

Discussion

Our analyses of capture-mark-recapture data of individual Eurasian red squirrels showed that scores

derived from the number of times a squirrel is trapped (trappability) and from the number of different traps

visited (trap diversity), during the first one or two years of presence, are repeatable across years and

therefore can be used as indices of an individual's personality. There was no correlation between boldness

or exploration scores and body size or body mass of the squirrels, suggesting that personality was not related

to body condition, a good proxy of an individual's quality. We found that the relationships between boldness

score and local survival/residency of individual squirrels differed between habitats, in males as well as in

384   females. Survival of bold individuals was higher than that of shy individuals in the habitat dominated by

385   Norway spruce (RHE), while in the other two study areas, a Scots pine dominated forest (OGA) and a mixed

386   spruce-fir forest (CED) bolder squirrels survived less well. The second PCA score, related to specific

387   exploration behavior, was negatively correlated with local survival in all habitats and in both sexes. For

388   females, the relationships between personality and body mass on one hand, and reproductive output

389   (number of litters in lifetime) on the other hand, were consistent across habitat types. Reproductive success

390   increased with female body mass, but decreased with the tendency to explore. Bolder females did not have

391   a reproductive advantage in years of poor food availability.

392

393   *Reliability of capture-mark-recapture data for deriving indices of personality and for estimating local survival*

394   In this study, we used two indirect indices of personality: trappability which is generally linked to risk

395   taking behavior, and the tendency to visit more different traps (trap diversity) which is considered as a

396   measure of exploration (Boon et al. 2008; Boyer et al. 2010). Similarly to studies on other Sciuridae we found

397   consistent individual differences across years in both indices suggesting they measure personality traits of

398   Eurasian red squirrels (Boon et al. 2008; Boyer et al. 2010; Montiglio et al. 2012; Le Coeur et al. 2015).

399   Moreover, capture probabilities of red squirrels tend to be high and this was the case also in the study areas

400   used here with high average capture probability per session which varied little over seasons or years (see

401   section "Study species", see also Wauters et al. 2008), allowing us to use and compare data over several

402   years.

403   Males were trapped on average more often and in more different traps than females, which is

404   consistent with space use differences between the sexes with males using larger home ranges than females

405   (Wauters and Dhondt 1992; Romeo et al. 2010; Di Pierro et al. 2011). Both sexes were captured in more

406   different traps in OGA and RHE than in CED, which may have been due to different numbers of available

407   traps. This potential bias among study areas was eliminated by standardizing trappability and trap diversity

408   within each study area. The first component of the PCA (PC1), measuring both risk taking and exploration

409   tendency and thus considered as a general boldness score, explained 88% of total variance and therefore

410   was the most relevant component. Nevertheless, we feel that PC2 is biologically relevant as it allowed us to

411   measure a pure exploration tendency. However, care is needed in using this component because of the low

412   variance explained, but where models show a significant contribution of PC2, it is not more prone to bias or

413   type I error compared to PC1.

414   We used the same capture-mark-recapture data to derive both personality and survival estimates,

415   which assumes the two estimates to be independent. Length of residency is commonly used in studies on

416   sciurids as an estimate of local survival (Gurnell et al. 2004; Wauters et al. 2004, 2007), with the precaution

417   to use only animals that stayed at least 6 month in the study area (eliminating dispersers) as we have done

418   here. Local survival was estimated from the entire trapping history of the individual and is only based on first

419   and last capture, while personality was estimated using all captures in each session, but only over the first

420   two years the individual was present (see methods). In principle, there could be a potential bias in that shy

421   individuals, which are trapped less often and visit fewer traps, would appear to have a shorter lifespan.

422   However, this was not the case in our study. As stated in the methods, estimated length of residency was

423   confirmed by data on radio-tracked animals. Moreover, in two out of three study areas shy animals (captured

424   fewer times) lived longer than bold ones, showing that the potential bias is weak or non-existent.

425

426   *Personality and phenotypic characteristics*

427   Since personality and body growth can be related, body size/mass should be taken into account when

428   testing for effects of personality on reproductive parameters (Rödel and Meyer 2011; Guenther and Trillmich,

429   2015). In some mammalian species, heavier animals were bolder and more explorative than conspecifics of

430   lower body mass, especially among pups (Rödel and Meyer 2011; Guenther and Trillmich, 2015; Vetter et al.

431   2016). Bolder animals tend to be more aggressive (proactive-reactive syndrome) (Huntingford 1976;

432   Koolhaas et al. 1999; Bell and Stamps 2004; Sih et al. 2004; Groothuis and Carere 2005) and, in our study

433   species, heavier squirrels were more aggressive than those in poorer condition (Wauters and Dhondt 1989).

434   However, here we found that personality scores of red squirrels were not correlated with body mass or size

435   (foot length). In high-density populations of red squirrels, where encounters between individuals are

436 frequent, body mass tends to increase with age and heavier, older males are more aggressive than lighter,

437 younger ones and these heavier males are more likely to mate (Wauters and Dhondt 1989; Wauters et al.

438 1990). Heavier, older females occupy higher quality (exclusive) core areas and have higher reproductive

439 success than animals of lower body mass (Wauters and Dhondt 1992, 1995). We must underline however

440 that in the alpine population studied here, densities were much lower (0.2 to 0.5 squirrels/ha against 0.8 to

441 1.5/ha in the lowland high-density populations) with less frequent encounters (our unpubl. data), which may

442 lead to animals being less aggressive independent of their body size/mass. This will be tested in future

443 research using Mirror Image Simulation (MIS) in arena tests (e.g. Réale 2007; Boon et al. 2008).

444

445 *Body condition, personality and survival*

446   In agreement with previous studies we showed that individual variation in body mass is a major factor

447 affecting survival: heavier squirrels of both sexes had a higher local survival than animals of lower body mass

448 (see also Wauters and Dhondt 1989; Wauters et al. 2007). This is a general pattern found in many mammals

449 for which there is a direct relationship between body mass and survival (Festa-Bianchet et al. 1997) and in

450 relation to food availability (Boutin and Larsen 1993). In fact, average survival was higher in the Scots pine

451 dominated forest of OGA where spatio-temporal variation in tree-seed availability was lower than in the

452 other two habitats (Table 1; see also Wauters et al. 2008; Salmaso et al. 2009). In our study, personality was

453 correlated to local survival of both male and female squirrels in different ways according to the study area.

454 In Norway spruce dominated forest (RHE), bolder squirrels of both sexes had a higher survival than shy ones,

455 although the pattern was more evident in females. Home range sizes of male and female red squirrels in this

456 habitat were much larger than in the Scots pine wood of OGA and the mixed conifer forest of CED (Wauters

457 et al. 2005; Romeo et al. 2010; Di Pierro et al. 2011). A tentative explanation is that when spatio-temporal

458 variation in food availability is high, having larger home ranges will allow better access to limited food

459 resources, and bolder/exploring animals may use larger ranges than shy ones (Bell 2007; van Overveld and

460 Matthysen 2010; Minderman et al. 2010). Alternatively, bold animals may have better resource acquisition

461 abilities when resources are scarce or more widely distributed (Biro and Stamps 2008), since their high

18

activity or exploration (compared to shy individuals) may bring more opportunities to discover essential resources in a heterogeneous environment (Wolf et al. 2007). In contrast, in our other two study areas (OGA and CED), bold animals had lower local survival than shy ones, which is in accordance with Boon et al. (2008) who found that the more active (higher trappability) female American red squirrels (*Tamiasciurus hudsonicus*) were less likely to survive until the spring of the following year. These habitat related differences could be explained by a higher cost of risk taking behavior in the latter two study areas, potentially due to higher risk of predation (Sih et al. 2004; Boon et al. 2008) or parasitism (Morand et al. 2006; Boyer et al. 2010; Patterson and Schulte-Hostedde 2011). Although Eurasian red squirrels have a poor macroparasite fauna (only one gastrointestinal helminth and two ectoparasites that are common, with prevalence > 10%), there is marked variation in parasite abundance and/or prevalence between individuals, at least partly related to variation in host body mass and habitat type (Romeo et al. 2013; Santicchia et al. 2015a). It should be further investigated whether bolder red squirrels indeed have higher parasite infections in some habitats, as was the case in Siberian chipmunks (*Eutamias sibiricus*; Boyer et al. 2010). We are aware that our study system lacks replication of the ecological variables mentioned here, at least for the highly-variable Norway spruce forest, but this does not weaken our main finding that the relationships between personality traits and survival differs among populations.

Another possible trade-off in costs/benefits of being bold was found in introduced Siberian chipmunks in France: bolder animals had a higher survival and reproductive success than shy ones in low resource years, but this was not the case when resources were abundant (Le Coeur et al. 2015). In great tits (*Parus major*), faster explorers were favored under lower densities but slower explorers under higher densities and temporal variation in local density represented the primary factor explaining personality-related variation in viability selection (Nicolaus et al. 2016). Our multi-year data on survival in different habitats produced rather similar patterns, with an advantage for bolder squirrels only in the habitat with higher variability in food abundance and squirrel density (RHE, Table 1; see also Wauters et al. 2008; Bisi et al. 2016).

487   In this study we separated a general boldness-exploration component of personality from a second

488   pure exploration component (see also Boon et al. 2008). Increased predation risk, encountering more

489   parasite infective stages and higher energy demands may all be involved in explaining why we always found

490   a negative effect of our pure exploration score (PC2) on local survival (both sexes) and on reproduction

491   (females). However, two points must be made when considering the effects of our exploration score. First,

492   as stated above, it explains only a limited amount of the variation among individual squirrels (12%); hence its

493   relationships should be interpreted with care. Second, we are measuring local survival of squirrels in the

494   study area: this measure might include animals that disappeared from our study areas due to emigration,

495   especially among those at the lower tail of the survival distribution (those with 6-12 months of local survival)

496   (e.g. Ergon and Gardner 2014). Although most dispersal in red squirrels occurs during the juvenile-subadult

497   phase (Wauters and Dhondt 1993; Wauters et al. 2010, 2011), some adults do undertake dispersal

498   movements (Wauters and Dhondt 1993; Lurz et al. 1997). However, in general site fidelity of adult red

499   squirrels is high and in our study areas 91 out of 107 (85%) radio-tracked adults remained within established

500   home ranges, with most cases of dispersal occurring in RHE in response to a poor seed-crop (e.g. Wauters et

501   al. 2005; Romeo et al. 2010; Di Pierro et al. 2011). We tried to remove dispersers as much as possible from

502   our dataset by using only adults that remained at least for 6 months on the study area and, among radio-

503   tracked animals, using only those that settled. Apart from this methodological point, our pure exploration

504   score (PC2) was negatively related to the fitness components studied (survival and reproduction). Only a few

505   studies found a small positive effect of exploration tendency on survival (and no relationship between

506   exploration and reproductive success, e.g. Smith and Blumstein 2008), whereas others reported negative

507   effects as in this study (Carter et al. 2010; Hall et al. 2015), although often related to early life-stages (Rödel

508   et al. 2015). We only used subadults and adults in our dataset, but still wider movements by pure explorers

509   might increase predation risk and/or levels of chronic stress compared to less explorative animals. How stress

510   levels may be linked to personality under differential conditions of habitat or population density are

511   challenges for future research (e.g. Dantzer et al. 2013, 2016).

512

Body condition, personality and female reproduction

513

514   We found that heavier females produced more litters than those of poorer body mass, in agreement

515   with previous studies on red squirrels (Wauters and Dhondt 1989, 1995; Wauters et al. 2007). Because of

516   such strong effects of a female's body condition, variation in personality might have only weak relationships

517   with reproductive success. In this study we found no effect of boldness on reproductive success but a

518   negative effect of exploration. Female red squirrels that explore a lot could be less efficient in obtaining and

519   defending exclusive core-areas (intrasexual territoriality, Wauters and Dhondt 1992), and/or spend less time

520   nursing their offspring. This hypothesis could be tested by radio-tracking squirrels, investigating the

521   relationships of personality with degree of core-area overlap and time spent away from the nest during

522   lactation. Another point to consider is that maybe we need more detailed data of reproductive success: not

523   only number of litters produced, but also data on number of young produced or weaned/litter (Wauters and

524   Dhondt 1995; Santicchia et al. 2015b) to reveal (weak) relationships between personality and reproductive

525   success. Negative effects of exploration on reproductive success were also found in other studies. For

526   example, Vetter et al. (2016) demonstrated that, under high food availability, being less aggressive and less

527   explorative positively influenced the post-weaning litter size in wild boar (*Sus scrofa*).

528   We believe that our study provides insight in how personality traits can produce fitness trade-offs

529   under different environmental conditions. Unfortunately, our sample size was too small to explore if and

530   how personality might relate to trade-offs among different fitness components, for example differential

531   investment in survival or reproduction. Hence, our results suggest the need for long-term studies measuring

532   individual variation in personality traits, phenotypic factors, space use (home range size, degree of overlap,

533   home range quality) and different fitness components combining data from populations living under different

534   abiotic conditions (habitat types, food supplies) to better assess the impacts of personality on an animal's

535   "performance" both before and during its period of reproductive activity.

536

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21

Compliance with ethical standards

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Ethical approval

All applicable international, national and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the current law on animal research in Italy and were carried out under permission of the authorities for wildlife research and management of Lombardy region (Decree n.18064 of 14/07/2000; Decree n.10816 of 10/06/2002; Decree n.1861 of 16/02/2004; Decree n.2456 of 07/03/2006) and Gran Paradiso National Park (Authorization prot. n. 1716/9.3.7 of 06/07/200 and prot. n 1071//9.3.7 of 07/05/2003). No specific approval from ethics committee was required.

Conflict of interest

The authors declare that they have no conflict of interests

Data availability

564 All data analysed during this study are included in this published article and its supplementary information

565 files.

566

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Table 1 Food abundance estimates (conifer seed-crop in 10^3 kJ/ha, mean ± SE) and number of red squirrels (males, females) trapped and used to measure personality per year in the three study areas. Total number of squirrels refers to sample size of different individuals used in the analyses

Year	Study areas CED		OGA		RHE	
	Food	Squirrels	Food	Squirrels	Food	Squirrels
1999	4357 ± 570		1732 ± 419			
2000	159 ± 63 *	4 (3, 1)	391 ± 82 *	16 (10, 6)	497 ± 252 *	11 (8, 3)
2001	3087 ± 440	10 (7, 3)	588 ± 83	20 (10, 10)	913 ± 109	18 (11, 7)
2002	1867 ± 296	14 (8, 6)	735 ± 153	23 (14,9)	1773 ± 154	21 (12, 9)
2003	846 ± 226 *	20 (11, 9)	552 ± 81	21 (13, 8)	1010 ± 130	20 (11, 9)
2004	6142 ± 728	18 (11, 7)	863 ± 111	21 (12, 9)	2402 ± 233	19 (11, 8)
2005	4022 ± 828	16 (10, 6)	352 ± 73 *	14 (8, 6)	22 ± 5 *	21 (10, 11)
2006	6249 ± 907	14 (9, 5)		5 (3, 2)	1363 ± 179	13 (8, 5)
2007	2547 ± 528	9 (7, 2)			1171 ± 133	8 (4, 4)
2008		1 (1, 0)			96 ± 27 *	4 (2, 2)
Mean/Total	3253 ± 849	45 (27, 18)	745 ± 192	40 (21, 19)	1027 ± 273	56 (30, 26)
% CV	66%		63%		75%	

*years of poor seed-crop

751 **Table 2** Pearson's correlation coefficient with significance level for correlations between foot length, body

752 mass and personality scores of red squirrels: a) all animals; b) and c) per sex. Sample size between brackets

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	Foot length	Boldness score (PC1)	Exploration score (PC2)
(a) Both sexes (n = 141)			
Body mass	$r = 0.49$, $P < 0.0001$	$r = 0.001$, $P = 0.98$	$r = -0.007$, $P = 0.93$
Foot length		$r = 0.06$, $P = 0.49$	$r = 0.04$, $P = 0.60$
(b) Males (n = 78)			
Body mass	$r = 0.63$, $P < 0.0001$	$r = 0.09$, $P = 0.44$	$r = -0.04$, $P = 0.73$
Foot length		$r = 0.08$, $P = 0.46$	$r = 0.01$, $P = 0.90$
(c) Females (n = 63)			
Body mass	$r = 0.38$, $P = 0.002$	$r = -0.04$, $P = 0.74$	$r = -0.03$, $P = 0.02$
Foot length		$r = -0.001$, $P = 0.99$	$r = 0.11$, $P = 0.39$

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766 **Table 3** General Linear Models with Poisson distribution of parameters affecting variation in longevity of male

767 red squirrels. After significant interactions of PC scores and foot length with study area, models were tested

768 separately for CED and OGA (interactions, all partial $P > 0.05$) and for RHE (interactions with both CED and

769 OGA, all partial $P < 0.05$)

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Fixed effects	Estimates	Chi-square (df = 1)	P
(a) CED & OGA (n = 45)			
Study area		32.6	< 0.0001
Body mass	0.014 ± 0.002	42.7	< 0.0001
Foot length	-0.058 ± 0.048	1.43	0.23
PC1 score	-0.047 ± 0.022	4.15	0.042
PC2 score	-0.376 ± 0.071	28.4	< 0.0001
(b) RHE (n = 29)			
Body mass	-0.0019 ± 0.0031	0.39	0.53
Foot length	0.221 ± 0.041	29.6	< 0.0001
PC1 score	0.037 ± 0.035	1.06	0.30
PC2 score	-0.478 ± 0.061	60.9	< 0.0001

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781   **Table 4** General Linear Models with Poisson distribution of parameters affecting variation in longevity of

782   female red squirrels. After significant interactions of PC scores with study area, models were tested

783   separately for CED and OGA (interactions, all partial $P > 0.05$) and for RHE (interactions with both CED and

784   OGA, all partial $P < 0.05$)

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Fixed effects	Estimates	Chi-square (df = 1)	P
(a) CED & OGA (n = 34)			
Study area		10.9	0.001
Body mass	0.0092 ± 0.0024	14.8	<0.0001
Foot length	-0.005 ± 0.037	0.02	0.89
PC1 score	-0.099 ± 0.056	3.11	0.078
PC2 score	-1.057 ± 0.120	77.6	< 0.0001
(b) RHE (n = 24)			
Body mass	0.0090 ± 0.0025	13.0	0.0003
Foot length	-0.124 ± 0.035	12.5	0.0004
PC1 score	0.158 ± 0.038	17.4	< 0.0001
PC2 score	-0.494 ± 0.115	18.6	< 0.0001

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793   **Fig. 1**

794   a) Trappability and b) trap diversity (mean ± SE) of male (triangles) and female (circles) red squirrels in

795   three study areas in the Italian Alps. Sample size per study area and sex above error flags

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