

Measuring personality traits in Eurasian red squirrels: a critical comparison of different methods

Reference:

Santicchia Francesca, Van Dongen Stefan, Martinoli Adriano, Preatoni Damiano, Wauters Luc.- Measuring personality traits in Eurasian red squirrels: a critical comparison of different methods

Ethology - ISSN 0179-1613 - Hoboken, Wiley, 127:2(2021), p. 187-201

Full text (Publisher's DOI): https://doi.org/10.1111/ETH.13117

To cite this reference: https://hdl.handle.net/10067/1743780151162165141

Measuring personality traits in Eurasian red squirrels: a critical comparison of different methods 1 Running title: Measuring personality in red squirrels 2 3 4 Santicchia Francesca^{a*}, Van Dongen Stefan^b, Martinoli Adriano^a, Preatoni Damiano^a, Wauters Lucas Armanda,b 5 6 7 ^aEnvironment Analysis and Management Unit - Guido Tosi Research Group - Department of Theoretical and Applied 8 Sciences, Università degli Studi dell'Insubria, Varese, Italy 9 ^b Evolutionary Ecology Group, Department of Biology, University of Antwerp, Wilrijk, Belgium 10 *Corresponding author (Santicchia F.): <u>f.santicchia@uninsubria.it</u> 11 12 Acknowledgements 13 We thank Regione Lombardia, Città Metropolitana di Torino, Stelvio National Park, natural reserve 'Bosco WWF di Vanzago' and the owners of private estates for permits and access to the study sites. We also thank 14 15 a number of dedicated field technicians and thesis students for helping with data collection. Constructive comments by the editor Luis Ebensperger and two anonymous reviewers helped us to improve the paper. 16 17 This study is part of the ASPER (Alpine Squirrel Population Ecology Research) project (paper # 32). **Conflict of interest** 18 19 The authors declare no conflict of interest. 20 21 **Authors' contributions** 22 FS and LAW developed the hypotheses and study design; LAW and FS collected data. FS and SVD analysed 23 data. FS led the writing of the manuscript. AM and DP contributed critically to the drafts. All authors gave 24 final approval for publication. 25 **Data Availability Statement** 26 27 The data that support the findings of this study are openly available in Zenodo at 28 https://doi.org/10.5281/zenodo.3889846

ABSTRACT

29

30

31

32

33

34

35

36

37

38

39

40

41

42

43

44

45

46

47

48

49

50

Animal personality, behavioural differences among individuals which are consistent through time and contexts, is generally described by one or more traits. Different methods are used to measure these traits, such as behavioural observations and trapping indices. Comparing several methods allows to validate different tests and to better identify which aspect of an animal's personality is being measured. Here we measured activity, exploration, and immobility of Eurasian red squirrels (Sciurus vulgaris) using observations from the open field test (OFT), and compared them with trappability and trap-diversity indices calculated from capture-mark-recapture data in six independent study sites. Trappability measures the willingness to enter a baited trap (boldness), while trap-diversity can be a proxy for exploration tendency. Our first aim was to test their repeatability, thus their appropriateness as candidate measures of personality traits. Next we explored the predictions that: (i) trappability, measuring boldness, does not correlate with any of the OFT personality traits, since risk-taking can not be expressed in our arena test; and (ii) trap-diversity correlates with exploration obtained from the OFT. Considering the species ecology and study design, we used multivariate Bayesian models based on different time-intervals (session/year) and habitat-types (alpine/plain). We found significant repeatabilities for trappability, for trap-diversity, and for most OFT personality traits, except exploration in the plain sites. Independently from habitat-type or time-interval, trappability did not correlate with either activity, exploration, or immobility from OFT, thus measuring a different personality axis, which we considered a proxy for boldness. Trap-diversity did not correlate with exploration from OFT, but seems related to a different aspect of red squirrels' exploration tendency. Our study emphasizes that caution is needed when using behaviours from OFT to measure multiple personality traits and that applying extra methods based on animals' responses to trapping can provide reliable proxies for boldness and exploration tendency.

51

52

53

KEYWORDS

Capture-mark-recapture, open field test, repeatability, Sciurus vulgaris, trappability, trap-diversity

56 INTRODUCTION

5/	Animal personality is defined as consistent among-individual differences in behaviour which persist through
58	time and in different contexts (Carter, Feeny, Marshall, Cowlishaw, & Heinsohn, 2013; Koski, 2014; Réale,
59	Reader, Sol, McDougall, & Dingemanse, 2007) and is commonly described by several underlying
60	personality traits, each of which reflects a particular aspect of an individual's behavioural repertoire (Carter
61	et al., 2013; Réale et al., 2007). Personality has been documented across taxa in several recent studies
62	(insects: Crall et al., 2018; fish: Barber, Mora, Payne, Weinersmith, & Sih, 2017; Jolles, Briggs, Araya-Ajoy,
63	& Boogert, 2019; reptiles: Horváth, Rodríguez-Ruiz, Martín, López, & Herczeg, 2019; Michelangeli,
64	Chapple, Goulet, Bertram, & Wong, 2019; birds: Morinay, Daniel, Gustafsson, & Doligez, 2019; Richardson
65	et al., 2019; mammals: Brehm, Mortelliti, Maynard, & Zydlewski, 2019; DeRango et al., 2019; Petelle,
66	Martin, & Blumstein, 2019) and personality traits such as activity (Michelangeli et al., 2019), exploration
67	(Arvidsson, Adriaensen, Van Dongen, De Stobbeleere, & Matthysen, 2017) and boldness-shyness (Jolly,
68	Webb, Gillespie, Hughes, & Phillips, 2019; Perals, Griffin, Bartomeus, & Sol, 2017) have been quantified
69	using different methods under laboratory conditions and in free-living populations in the wild (Krebs,
70	Linnenbrink, & Guenther, 2019; Réale et al., 2007; Slipogor, Burkart, Martin, Bugnyar, & Koski, 2020;
71	Tkaczynski et al., 2019).
72	One of the most common assays used in behavioural ecology studies is the open field test (OFT, Walsh &
73	Cummins, 1976; Carter et al., 2013; Montiglio, Garant, Pelletier, & Réale, 2012), where an animal's
74	behaviour in a novel situation is observed. The OFT allows a relatively simple and rapid measurement of an
75	animal's behaviour (Perals et al., 2017) and the quantification of a variety of different personality traits (i.e.,
76	boldness: Jolly et al., 2019; Yuen, Schoepf, Schradin, & Pillay, 2017; exploration: Montiglio et al., 2012;
77	activity: Boon, Reale, & Boutin, 2008). Its effectiveness has been recently criticized for simultaneously
78	measuring multiple traits (Carter et al., 2013; Réale et al., 2007), which could lead to difficulties in
79	quantifying a targeted trait (Carter et al., 2013). Nevertheless, combined measures are usually more
80	significant from an ecological perspective and allow to consider possible confounding effects of other traits
81	(Jolly et al., 2019; Koski, 2014), and/or to look for behavioural syndromes (Sih, Bell, & Johnson, 2004; Sih,
82	Cote, Evans, Fogarty, & Pruitt, 2012). Hence, a careful use of the OFT, also relying on biological knowledge
83	and proper metric validation is advocated (Carter et al. 2013; Krebs et al. 2019; Perals et al. 2017). In this

light, measuring different traits with multiple tests increases the certainty of applying relevant tests and the 84 understanding about what they are quantifying (i.e. multi-traits and multi-test approach, Carter et al., 2013; 85 86 Koski, 2014; Krebs et al., 2019). 87 Studies in natural populations based on capture-mark-recapture of animals can rely on the sampling method 88 itself to obtain measure of individual behaviour and/or personality. Indeed, individual differences in 89 willingness to enter a baited trap (trappability) can be considered as a measure of an animal's propensity for 90 risk-taking (Bisi et al., 2011; Boon et al., 2008; Boyer, Réale, Marmet, Pisanu, & Chapuis, 2010; Le Coeur et 91 al., 2015; Montiglio et al., 2012; Réale, Gallant, Leblanc, & Festa-Bianchet, 2000; Santicchia et al., 2018a, 92 2019). Reactions to risky situations, excluding any component of novelty which is exclusively related to exploration propensity (Réale et al., 2007), have been identified in literature as a measure of individual 93 94 boldness (Réale et al., 2007). Nevertheless, correlations between exploration and risk-taking behaviour have 95 been found (van Oers, Drent, de Goede, & van Noordwijk, 2004) and some studies highlighted that exploration of new environments itself increases the risk of predation (Larsen & Boutin, 1994). Thus, the 96 97 intrinsic relationship between boldness and exploration needs to be considered and accounted for to properly 98 identify which aspect of an individual's behaviour or personality is measured (Carter et al., 2013; Koski, 99 2014). 100 Moreover, also the number of different traps visited (trap diversity) can give insights about an animal's 101 movements in the wild (Boyer et al., 2010; Brehm & Mortelliti, 2018; Santicchia et al., 2018a, 2019; Vanden 102 Broecke et al., 2018). This measure can be both informative of an individual's exploration tendency or its 103 space use (Boyer et al., 2010; Réale et al., 2007). Indeed, in some studies individuals are defined as explorers 104 when they move farther from their core-area in order to obtain information of nearby habitat quality or food resources (Bruinzeel & van de Pol, 2004; Fedy & Stutchbury, 2004; Fraser, Gilliam, Daley, Le, & Skalski, 105 106 2001; Tebbich, Fessl, & Blomqvist, 2009; Verbeek, Drent, & Wiepkema, 1994) or potential partners 107 (Neudorf, Stutchbury, & Piper, 1997; Pedersen, Dunn, & Whittingham, 2006). Consequently, exploration 108 has been found to be correlated with movements in the wild, such as dispersal distance (Dingemanse, Both, 109 van Noordwijk, Rutten, & Drent, 2003; Fraser et al., 2001), home range size (Minderman et al., 2010; van 110 Overveld, Adriaensen, & Matthysen, 2011) and number of foraging sites used (Herborn et al., 2010).

Personality trait differences between individuals, measured in studies which rely on the usage of passive 111 trapping methods (Boon et al., 2008; Boyer et al., 2010; Carter, Heinsohn, Goldizen, & Biro, 2012; 112 113 Michelangeli, Wong, & Chapple, 2016), have been suggested to influence their trappability resulting in a sampling biased towards 'trap-happy/trap-shy' animals (Brehm & Mortelliti, 2018; Carter et al., 2012). 114 However, recent studies highlighted that this, apparently inevitable, bias can be overcome considering a 115 study design and sampling methods based on the animal's ecology and on the assessment of measured traits 116 117 though a multi-test approach (i.e. convergent/discriminant validity, Carter et al., 2013; Jolly et al., 2019; 118 Michelangeli et al., 2016). 119 Here we used the OFT to measure activity, exploration and immobility in the Eurasian red squirrel (Sciurus vulgaris; Mazzamuto et al., 2019; Santicchia et al., 2020a; Wauters et al., 2019) and capture-mark-recapture 120 data to calculate trappability and trap-diversity indices (Santicchia et al., 2018a, 2019). The main objective 121 122 was to compare personality traits derived from different methodological approaches. For instance, in sciurid 123 rodents, such methods comparisons have been carried out on the Siberian chipmunk (Tamias sibiricus; Boyer 124 et al., 2010) and the North American red squirrel (Tamiasciurus hudsonicus; Boon et al., 2008; Brehm & 125 Mortelliti, 2018). Both species are ecologically different from the Eurasian red squirrel. Indeed, North 126 American red squirrels are strictly territorial and actively defend (with aggressive behaviours) a central 127 larderhoard (Boon et al., 2008), while Siberian chipmunks spend most of their time foraging on the ground, caching food in their burrows, which are defended against conspecifics (Tsytsulina, Formozov, Shar, 128 129 Lkhagvasuren, & Sheftel, 2016). Conversely, the Eurasian red squirrel has a sex-specific social organization 130 with overlapping home ranges, and aggressive behavior and social status vary with body mass, age and ecological context (availability and predictability of food resources; e.g. Wauters & Dhondt, 1989; 1992). 131 132 Therefore, comparison and validation of methods applied to measure personality traits are required, due to their high species-specificity in rodents (Brehm & Mortelliti, 2018 and references therein) as well as in other 133 134 wild animals (Tkaczynski et al., 2019). First, we investigated whether activity, exploration and immobility, as well as trappability and trap-diversity 135 136 indices, were repeatable and, thus, could be considered as personality traits (Brehm & Mortelliti, 2018). Secondly, we tested if trappability correlates with personality traits from OFT. Since, trappability in our 137 study system reflects risk-taking behaviour (boldness; Santicchia et al., 2018a, 2019), we predicted that it 138

will not correlate with any of the personality traits measured in the OFT, since the arena test we performed is not designed to measure boldness (discriminant validity, Carter et al., 2013). Lack of correlation would indeed indicate that trappability measures a different axis of personality variation than either activity, exploration, or immobility from OFT, supporting the use of trappability as a proxy for boldness.

Furthermore, we tested whether trap-diversity, which could reflect exploration tendency (Santicchia et al., 2018a, 2019), correlates with exploration obtained from the OFT, thus capturing the same axis of personality variation (convergent validity, Carter et al., 2013). Here, a lack of correlation would suggest that trap-diversity measures a different personality trait then exploration derived from OFT, possibly due to ecological factors (e.g., squirrel density, habitat patchiness) that might influence trap-diversity but not the behaviour in the arena.

MATERIALS AND METHODS

Study species

Male and female Eurasian red squirrel differ in social organization. Adult females have food-based home ranges and defend their core-areas (most intensively used parts in the home range) against other females (intrasexual territoriality; Wauters & Dhondt, 1992). Older, heavier males are dominant and use the largest home ranges, overlapping with more females than younger males of lower body mass (Romeo, Wauters, Preatoni, Tosi, & Martinoli, 2010; Wauters & Dhondt, 1992). The mating system is promiscuous, although most females only mate with a dominant male of high body mass (Wauters, Dhondt, & De Vos, 1990). Reproduction is seasonal, with one to two litters per year, and is strongly affected by the female's body condition, food availability and, in the mountains, elevation (Rodrigues et al., 2010; Wauters & Dhondt, 1995; Wauters et al., 2008). The species occupies a wide variety of forest types, occurring in both continuous forests and fragmented woodlands. Although red squirrels are well adapted to fragmented habitats and have good dispersal capacities (Thomas, Teich, Dausmann, Reher, & Turner, 2018; Wauters, Verbeylen, Preatoni, Martinoli, & Matthysen, 2010), populations inhabiting forest fragments have lower densities and reduced genetic diversity, and higher endoparasite loads than those in continuous forests (Santicchia et al., 2015;

Wauters, Hutchinson, Parkin, & Dhondt, 1994). Most animals disperse as juveniles and subadults (from 4 to 10 months old, Wauters et al., 2010).

Study sites, trapping and handling squirrels

165

166

167

168

169

170

171

172

173

174

175

176

177

178

179

180

181

182

183

184

185

186

187

188

189

190

191

192

We trapped red squirrels in three study sites in alpine habitat (Bormio, Cancano, Valfurva) and three in plain habitat (Castelbarco, Vanzago, Passatempo) between January 2016 and December 2019 (Supporting Information Table S1). In alpine habitat only red squirrels were present, while in the study sites in the plain habitat, red squirrels co-occurred with invasive alien grey squirrels (Sciurus carolinensis). Since the alien species was controlled for red squirrel conservation, its numbers were low throughout the study (Santicchia et al., 2018b; Wauters et al., 2019). In both habitats, two study sites were high-quality forests or woodlands, and one study site in each habitat-type was of lower quality (fewer food resources and/or extreme weather conditions in winter; Supporting Information S1). Capture-mark-recapture (CMR) sessions were carried out two times per year in the alpine sites and from two to six times per year in the plain sites, each session lasted from three to six days. Number of traps varied between study sites (Supporting Information Table S1). We used Tomahawk "squirrel" traps (Model 202, Tomahawk Live Trap Co., Hazelhurst, WI, USA), placed on the ground or at breast height against tree trunks. Traps were more or less homogeneously distributed over the study site, with distances of 50-150 m between them and average trap-density ranging from 0.29 to 1.05 traps ha⁻¹ (details in Supporting Information Table S1). We pre-baited traps with hazelnuts three to four times over a 30 day period, then baited and set for capture session. We partly covered the traps with dark plastic bag to provide animals with shelter, and checked traps three times/day to minimize time in trap. Before handling, we completely covered the trap with a cloth to reduce stress. We flushed the trapped animal in a zipper-tube handling bag to reduce direct contact with the operator. At first capture, we marked each squirrel with a Monel 1005 1L1 ear-tag (size 2.3 – 10 mm, 0.2 g or less than 0.1% of squirrel's body mass; National Band & Tag Co. Newport, KY, USA), putting the tag near the base of the ear to reduce risk of injury. To reduce stress, only trained researchers handled the squirrels, and handling time was kept as short as possible (< 5 minutes). Each animal was weighed to the nearest 5 g using a spring-balance (Pesola AG, Baar, Switzerland) (Wauters et al., 2007). Sex and age class were determined from external genitalia and body mass, with juvenile red squirrels weighing less than 250 g (Wauters & Dhondt, 1989). Only two juveniles were included in our dataset.

Arena test personality measures

After checking a red squirrel's identity, we released it inside a portable arena by opening a sliding door and allowing the animal to move from the handling bag into the arena (Mazzamuto et al., 2019). The arena was placed within 20 m of the trap location. We performed the OFT (4 minutes) which serves to estimate activity, exploration and immobility in a novel environment (Mazzamuto et al., 2019; Santicchia et al., 2020a; Wauters et al., 2019; details in Supporting Information S2). At the end of the experiment, the squirrel was released by opening the sliding door. For each experiment we calculated the time that individuals spent in each behavioural state (behaviours defined in Table S2) using the CowLog 3.0.2 software (Hänninen & Pastell, 2009). To reduce the number of behaviours observed into few personality-linked variables we used the expert-based method (EB; Mazzamuto et al., 2019). The EB approach is a classification of behaviours into groups, summing the values of the single behaviours to obtain scores for few personality-linked variables, based on researchers' previous knowledge. This method was validated (Carter et al., 2013) for red squirrels by comparing its classification outcome and scores with those derived from PCA or Factor Analysis (Mazzamuto et al., 2019). Ethogram description and details in Supporting Information S2 and Table S2. To check the assumptions of repeatability of the OFT traits, the majority of squirrels were tested multiple times to have repeated measures for most individuals.

Ethical note

Trapping, marking and handling of red squirrels and arena test experiments were carried out in accordance with the Guidelines for the treatment of animals in behavioural research and teaching (Animal Behaviour, 2020, 159, I-XI; https://doi.org/10.1016/j.anbehav.2019.11.002). Approval and legal requirements according to the Italian Wildlife Protection and Hunting Law L.N. 157 from 1992 and authorizations N. 294-34626 of 12/09/2014 (2014-2016) from the Provincia di Torino and N. 62-3025 (2017-2019) from the Città Metropolitana di Torino, and Decreto N. 11190 (29/11/2013) and decrees N. 9523 of 15/10/2014 and N. 198 (13/01/2017) from Direzione Generale Agricoltura, Regione Lombardia; and the permission Protocol N. 414 of 28/02/2014 of the Stelvio National Park.

220

245

246

221 For each individual we calculated a trappability and a trap-diversity index, and investigated whether they can 222 be considered personality-linked variables in our study species and populations. In previous studies 223 trappability was considered a proxy of the tendency to take risks (boldness) and trap-diversity a proxy of the 224 propensity to explore the environment (exploration) (Santicchia et al., 2018a). As outlined by Brehm and 225 Mortelliti (2018), caution is necessary when considering these indices as proxies of personality. In effect, 226 trappability has been demonstrated to differ between sexes, ages, study sites, seasons and years (see Brehm 227 & Mortelliti, 2018 and references therein). Therefore, we calculated trappability and trap-diversity at different time-intervals; per trapping session and per year; as well as for both habitat-types (alpine and plain) 228 separately. We included only individuals that were captured at least in two capture sessions, during the 229 230 period of the study, to avoid sampling bias due to: (i) potential dispersers (i.e. animals that were captured 231 only one time and dispersed away from the study site); (ii) old animals (i.e. animals that were captured only one time because they died at the start of the study period); and (iii) new animals caught only at the end of 232 233 the study (i.e. animals that were captured only one time because settled in the study site at the end of the 234 study period). Number of available traps per study site did not change during the study period (details in 235 Supporting Information Table S1). Trappability per session (TBs) was estimated from the ratio of number of captures in session i on the number 236 237 of capture days in session i. Trap-diversity per session (TDs) was calculated from the ratio of the number of 238 different traps an individual was captured in session i on the number of available traps. TBs (trappability session i) = n. captures session i / n. capture days session i239 240 TDs (trap-diversity session i) = n. different traps captured session i / n. available traps site 241 Trappability per year (TBy) was calculated from the ratio of the number of captures in year i on the number 242 of capture days an individual was present in year i. Each individual was considered present in the study site, 243 thus potentially catchable, from the first to the last session in which it was captured. Number of capture days 244 an individual was present in the study site included all capture days of the first and the last session an animal

was captured, and also all capture days of sessions in-between these two. This allowed us to estimate number

of capture days an individual was present on a yearly basis. Trap-diversity per year (TDy) was estimated

- from the ratio of the number of different traps an individual was captured in year *i* on the number of available traps.
- TBy (trappability year i) = n. captures year i / n. capture days presence year i
- TDy (trap-diversity year i) = n. different traps captured year i / n. available traps site

- 252 Repeatability of OFT personality traits, trappability and trap-diversity
- We estimated the repeatability of the OFT personality traits and of the trappability and trap-diversity indices
- for each habitat-type (alpine and plain) separately and for both session and year time-periods (Table 1).
- Repeatabilities were calculated with a Linear Mixed Model (LMM; Nakagawa & Schielzeth, 2010) using the
- R package 'rptR' v 0.9.22 (CI = 95%, number of parametric bootstraps for interval estimation = 2000,
- number of permutations used when calculating asymptotic p-values = 1000; Stoffel, Nakagawa, &
- Schielzeth, 2017) and estimates were considered significant based on confidence intervals and the p-value of
- a Likelihood Ratio Test (LRT), that compares the fit of a model with ID as random effect (estimating the
- within-individual variance) and the same model without the random effect (Nakagawa & Schielzeth, 2010;
- 261 Table 1).
- Each model with one of the OFT personality trait as dependent variable (activity, immobility, exploration)
- included study site, sex, year, arena test order (categorical factor: first [coded as 1] vs. subsequent ones [all
- coded as 0], based on results from earlier studies which showed that scores of OFT personality traits differed
- between the first arena and all the subsequent ones; Dingemanse et al., 2012; Santicchia et al., 2020a;
- Wauters et al., 2019), and number of days from the previous arena test as fixed effects. Squirrel identity (ID)
- was added as random effect. Arena test order and number of days from the previous test were included to
- account for habituation and temporal proximity between two tests (number of days between subsequent tests:
- alpine sites, median 132, mean \pm SE = 185 \pm 12, range 1 611 days; plain sites, median 146, mean \pm SE =
- 157 \pm 10, range 1 622 days; details in Supporting Information S3) (Mazzamuto et al., 2019; Montiglio,
- Garant, Thomas, & Réale, 2010; Dingemanse et al., 2012). All repeatabilities were calculated on squareroot
- transformed values of proportion time for each OFT personality trait and assumptions of normality of the

residuals was confirmed by Shapiro-Wilk's test (W > 0.90). Also squirrels that had only one estimate for the OFT personality traits were included in the repeatability estimates (following Martin, Nussey, Wilson, &

We calculated repeatability of trappability and trap-diversity for individuals with at least one arena test (see Table 1). We run four separate models for these indices (TBs, TDs, TBy, TDy) with each of them as

dependent variable and study site, sex, year as fixed effect, and squirrel identity as random effect. All

repeatabilities were calculated on squareroot transformed values of trappability and trap-diversity, and

assumptions of normality of the residuals was confirmed by Shapiro-Wilk's test (W > 0.90). Full model

outputs are provided in Supporting Information, Tables S3 and S4.

Réale, 2011).

Relationship between OFT personality traits, trappability and trap-diversity

Since we calculated trappability and trap-diversity both based on session and year, and since the relationship between them and the OFT personality traits can be influenced by differences in habitat-type (alpine or plain; see Brehm & Mortelliti, 2018), we performed four multivariate Bayesian generalized linear mixed effects models based on a Markov Chain Monte Carlo algorithm with the R package MCMCglmm version 2.29 (Hadfield, 2010). Before the analysis we selected our data including individuals that were present at least in two capture sessions to avoid any bias (as described above in '*Trappability and trap-diversity indices*') and excluding missing values for OFT personality traits and trappability, trap-diversity indices.

Models based on session were conducted on a subset (alpine sites: n = 182, ID = 69, males/females = 44/25; plain sites: n = 244, ID = 90, males/females = 51/39) which included personality traits derived from the first OFT of each session for each red squirrel and the relative TBs (trappability/session) and TDs (trapdiversity/session) value. While models based on year were conducted on another subset (alpine sites: n = 127, ID = 69, males/females = 44/25; plain sites: n = 165, ID = 90, males/females = 51/39) which included personality traits derived from the first OFT of each year for each red squirrel and the relative TBy

(trappability/year) and TDy (trap-diversity/year) value.

The OFT personality traits squareroot transformed scores (immobility, activity and exploration) were treated as dependent variables after centering and scaling $[(x_i - \text{mean } x)/\text{SD } x]$ with a Gaussian residual error distribution. In the plain sites exploration was not repeatable but was included in the models to allow comparisons between model outputs. Also squareroot transformed values of indices (TBs, TDs, TBy, TDy) were included as dependent variables after standardization within study site because of site-related differences in capture histories and available traps (details in Supporting Information Table S1). In addition, sex, year, arena test order (categorical factor: first [coded as 1] vs. subsequent ones [all coded as 0], see Santicchia et al., 2020a; Wauters et al., 2019), study site, and body mass (centered and scaled) were added as fixed effects. In all models, the effect of arena test order and study site was only estimated for the OFT personality traits. Models based on session included also season [winter (December to February); springsummer (March to July); autumn (September to November)] as fixed effect, which was only estimated for trappability and trap-diversity indices, since variation in food availability across seasons could influence the attractiveness of the baited traps. As repeated observations were present, and to estimate both amongindividual and within-individual variation of the dependent variables, individual (ID) was added as random effect. Assumption of normality of the dependent variables was supported by their QQ-plots. For both the residual and between-individual variation, an unstructured variance-covariance matrix was modelled, allowing the estimation of correlations among the dependent variables (covariance divided by the square root of the product of the variances). Posterior distributions were based on 1050000 iterations with a burn-in of 50000 iterations and thinning of 400, such that 2500 iterations were used to obtain point estimates and 95% credibility intervals. For all fixed effects related parameters (i.e., intercept, slopes, differences), the prior distribution was Gaussian with zero mean and variance equal to 10⁸ (default setting in MCMCglmm). We used non-informative (parameter-expanded) inverse Wishart prior [prior specifications: R structure degree of belief (nu) = 0.002; G structure degree of belief (nu) = 5, alpha.mu = rep (0, 5), alpha.V = diag (25², 5, 5); Houslay & Wilson, 2017]. We applied the Gelman-Rubin statistic (Gelman & Rubin, 1992) and Geweke diagnostic (Geweke, 1992) which confirmed model consistency and convergence. Full model outputs are provided in Supporting Information, Tables S5, S6, S7 and S8.

298

299

300

301

302

303

304

305

306

307

308

309

310

311

312

313

314

315

316

317

318

319

320

321

322

RESULTS

OFT personality traits

We performed 273 OFT on 144 different red squirrels (95 males, 49 females) in alpine sites and 309 OFT of 120 individuals (65 males, 55 females) in plain sites (Table 1). In the Alps, 68 animals were tested more than 1 time (197 arena tests) while 76 animals were tested only once. In the plain, 76 individuals were tested more than 1 time (265 arena tests) and 44 animals tested only once. During OFT, red squirrels in both habitat-types spent most time in behaviours related to activity and immobility and little time in exploration (Table 1). We found moderate repeatabilities (R > 0.31; see also Bell, Hankinson, & Laskowski, 2009) for activity and immobility in alpine and plain sites and low repeatabilities (R < 0.20; Bell et al., 2009) for exploration in alpine sites (Table 1). The repeatability of exploration in plain sites was low and not significant (Table 1).

Trappability and trap-diversity indices

We calculated trappability and trap-diversity per session and year on 70 red squirrels (45 males, 25 females) in alpine sites and on 90 red squirrels (51 males, 39 females) in plain sites (Table 1). Number of captures, number of different traps, and number of capture days, calculated for each individual, based on different habitat-types and time-intervals, are described in Table 2. Trappability and trap diversity reported a moderate repeatability (all R > 0.30) in alpine sites, but a lower repeatability in plain sites (all R < 0.30; Table 1). In both habitat-types, repeatability values of indices based on year are higher than those based on session, although confidence intervals largely overlap (see Table 1 for details).

OFT personality traits, trappability and trap-diversity relationships

346 Alpine sites

In alpine sites, the model with personality traits, trappability (TBs) and trap-diversity (TDs) indices based on session, reported a strong and negative correlation between immobility and activity (r = -0.85; 95% CI = -0.98 to -0.62; Figure 1, Table S9) and a strong positive correlation between TBs and TDs (r = 0.82; 95% CI

= 0.13 to 0.99; Figure 1, Table S9). Moreover, there was a positive correlation between immobility and TDs (r = 0.71; 95% CI = 0.09 to 0.99; Figure 1, Table S9). All the other correlations between immobility, activity and exploration, TBs and TDs had 95% CIs that included 0 and thus can be considered not significant (Figure 1). Males had higher TBs and TDs than females and squirrel body mass was positively related with exploration and TDs (details on the MCMCglmm output in Table S5). In the model based on year, all correlations between the dependent variables included 0 in the 95% CIs (Figure 1). Males had a higher TBy than females, while there was no effect of sex on TDy or on any of the OFT personality traits. Body mass did not affect any of the dependent variables (details on the MCMCglmm output in S7).

Plain sites

For the plain sites, the model based on session reported only a strong and negative correlation between immobility and activity (r = -0.92; 95% CI = -0.99 to -0.81; Figure 1, Table S9). All the other correlations between immobility, activity and exploration and TBs and TDs were not significant (Figure 1, Table S9). Males had higher TBs and TDs than females but there was no significant relationship of body mass with any of the dependent variables (details on the MCMCglmm output in Table S6). Similarly, the same model based on year had no significant correlations among the OFT personality traits (immobility, activity and exploration) or between OFT traits and TBy and/or TDy (Figure 1, Table S9). In this habitat-type, males had both higher TBy and higher TDy than females, while there was no relationship

DISCUSSION

Through the use of the OFT we measured activity, exploration and immobility in the Eurasian red squirrel (*Sciurus vulgaris*), while capture-mark-recapture allowed us to estimate trappability and trap-diversity indices, which can be related to boldness and exploration, respectively. We tested their repeatability, thus their appropriateness as candidate variables of personality traits, and, to test our hypotheses, explored their

of body mass with any of the dependent variables (details on the MCMCglmm output in Table S8).

posterior correlations derived from the multivariate MCMCglmm models. We found significant repeatabilities for all five variables, except for exploration from OFT in the plain habitat-type. Trappability did not correlate with any of the personality traits measured in the OFT, and trap-diversity did not correlate with exploration measured in the OFT.

380

381

382

383

384

385

386

387

388

389

390

391

392

393

394

395

396

397

398

399

400

401

402

376

377

378

379

Repeatability of OFT personality traits

Personality traits activity and immobility, measured in the OFT, had a moderate repeatability, suggesting they are reliable personality traits for red squirrels, in both alpine and plain sites (Brehm & Mortelliti, 2018; Carter et al., 2013). This is similar to other studies on the same species, where repeatabilities for activity and immobility were also moderate (Mazzamuto et al., 2019; Santicchia et al., 2020a; Wauters et al., 2019), and on other studies on rodents where repeatability of activity measured in the OFT were from moderate to high (Tamiasciurus hudsonicus: Boon et al., 2008; Tamias striatus: Montiglio et al., 2012; Sciurus carolinensis: Mazzamuto et al., 2019, Santicchia et al., 2020b; Marmota flaviventer: Petelle et al., 2019; Peromyscus maniculatus, Myodes gapperi, Blarina brevicauda: Brehm et al., 2019, Brehm, Tironi, & Mortelliti, 2020). Conversely, exploration had a low repeatability in alpine sites (R=0.18), and repeatability was not significant in plain sites. Recent studies on rodents measured exploration in the OFT using different variables, such as duration or frequency of behaviours observed, and reported repeatabilities from low to moderate (Marmota flaviventer: Petelle et al., 2019; Myodes glareolus: Schirmer, Herde, Eccard, & Dammhahn, 2019). Previous studies on the same species and on a different squirrel species also found low repeatability values for exploration measured in the OFT (Sciurus vulgaris: Santicchia et al., 2020a; Wauters et al., 2019; Sciurus carolinensis: Santicchia et al., 2020b) and among-individual variation in the duration of exploration behaviours in the OFT was low, compared to other behavioural measures taken during the same tests (see Table S2, Santicchia et al., 2020b; Table 1, Santicchia et al., 2020a; Table 2, Wauters et al., 2019). Hence, behaviours related to pure exploration by this species occur rarely in such tests. Furthermore, studies on other squirrel species which measured personality in the OFT found that, when applying multivariate reduction techniques, behaviours related to activity and exploration grouped on the same component (Tamias striatus: Martin & Réale, 2008; Tamiasciurus hudsonicus: Boon et al., 2008), even when appropriate tests were designed to separate measures of the two personality traits (i.e. hole-board test: File & Wardill, 1975). Hence, separating exploration from activity is critical and not always possible, since they are strongly and positively associated in several squirrel species (Boon et al., 2008; Boyer et al., 2010; Martin & Réale, 2008; Patterson & Shulte-Hostedde, 2011). This highlights how, in different squirrel species, the OFT might not be the best way to measure exploration separately from activity (Boon et al., 2008; Boyer et al., 2010; Martin & Réale, 2008; Santicchia et al., 2020a,b; Wauters et al., 2019).

Moreover, aside this criticism, the low or even non-significant repeatability values of exploration found in the present study could also be related to high levels of plasticity in exploration behaviours (flexible component of personality, e.g., Dingemanse et al., 2012). This has been suggested, but on a different personality trait, in a previous study on the same species, which measured the personality trait "sociability" with and without an invasive competitor present (Wauters et al., 2019). In our plain study sites, red squirrels are in syntopy with the alien Eastern grey squirrel (*S. carolinensis*), contrary to alpine sites where they occur without other tree squirrels competitors, and it is not unlikely that the presence of the invasive species could advantage individual red squirrels with more flexible exploration behaviours (context related plasticity; see also Sih et al., 2012; Wauters & Dhondt, 1993).

Repeatability of trappability and trap-diversity

Trappability has been measured in several studies on animal personality and, as examined by Brehm and Mortelliti (2018), erroneously used as a proxy for personality traits based solely on its correlation with other traits without testing its own repeatability. Moreover, in their study, these authors highlighted how a trappability measure can be highly species specific and contingent on environmental factors. Hence, the need to estimate the repeatability of trappability, separately from other traits, before using it as a proxy for personality. This is paramount for every candidate personality variable, and should be common practice in animal personality studies (Brehm & Mortelliti, 2018; Carter et al., 2013).

Here we found moderate repeatabilities of trappability and trap-diversity in alpine sites [annual 0.33 and 0.50 respectively; Table 1], while in plain sites they were lower [annual 0.27 and 0.20 respectively; Table 1]. Both these indices have been found to measure individual differences in personality also in other studies on sciurid

rodents, which reported moderate to high repeatabilities (Tamias sibiricus: Boyer et al., 2010; Le Coeur et al., 2015; Sciurus vulgaris: Santicchia et al., 2018a; Sciurus carolinensis: Santicchia et al., 2019).

432

455

456

430

431

433 Repeatabilities differences by habitat-type and time-intervals 434 In the present study, we measured personality traits in two different habitat types (alpine and plain) which 435 differ in forest type, thus in resources availability (Supporting Information S1). Previous studies showed that 436 spatio-temporal variation in habitat quality (in particular tree-seed availability) influences tree squirrel 437 population dynamics, space use and behaviour (Boutin et al., 2006; Lurz, Garson, & Wauters, 2000; Thomas 438 et al., 2018; Wauters & Dhondt, 1992; Zong et al., 2014). Hence, also the costs and benefits of certain 439 personality traits may vary in space (habitat) and/or over time. 440 As far as habitat type was concerned, trappability and trap-diversity repeatabilities, as well as those 441 calculated for activity, immobility and exploration measured in the OFT, seemed to be higher in alpine sites 442 than in plain sites. Differences in behavioural consistency between habitat types have been investigated 443 comparing urban and rural populations (Hardman & Dalesman, 2018) and individuals with a high 444 behavioural flexibility have been suggested to adapt better to urban landscapes (Lowry, Lill, & Wong, 2013). 445 This suggests that Eurasian red squirrels inhabiting plain sites, which are not urbanized but still more 446 anthropogenically disturbed semi-natural sites, are likely to have higher flexibility in their behaviours 447 compared to populations in alpine sites. However, this was not confirmed by our data since the confidence 448 intervals of repeatability estimates partially overlap (see Table 1 for details; Hardman & Dalesman, 2018). 449 Comparisons of personality traits repeatability across populations and/or habitat-types is beyond our scope, 450 but future studies may wish to explore this, since it has been rarely investigated (Dingemanse et al., 2012; 451 van Dongen, Maldonado, Sabat, & Vásquez, 2010; Hardman & Dalesman, 2018). Moreover, our study has been conducted across four consecutive years, which allowed us to measure 452 453 personality of red squirrels during the major part of their lifetime (average lifespan 3-4 years; Lurz, Gurnell, 454 & Magris, 2005; Wauters & Dhondt, 1995). As detailed in methods section, we calculated trappability and

trap-diversity for different time-intervals (session and year), where the short time-interval measure, allowed us to control for possible confounding effect due to seasonal variation in capture rates. Conversely, a long

time-interval, covers a wider range of individual responses to trapping, and thus could allow to distinguish more clearly bold from shy animals and high from low explorers. Also, studies on other rodent species measured the repeatability of personality variables on an appropriate timescale based on study species lifespan: trappability on a yearly basis (Siberian chipmunk generation length 3-4 years; Boyer et al., 2010; Tsytsulina et al., 2016); or within a single capture session (several small rodent species that have a nearly complete population turnover from one year to the next, Brehm & Mortelliti, 2018). In red squirrels, we indeed found slightly higher year-based than session-based repeatabilities of trappability and trap-diversity, in both habitat-types, albeit with overlapping confidence intervals (Table 1). As mentioned above, this difference might be due to a higher among-individual variance in personality traits measured on a yearly than on a short-term (session) basis. A relatively higher variance accounted for by differences among individuals in relation to within-individual variance would indeed result in higher repeatability values (Bell et al., 2009; Brehm & Mortelliti, 2018; Carlson & Tetzlaff, 2020; Nakagawa & Schielzeth, 2010). This could be related to the relative stability of capture rates measured over a longer time-interval (year) compared to those based on shorter time-intervals (session). Indeed, a shorter time-interval measure (session) is more sensitive to stochastic (e.g. seasonal) factors affecting capture rates (e.g. Tkaczynski et al., 2020).

Bias of trappability and trap-diversity

In the present study, trappability and trap-diversity, for both habitat-types and based on session and year, has been found to be repeatable, thus a measure of personality traits. However, measures obtained from passive trapping methods, such as the baited traps that we used here, have been criticized for causing personality-biased sampling towards the boldest individuals in a population, leading to a lack of sampling on those animals that are hard to capture (Biro & Dingemanse, 2009; Jolly et al., 2019; Michelangeli et al., 2016). Recent studies on rodents explored this issue and highlighted how different aspects, mainly related to sampling design and species ecology, need to be accounted for in such studies (Brehm & Mortelliti, 2018; Jolly et al., 2019).

Studies on capture-mark-recapture of Eurasian red squirrels in alpine habitats found how in the same session recapture probabilities were high, suggesting that the probability to miss squirrels present in the study site

were low (Wauters et al., 2008). Also, studies on the same species in lowland habitat detailed that after a certain number of days (five days) no additional new unmarked squirrels were trapped (Wauters & Dhondt, 1993; Wauters, Matthysen, Adriaensen, & Tosi, 2004). In general, in the present study, we observed that during the lasts days of capture in each session nearly all captures were related to already marked squirrels. Nevertheless, we cannot entirely rule out the possibility that we missed some extremely shy individuals, but at worst, this makes our data and comparisons more conservative. That we sampled a broad range of responses to the traps is further supported by the high variation in our trappability and trap-diversity measures (see Table 1 for details). Thus, we are confident that our measure of trappability and trap-diversity are only minimally biased towards bolder and more explorative animals (Biro & Dingemanse, 2009). Also neophobia has to be considered in studies which rely on passive trapping methods (Jolly et al., 2019; Michelangeli et al., 2016). The capture-mark-recapture method applied on squirrels relies also on a prebaiting phase, which consist in placing inactive baited traps at fixed points in the study sites and repeatedly replenish the bait over a 30 day period before each trapping sessions (Wauters et al., 2008). Therefore, a repeated exposure to the baited traps before capture sessions, along with increasing trapping success, decreases the possibility of rejection by neophobic/shy individuals (Michelangeli et al., 2016). Finally, a careful sampling design which provides an appropriate number of available traps to avoid trap saturation must be considered (Jolly et al., 2019). Indeed, the presence of alien species competitors, as in our plain sites, could decrease trap availability for the target species since in those sites there is no niche partitioning between the species (Santicchia et al., 2018b; Wauters, Gurnell, Martinoli, & Tosi, 2002; Wauters et al., 2019). In the present study this is unlikely since in the majority of trapping sessions less than 30% of the traps were occupied during a trap-control round [in alpine sites on average 30% (range 5-60% per trapping occassion) of traps were simultaneously unavailable, while in plain sites the average was 20% (range 2-46%)].

507

508

509

510

484

485

486

487

488

489

490

491

492

493

494

495

496

497

498

499

500

501

502

503

504

505

506

Relationships between OFT personality traits, trappability and trap-diversity

Among the three personality traits measured with OFT, activity and immobility were negatively correlated in both habitat types, but only when estimated in session. This was expected since these two traits are measured

along a continuum of high to low time spent moving in the arena (Mazzamuto et al., 2019). That the correlations were stronger at the session rather than the annual level was probably due to having used more arena tests per individual at the session level. Therefore, it is likely we obtained more accurate estimates of traits measured in sessions, leading to greater statistical power to detect the correlations. In the alpine sites, we found a positive correlation between immobility from OFT and trap-diversity. This correlation was evident only at session level, and only in this habitat-type; hence it could be a spurious result. In fact it is counter intuitive, since these squirrels with high trap-diversity were mostly males and/or animals of high body mass; hence individuals expected to use large home ranges (Romeo et al., 2010; Wauters & Dhondt, 1992). An alternative explanation is that squirrels show habituation to the OFT, indeed repeated exposition to the same test can cause a decrease in responses to novelty (Martin & Réale, 2008; Réale et al., 2007) as already observed in some traits (Dingemanse et al., 2012; Perals et al., 2017). Hence, this potential habituation, measured by an increase in expression of immobility-related behaviours (see Supporting Information Table S5), seems to be stronger in animals with high trap-diversity. Following the general goal to capture a wide range of traits to increase awareness of what is actually measured (Carter et al., 2013; Koski, 2014), we compared personality traits obtained from the OFT with trappability and trap-diversity indices. Since the personality traits that we measured in the OFT were related to activity, immobility and exploration (Mazzamuto et al., 2019; Santicchia et al., 2020a; Wauters et al., 2019), we predicted that trappability (boldness; Santicchia et al., 2018a, 2019) would not correlate with any of them. Our results demonstrated that trappability, whether based on sessions or year, was not correlated with any of the personality traits measured in the OFT (Figure 1), thus measures a different axis of personality variation. These findings, found in both habitat types, support that trappability is a proxy for boldness in red squirrels (see Santicchia et al., 2018a, 2019). Moreover, this measure is based on the individual number of captures, thus the propensity of each animal to enter in a trap. Since entering a trap also results in the animal being handled, the entire process is likely to be stressful, but despite this, the animals overcome the fear in order to obtain the bait (i.e. bighorn sheep; Réale et al., 2000). Hence, we are confident that our trappability actually measures the willingness to take risks (boldness; Réale et al., 2007). Previous studies on rodents explored the relationship between personality traits measured in the OFT and number of captures (trappability) reporting different results. Boon et al. (2008) found that activity-

511

512

513

514

515

516

517

518

519

520

521

522

523

524

525

526

527

528

529

530

531

532

533

534

535

536

537

exploration of the North American red squirrel (Tamiasciurus hudsonicus) was positively related with the number of captures, but they did not test repeatability of the latter. Boyer et al. (2010), found a positive relationship between *Tamias sibiricus* activity-exploration in an arena test and trappability, both having significant repeatabilities. Also, they found a positive relationship between number of captures (trappability) and number of different traps (trap-diversity) used by an individual. Similarly, in this study, as in other studies on tree squirrels (Santicchia et al., 2018a, 2019), we found a strong and positive correlation between the two capture indices based on session, but only in alpine sites (Figure 1). That they are related to some degree is inherent to the estimates; a squirrel can not have a high trap-diversity index when trapped very few times (low trappability). In contrast, animals with high trappability might be captured nearly always in the same trap, hence having a low trap diversity score. The fact that we found a positive correlation only in one habitat-type and only when estimated per session, suggest that the two trapping indices indeed measure two different personality traits. Some studies found contrasting results. In a large-scale experiment on four rodent species and a shrew, Brehm and Mortelliti (2018) found that number of captures in a session (trappability) was not repeatable and that there was no correlation between trappability and activity-exploration measured in an OFT. These examples highlight that trappability not always reflects a personality trait and its applicability is speciesspecific (Brehm & Mortelliti, 2018). Finally, we predicted that trap-diversity (exploration; Santicchia et al., 2018a, 2019) would correlate with exploration measured in the OFT, capturing the same axis of personality variation. Our results did not confirmed our prediction, indeed we found that trap-diversity, albeit repeatable, was not correlated with exploration from OFT, for both habitat-types and time-intervals (Figure 1). Similarly, in introduced Siberian chipmunks (Tamias sibiricus) there was no association between trap-diversity and exploration measured with arena-tests (Boyer et al., 2010). They suggested that trap-diversity was mainly a proxy for space use, which apparently was independent from activity-exploration propensity of chipmunks. In contrast, in territorial American red squirrels (Tamiasciurus hudsonicus), activity-exploration was positively related with the number of different trapping locations (Boon et al., 2008), suggesting that a high number of different trapping locations was positively related to a high number of extra-territorial exploratory movements.

539

540

541

542

543

544

545

546

547

548

549

550

551

552

553

554

555

556

557

558

559

560

561

562

563

564

Our alternative prediction included the possibility that trap-diversity measures a different axis of personality variation than exploration obtained from the OFT. In this study, trap-diversity measures were based on capture-mark-recapture data that rely on how squirrels move inside their home ranges and visit the available traps. Therefore, it is likely that trap-diversity actually measures an individual's exploration in a known environment (its home range). Conversely, exploration in the OFT was measured in a context different from the natural environment, probably mainly related to the novelty aspect of exploration as defined by Réale et al. (2007). It is likely that these intrinsic differences between the two measures of exploration are responsible for the lack of correlation between trap-diversity and exploration derived from the OFT; in other words they are measuring different personality traits. That estimates of exploration behaviour in a species can be highly context (test situation) specific was also demonstrated by Arvidsson et al. (2017) who found that an activityexploration score of individual great tits (Parus major) derived from the classical arena design was not correlated with scores obtained from tests in a different, much larger arena structure. Furthermore, in our species and study design, both the expression of exploration-linked behaviours in the OFT and the repeatability of exploration itself where low. Hence, the OFT does not seem a reliable method to quantify exploration tendency in Eurasian red squirrels. Finally, for several of our correlations the CI's are wide, in particular for variables with low repeatabilities (Bell et al., 2009). In such instances among-individual variation may be insufficient to detect the covariations reducing the biological meaning of the nonsignificant correlations.

584

585

586

587

588

589

590

591

592

566

567

568

569

570

571

572

573

574

575

576

577

578

579

580

581

582

583

CONCLUSIONS

We conclude that activity and immobility obtained from the OFT are reliable measures of red squirrel's personality, as well as trappability and trap-diversity indices derived from capture-mark-recapture data. These personality traits are consistent in different habitat-types (alpine and plain) and when measured over different time-periods (per session or per year). In contrast, exploration measured in the OFT, occurred at low frequencies and had poor (alpine habitat-type) or even non-significant repeatabilities (plain habitat-type). Based on our findings we are confident that trappability is indeed an appropriate measure of boldness, while, contrary to our expectation, trap-diversity does not reflect exploration obtained from the OFT but seems to

be related to a different aspect of red squirrels' exploration tendency. Albeit our hypotheses were mainly focused on exploring relationships between different methods to measure personality traits (testing convergent/discriminant validity, Carter et al., 2013), this study underscores that careful application is needed when using OFTs or animals' responses to traps in studies of personality, and that it is paramount to consider the environmental context in which the species is studied, and its social organization and lifehistory.

616 **REFERENCES**

641

642

doi:10.1111/ele.13324

617	Arvidsson, L. K., Adriaensen, F., van Dongen, S., De Stobbeleere, N., & Matthysen, E. (2017). Exploration
618	behaviour in a different light: testing cross-context consistency of a common personality trait.
619	Animal Behaviour, 123, 151–158. doi:10.1016/j.anbehav.2016.09.005
620	Barber, I., Mora, A. B., Payne, E. M., Weinersmith, K. L., & Sih, A. (2017). Parasitism, personality and
621	cognition in fish. Behavioural Processes, 141, 205–219. doi:10.1016/j.beproc.2016.11.012
622	Bell, A. M., Hankinson, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: a meta-analysis.
623	Animal Behaviour, 77, 771–783. doi:10.1016/j.anbehav.2008.12.022
624	Biro, P. A., & Dingemanse, N. J. (2009). Sampling bias resulting from animal personality. <i>Trends in Ecology</i>
625	and Evolution, 24, 66-7. doi:10.1016/j.tree.2008.11.001
626	Bisi, F., Newey, S., Nodari, M., Wauters, L. A., Harrison, A., Thirgood, S., & Martinoli, A. (2011). The
627	strong and the hungry: bias in capture methods for mountain hares Lepus timidus. Wildlife Biology,
628	17, 311–316. doi:10.2981/10-133
629	Boon, A. K., Réale, D., & Boutin, S. (2008). Personality, habitat use, and their consequences for survival in
630	North American red squirrels Tamiasciurus hudsonicus. Oikos, 117, 1321-1328. doi:10.1111/j.0030-
631	1299.2008.16567.x
632	Boutin, S., Wauters, L. A., McAdam, A. G., Humphries, M. M., Tosi, G., & Dhondt, A. A. (2006).
633	Anticipatory reproduction and population growth in seed predators. Science, 314, 1928–1930.
634	doi:10.1126/science.1135520
635	Boyer, N., Réale, D., Marmet, J., Pisanu, B., & Chapuis, J-L. (2010). Personality, space use and tick load in
636	an introduced population of Siberian chipmunks Tamias sibiricus. Journal of Animal Ecology, 79,
637	538–547. doi:10.1111/j.1365-2656.2010.01659.x
638	Brehm, A. M., & Mortelliti, A. (2018). Mind the trap: large-scale field experiment shows that trappability is
639	not a proxy for personality. Animal Behaviour, 142, 101-112. doi:10.1016/j.anbehav.2018.06.009
640	Brehm, A. M., Mortelliti, A., Maynard, G. A., & Zydlewski, J. (2019). Land-use change and the ecological

consequences of personality in small mammals. *Ecology Letters*, 22, 1387–1395.

- Brehm, A. M., Tironi, S., & Mortelliti, A. (2020). Effects of trap confinement on personality measurements
- in two terrestrial rodents. *PLoS ONE*, 15, e0221136. doi:10.1371/journal.pone.0221136
- Bruinzeel, L. W., & van de Pol, M. (2004). Site attachment of floaters predicts success in territory
- acquisition. Behavioral Ecology, 15, 290–296. doi:10.1093/beheco/arh019
- 647 Carlson, B. E., & Tetzlaff, S. J. (2020). Long-term behavioral repeatability in wild adult and captive juvenile
- turtles (*Terrapene carolina*): Implications for personality development. *Ethology*, 126, 668–678.
- doi:10.1111/eth.13024
- 650 Carter, A. J., Heinsohn, R., Goldizen, A. W., & Biro, P. A. (2012). Boldness, trappability and sampling bias
- 651 in wild lizards. *Animal Behaviour*, 83, 1051–1058. doi:10.1016/j.anbehav.2012.01.033
- 652 Carter, A. J., Feeney, W. E., Marshall, H. H., Cowlishaw, G., & Heinsohn, R. (2013). Animal personality:
- what are behavioural ecologists measuring? *Biological Reviews*, 88, 465–475.
- doi:10.1111/brv.12007
- 655 Crall, J. D., Gravish, N., Mountcastle, A. M., Kocher, S. D., Oppenheimer, R. L., Pierce, N. E., & Combes,
- S. A. (2018). Spatial fidelity of workers predicts collective response to disturbance in a social insect.
- Nature Communications, 9, 1201. doi:10.1038/s41467-018-03561-w
- 658 DeRango, E. J., Schwarz, J. F. L., Kalberer, S., Piedrahita, P., Páez-Rosas, D., & Krüger, O. (2019). Intrinsic
- and maternal traits influence personality during early life in Galápagos sea lion, Zalophus
- 660 *wollebaeki*, pups. *Animal Behaviour*, 154, 111–120. doi:10.1016/j.anbehav.2019.06.011.
- 661 Dingemanse, N. J., Both, C., van Noordwijk, A. J., Rutten, A. L., & Drent, P. J. (2003). Natal dispersal and
- personalities in great tits (*Parus major*). *Proceedings of the Royal Society B: Biological Sciences*,
- 663 270, 741–747. doi:10.1098/rspb.2002.2300.
- Dingemanse, N. J., Bouwman, K. M., van de Pol, M., van Overveld, T., Patrick, S. C., Matthysen, E., &
- Quinn, J. L. (2012). Variation in personality and behavioural plasticity across four populations of the
- great tit *Parus major*: population variation in personality and behavioural plasticity. *Journal of*
- 667 Animal Ecology, 81, 116–126. doi:10.1111/j.1365-2656.2011.01877.x
- van Dongen, W. F. D., Maldonado, K., Sabat, P., & Vásquez, R. A. (2010). Geographic variation in the
- repeatability of a personality trait. *Behavioral Ecology*, 21, 1243–1250. doi:10.1093/beheco/arq145

- Fedy, B. C., & Stutchbury, B. J. M. (2004). Territory switching and floating in white-bellied antibrids
- 671 (*Myrmeciza longipes*), a resident tropical passerine in Panama. *The Auk, 121*, 486–496.
- doi:10.2307/4090412
- File, S. E., & Wardill, A. G. (1975). Validity of Head-Dipping as a Measure of Exploration in a Modified
- 674 Hole-Board. *Psychopharmacologia (Berl.)*, 44, 53–59. doi:10.1007/BF00421184
- 675 Fraser, D. F., Gilliam, J. F., Daley, M. J., Le, A. N., & Skalski, G. T. (2001). Explaining leptokurtic
- movement distributions intrapopulation variation in boldness and exploration. *American Naturalist*,
- 678 Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical*
- 679 *Science*, 7, 457–472. doi:10.1214/ss/1177011136
- 680 Geweke, J. (1992). Evaluating the accuracy of sampling-based approaches to the calculation of posterior
- moments. In: Bernardo, J. M., Berger, A. P., Dawid, A. P., Smith, A. F. M., editors. Bayesian
- Statistics 4. Oxford:Oxford University Press. 169–193.
- Hadfield, J. D. (2010). MCMC Methods for Multi-Response Generalized Linear Mixed Models: The
- MCMCglmm R Package. *Journal of Statistical Software*, 33, 1–22. doi:10.18637/jss.v033.i02.
- Hänninen, L., & Pastell, M. (2009). CowLog: open-source software for coding behaviors from digital video.
- *Behavior Research Methods*, 41, 472–476. doi:10.3758%2FBRM.41.2.472
- Hardman, S. I., & Dalesman, S. (2018). Repeatability and degree of territorial aggression differs among
- 688 urban and rural great tits (*Parus major*). *Scientific Reports*, 8, 5042. doi:10.1038/s41598-018-23463-
- 689 7
- 690 Herborn, K. A., Macleod, R., Miles, W. T., Schofield, A. N., Alexander, L., & Arnold, K. E. (2010).
- 691 Personality in captivity reflects personality in the wild. *Animal Behaviour*, 79, 835–843.
- 692 doi:10.1016/j.anbehav.2009.12.026
- 693 Horváth, G., Rodríguez-Ruiz, G., Martín, J., López, P., & Herczeg, G. (2019). Maternal diet affects juvenile
- 694 Carpetan rock lizard performance and personality. *Ecology and Evolution*, 9, 14476–14488.
- 695 doi:10.1002/ece3.5882
- Houslay, T. M., & Wilson, A. J. (2017). Avoiding the misuse of BLUP in behavioural ecology. *Behavioral*
- 697 *Ecology*, 28, 948–952. doi:10.1093/beheco/arx023

- Jolles, J. W., Briggs, H. D., Araya-Ajoy, Y. G., & Boogert, N. J. (2019). Personality, plasticity and
- predictability in sticklebacks: bold fish are less plastic and more predictable than shy fish. *Animal*
- 700 *Behaviour, 154,* 193–202. doi:10.1016/j.anbehav.2019.06.022
- Jolly, C. J., Webb, J. K., Gillespie, G. R., Hughes, N. K., & Phillips, B. L. (2019). Bias averted: personality
- may not influence trappability. Behavioral Ecology and Sociobiology, 73, 129. doi:10.1007/s00265-
- 703 019-2742-4
- Koski, S. E. (2014). Broader horizons for animal personality research. Frontiers in Ecology and Evolution, 2,
- 705 1–6. doi:10.3389/fevo.2014.00070
- 706 Krebs, R., Linnenbrink, M., & Guenther, A. (2019). Validating standardised personality tests under semi-
- natural conditions in wild house mice (*Mus musculus domesticus*). *Ethology*, 125, 761–773.
- 708 doi:10.1111/eth.12930
- 709 Larsen, K. W., & Boutin, S. (1994). Movements, survival and settlement of red squirrel (Tamiasciurus
- 710 *hudsonicus*) offspring. *Ecology*, 75, 214–223. doi:10.2307/1939395
- Le Coeur, C., Thibault, M., Pisanu, B., Thibault, S., Chapuis, J-L., & Baudry, E. (2015). Temporally
- fluctuating selection on a personality trait in a wild rodent population. *Behavioral Ecology*, 26,
- 713 1285–1291. doi:10.1093/beheco/arv074
- Lowry, H., Lill, A., & Wong, B. B. M. (2013). Behavioural responses of wildlife to urban environments.
- 715 *Biological Reviews*, 88, 537–549. doi:10.1111/brv.12012
- Lurz, P. W. W., Garson, P. J., & Wauters, L. (2000). Effects of temporal and spatial variations in food supply
- on the space and habitat use of red squirrels, *Sciurus vulgaris* L. *Journal of Zoology*, 251, 167–178.
- 718 doi:10.1111/j.1469-7998.2000.tb00601.x
- 719 Lurz, P. W. W., Gurnell, J., & Magris, L. (2005). Sciurus vulgaris. Mammalian Species, 769, 1–10.
- 720 doi:10.2307/3504523
- Martin, J. G. A., & Réale, D. (2008). Temperament, risk assessment and habituation to novelty in eastern
- 722 chipmunks, Tamias striatus. Animal Behaviour, 75, 309–318. doi:10.1016/j.anbehav.2007.05.026
- 723 Martin, J. G. A., Nussey, D. H., Wilson, A. J., & Réale, D. (2011). Measuring individual differences in
- reaction norms in field and experimental studies: a power analysis of random regression models.
- 725 *Methods in Ecology and Evolution*, 2, 362–374. doi:10.1111/j.2041-210X.2010.00084.x

- 726 Mazzamuto, M. V., Cremonesi, G., Santicchia, F., Preatoni, D. G., Martinoli, A., & Wauters, L. A. (2019).
- Rodents in the arena: a critical evaluation of methods measuring personality traits. *Ethology, Ecology*
- 728 and Evolution, 31, 38–58. doi:10.1080/03949370.2018.1488768
- Michelangeli, M., Wong, B. B. M., & Chapple, D. G. (2016). It's a trap: sampling bias due to animal
- personality is not always inevitable. *Behavioral Ecology*, 27, 62–67. doi:10.1093/beheco/arv123
- 731 Michelangeli, M., Chapple, D. G., Goulet, C. T., Bertram, M. G., & Wong, B. B. M. (2019). Behavioral
- syndromes vary among geographically distinct populations in a reptile. *Behavioral Ecology*, 30,
- 733 393–401. doi:10.1093/beheco/ary178
- Minderman, J., Reid, J. M., Hughes, M., Denny, M. J. H., Hogg, S., Evans, P. G. H., & Whittingham, M. J.
- 735 (2010). Novel environment exploration and home range size in starlings *Sturnus vulgaris*.
- 736 Behavioral Ecology, 21, 1321–1329. doi:10.1093/beheco/arq151
- Montiglio, P-O., Garant, D., Thomas, D., & Réale, D. (2010). Individual variation in temporal activity
- patterns in open-field tests. *Animal Behaviour*, 80, 905–912. doi:10.1016/j.anbehav.2010.08.014
- Montiglio, P-O., Garant, D., Pelletier, F., & Réale, D. (2012). Personality differences are related to longterm
- stress reactivity in a population of wild eastern chipmunks, *Tamias striatus*. *Animal Behaviour*, 84,
- 741 1071–1079. doi:10.1016/j.anbehav.2012.08.010
- Morinay, J., Daniel, G., Gustafsson, L., & Doligez, B. (2019). No evidence for behavioural syndrome and
- 743 genetic basis for three personality traits in a wild bird population. *Animal Behaviour*, 153, 69–82.
- 744 doi:10.1016/j.anbehav.2019.05.001
- Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: a practical guide
- 746 for biologists. *Biological Reviews*, 85, 935–956. doi:10.1111/j.1469-185X.2010.00141.x
- Neudorf, D. L., Stutchbury, B. J. M., & Piper, W. H. (1997). Covert extraterritorial behavior of female
- 748 hooded warblers. *Behavioral Ecology*, 8, 595–600. doi:10.1093/beheco/8.6.595
- van Oers, K., Drent, P. J., de Goede, P., & van Noordwijk, A. J. (2004). Realized heritability and
- 750 repeatability of risk-taking behaviour in relation to avian personalities. *Proceedings of the Royal*
- 751 Society B: Biological Sciences, 271, 65–73. doi:10.1098/rspb.2003.2518

- van Overveld, T., Adriaensen, F., & Matthysen, E. (2011). Postfledging family space use in great tits in
- relation to environmental and parental characteristics. *Behavioral Ecology*, 22, 899–907.
- 754 doi:10.1093/beheco/arr063
- Patterson, L. D., & Schulte-Hostedde, A. I. (2011). Behavioural correlates of parasitism and reproductive
- success in male eastern chipmunks, *Tamias striatus*. *Animal Behaviour*, 81, 1129–1137.
- 757 doi:10.1016/j.anbehav.2011.02.016
- Pedersen, M. C., Dunn, P. O., & Whittingham, L. A. (2006). Extraterritorial forays are related to a male
- ornamental trait in the common yellowthroat. *Animal Behaviour*, 72, 479–486.
- 760 doi:10.1016/j.anbehav.2006.02.010
- Perals, D., Griffin, A. S., Bartomeus, I., & Sol, D. (2017). Revisiting the open-field test: what does it really
- tell us about animal personality? *Animal Behaviour*, 123, 69–79. doi:10.1016/j.anbehav.2016.10.006
- Petelle, M. B., Martin, J. G. A., & Blumstein, D. T. (2019). Mixed support for state maintaining risky
- personality traits in yellow-bellied marmots. *Animal Behaviour*, 150, 177–188.
- 765 doi:10.1016/j.anbehav.2019.02.008
- 766 R Core Team. (2019). R: A language and environment for statistical computing. Vienna, Austria: R
- Foundation for Statistical Computing. Retrieved from https://www.R-project.org/
- Réale, D., Gallant, B. Y., Leblanc, M., & Festa-Bianchet, M. (2000). Consistency of temperament in bighorn
- 769 ewes and correlates with behaviour and life history. *Animal Behaviour*, 60, 589–597.
- 770 doi:10.1006/anbe.2000.1530
- Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal
- temperament within ecology and evolution. *Biological Reviews*, 82, 291–318. doi:10.1111/j.1469-
- 773 185X.2007.00010.x
- Richardson, K. M., Parlato, E. H., Walker, L. K., Parker, K. A., Ewen, J. G., & Armstrong, D. P. (2019).
- Links between personality, early natal nutrition and survival of a threatened bird. *Philosophical*
- 776 Transactions of the Royal Society B: Biological Sciences, 374, 20190373.
- 777 doi:10.1098/rstb.2019.0373

- Rodrigues, D., Wauters, L. A., Romeo, C., Mari, V., Preatoni, D., Mathias, M. L., ... Martinoli, A. (2010).
- Living on the edge: can Eurasian red squirrels (Sciurus vulgaris) persist in extreme high-elevation
- 780 habitats? Arctic, Antarctic, and Alpine Research, 42, 106–112. doi:10.1657/1938-4246-42.1.106
- Romeo, C., Wauters, L., Preatoni, D., Tosi, G., & Martinoli, A. (2010). Living on the edge: space use of
- Eurasian red squirrels in marginal high elevation habitat. *Acta Oecologica*, *36*, 604–610.
- 783 doi:10.1016/j.actao.2010.09.005
- Santicchia, F., Romeo, C., Martinoli, A., Lanfranchi, P., Wauters, L.A., & Ferrari, N. (2015). Effects of
- habitat quality on parasite abundance: do forest fragmentation and food availability affect helminth
- infection in the Eurasian red squirrel? *Journal of Zoology*, 296, 38–44. doi:10.1111/jzo.12215
- Santicchia, F., Gagnaison, C., Bisi, F., Martinoli, A., Matthysen, E., Bertolino, S., & Wauters, L. A. (2018a).
- Habitat-dependent effects of personality on survival and reproduction in red squirrels. *Behavioral*
- 789 *Ecology and Sociobiology*, 72, 134. doi:10.1007/s00265-018-2546-y
- Santicchia, F., Dantzer, B., van Kesteren, F., Palme, R., Martinoli, A., Ferrari, N., & Wauters, L. A. (2018b).
- 791 Stress in biological invasions: introduced invasive grey squirrels increase physiological stress in
- native Eurasian red squirrels. *Journal of Animal Ecology*, 87, 1342–1352. doi:10.1111/1365-
- 793 2656.12853
- Santicchia, F., Romeo, C., Ferrari, N., Matthysen, E., Vanlauwe, L., Wauters, L. A., & Martinoli, A. (2019).
- 795 The price of being bold? Relationship between personality and endoparasitic infection in a tree
- 796 squirrel. *Mammalian Biology*, 97, 1–8. doi:10.1016/j.mambio.2019.04.007
- 797 Santicchia, F., Wauters, L. A., Piscitelli, A. P., Van Dongen, S., Martinoli, A., Preatoni, D., ... Ferrari, N.
- 798 (2020a). Spillover of an alien parasite reduces expression of costly behaviour in native host species.
- 799 *Journal of Animal Ecology*, 89, 1559–1569. doi:10.1111/1365-2656.13219
- Santicchia, F., Wauters, L. A., Dantzer, B., Westrick, S. E., Ferrari, N., Romeo, C., ... Martinoli, A. (2020b).
- Relationships between personality traits and the physiological stress response in a wild mammal.
- 802 *Current Zoology*, 66, 197–204. doi: 10.1093/cz/zoz040
- [dataset] Santicchia, F., Van Dongen, S., Martinoli, A., Preatoni, D., & Wauters, L. A. (2020). Measuring
- personality traits in Eurasian red squirrels: a critical comparison of different methods. Zenodo;
- 805 https://doi.org/10.5281/zenodo.3889846

806 Schirmer, A., Herde, A., Eccard, J. A., & Dammhahn, M. (2019). Individuals in space: personality-807 dependent space use, movement and microhabitat use facilitate individual spatial niche 808 specialization. Oecologia, 189, 647-660. doi:10.1007/s00442-019-04365-5 Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: an ecological and evolutionary overview. 809 Trends in Ecology and Evolution, 19, 372–378. doi:10.1016/j.tree.2004.04.009 810 Sih, A., Cote, J., Evans, M., Fogarty, S., & Pruitt, J. (2012). Ecological implications of behavioural 811 syndromes. *Ecology Letters*, 15, 278–289. doi:10.1016/j.anbehav.2017.09.008 812 813 Šlipogor, V., Burkart, J. M., Martin, J. S., Bugnyar, T., & Koski, S. E. (2020). Personality method validation in common marmosets (Callithrix jacchus): Getting the best of both worlds. Journal of Comparative 814 Psychology, 134, 52-70. doi:10.1037/com0000188 815 Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2017). rptR: repeatability estimation and variance 816 decomposition by generalized linear mixed-effects models. Methods in Ecology and Evolution, 8, 817 818 1639–1644. doi:10.1111/2041-210X.12797 Tebbich, S., Fessl, B., & Blomqvist, D. (2009). Exploration and ecology in Darwin's finches. Evolutionary 819 820 Ecology, 23, 591–605. doi:10.1007/s10682-008-9257-1 Thomas, L. S., Teich, E., Dausmann, K. H., Reher, S., & Turner, J. M. (2018). Degree of urbanisation affects 821 Eurasian red squirrel activity patterns. Hystrix, the Italian Journal of Mammalogy, 29, 175–180. 822 doi:10.4404/hystrix-00065-2018 823 824 Tkaczynski, P. J., Ross, C., MacLarnon, A., Mouna, M., Majolo, B., & Lehmann, J. (2019). Measuring 825 personality in the field: An in situ comparison of personality quantification methods in wild Barbary 826 macaques (Macaca sylvanus). Journal of Comparative Psychology, 133, 313–325. doi:10.1037/com0000163 827 Tkaczynski, P. J., Mielke, A., Samuni, L., Preis, A., Wittig, R. M., & Crockford, C. (2020) Long-term 828 829 repeatability in social behaviour suggests stable social phenotypes in wild chimpanzees. Royal Society Open Science, 7: 200454. doi:10.1098/rsos.200454 830 Tsytsulina, K., Formozov, N., Shar, S., Lkhagvasuren, D., & Sheftel, B. (2016). Eutamias sibiricus. The 831 IUCN Red List of Threatened Species 2016: e.T21360A115161465. doi:10.2305/IUCN.UK.2016-832

833

3.RLTS.T21360A22268598.en

- 834 Vanden Broecke, B., Borremans, B., Mariën, J., Makundi, R. H., Massawe, A. W., Leirs, H., & Hughes, N. K. (2018). Does exploratory behavior or activity in a wild mouse explain susceptibility to virus 835 836 infection? Current Zoology, 64, 585-592. doi:10.1093/cz/zox053 Verbeek, M., Drent, P. J., & Wiepkema, P. R. (1994). Consistent individual differences in early exploratory 837 behaviour of male great tits. Animal Behaviour, 44, 1113-1121. doi:10.1006/anbe.1994.1344 838 Walsh, R. N. & Cummins, R. A. (1976). The open-field test: a critical review. Psychological Bulletin, 83, 839 482-504. doi:10.1037/0033-2909.83.3.482 840 841 Wauters, L. A., & Dhondt, A. A. (1989). Body weight, longevity and reproductive success in red squirrels
- (Sciurus vulgaris). Journal of Animal Ecology, 58, 637–651. doi:10.2307/4853
 Wauters, L. A., & Dhondt, A. A. (1992). Spacing behaviour of red squirrels, Sciurus vulgaris: variation
- between habitats and the sexes. *Animal Behaviour*, *43*, 297–311. doi:10.1016/S0003-3472(05)80225-845
- Wauters, L. A., & Dhondt, A. A. (1993). Immigration pattern and success in red squirrels. *Behavioral Ecology and Sociobiology*, 33, 159–167. doi:10.1007/BF00216596
- Wauters, L. A., & Dhondt, A. A. (1995). Lifetime reproductive success and its correlates in female Eurasian
 red squirrels. *Oikos*, 72, 402–410. doi:10.2307/3546126
- Wauters, L. A., Dhondt, A. A., & De Vos, R. (1990). Factors affecting male mating success in red squirrels
 (Sciurus vulgaris). Ethology, Ecology and Evolution, 2, 195–204.
- 852 doi:10.1080/08927014.1990.9525486
- Wauters, L. A., Hutchinson, Y., Parkin, D. T., & Dhondt, A. A. (1994). The effects of habitat fragmentation
 on demography and on the loss of genetic variation in the red squirrel. *Proceedings of the Royal Society B: Biological Sciences*, 225, 107–111. doi:10.1098/rspb.1994.0015
- Wauters, L. A., Gurnell, J., Martinoli, A., & Tosi, G. (2002). Interspecific competition between native
 Eurasian red squirrels and alien grey squirrels: does resource partitioning occur? *Behavioral Ecology* and Sociobiology, 52, 332–341. doi:10.1007/s00265-002-0516-9
- Wauters, L. A., Matthysen, E., Adriaensen, F., & Tosi, G. (2004). Within-sex density dependence and population dynamics of red squirrels *Sciurus vulgaris*. *Journal of Animal Ecology*, 73, 11–25. doi:10.1111/j.1365-2656.2004.00792.x

862	Wauters, L. A., Vermeulen, M., Van Dongen, S., Bertolino, S., Molinari, A., Tosi, G., & Matthysen, E.
863	(2007). Effects of spatio-temporal variation in food supply on red squirrel Sciurus vulgaris body size
864	and body mass and its consequences for some fitness components. <i>Ecography</i> , 30, 51-65.
865	doi:10.1111/j.2006.0906-7590.04646.x
866	Wauters, L. A., Githiru, M., Bertolino, S., Molinari, A., Tosi, G., & Lens, L. (2008). Demography of alpine
867	red squirrel populations in relation to fluctuations in seed crop size. Ecography, 31, 104–114.
868	doi:10.1111/j.2007.0906-7590.05251.x
869	Wauters, L. A., Verbeylen, G., Preatoni, D., Martinoli, A., & Matthysen, E. (2010). Dispersal and habitat
870	cuing of Eurasian red squirrels in fragmented habitats. <i>Population Ecology</i> , 52, 527–536. doi:
871	10.1007/s10144-010-0203-z
872	Wauters, L. A., Mazzamuto, M. V., Santicchia, F., Van Dongen, S., Preatoni, D. G., & Martinoli, A. (2019).
873	Interspecific competition affects the expression of personality traits in natural populations. Scientific
874	Reports, 9, 11189. doi:10.1038/s41598-019-47694-4
875	Yuen, C. H., Schoepf, I., Schradin, C., & Pillay, N. (2017). Boldness: are open field and startle tests
876	measuring the same personality trait? Animal Behaviour, 128, 143–151. doi:
877	10.1016/j.anbehav.2017.04.009
878	Zong, C., Suonancuo, M., Santicchia, F., Wauters, L. A., Preatoni, D. G., & Martinoli, A. (2014). Habitat
879	effects on hoarding plasticity in the Eurasian red squirrel (Sciurus vulgaris). Hystrix, the Italian
880	Journal of Mammalogy, 25, 14-17. doi:10.4404/hystrix-25.1-10160

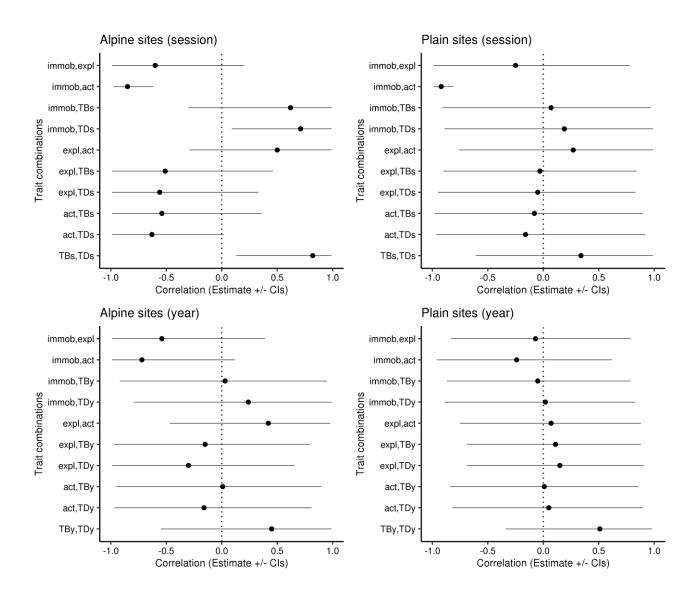
Table 1. The average proportion of time (raw data), red squirrels were engaged in behaviours related to the different OFT personality traits (see Table S2 for details). Followed by the average (raw data) trappability (TB) and trap-diversity (TD) calculated for each session and each year. Data grouped by habitat-type (alpine and plain). Each type of different personality measure reported the sample sizes (n) and the relative number of different squirrels (ID). Data shown are the minimum and maximum values, mean with standard deviation (SD) and the 95% confidence intervals. Repeatability (R), confidence intervals (95% CI) and likelihood ratio test (LRT; df; p) were estimated on squareroot transformed personality measures.

Personality measure	Habitat-type	Personality trait						Repeatability					
Tersonanty measure	павнае-гурс	1 crsonanty trait	min max		Mean	SD	95% CI	R	95% CI	LRT	df	p	
		Activity	0.004	0.92	0.33	0.19	0.19 - 0.44	0.47	0.34 - 0.62	34.3	1	< 0.001	
	Alpine (n=273; ID=144)	Immobility	0.01	0.99	0.60	0.22	0.46 - 0.77	0.46	0.34 - 0.62	23.4	1	< 0.001	
Onen Field Test		Exploration	0	0.31	0.05	0.05	0.01 - 0.07	0.18	0.04 - 0.37	5.2	1	0.01	
Open Field Test	Plain (n=309; ID=120)	Activity	0.03	0.97	0.36	0.23	0.17 - 0.52	0.35	0.22 - 0.49	36.5	1	< 0.001	
		Immobility	0	0.95	0.54	0.28	0.34 - 0.78	0.31	0.18 - 0.45	25.1	1	< 0.001	
		Exploration	0	0.42	0.07	0.08	0.02 - 0.09	0.10	3.3e-16-0.25	2.15	1	0.07	
	Alpine	TBs	0.17	1.33	0.44	0.25	0.25 - 0.50	0.33	0.18 - 0.50	20.4	1	<0.001	
TB, TD indices	(n=203; ID=70)	TDs	0.05	0.22	0.08	0.05	0.05 - 0.10	0.41	0.26 - 0.56	28.7	1	< 0.001	
session	Plain	TBs	0.20	2	0.53	0.32	0.25 - 0.75	0.17	0.07 - 0.26	22.2	1	< 0.001	
	(n=452; ID=90)	TDs	0.03	0.29	0.07	0.05	0.03 - 0.08	0.18	0.09 - 0.28	23.6	1	<0.001	
	Alpine	ТВу	0.11	1	0.39	0.23	0.25 - 0.50	0.33	0.13 - 0.56	8.28	1	0.002	
TB, TD indices	(n=138; ID=70)	TDy	0.05	0.44	0.10	0.07	0.05 - 0.10	0.55	0.38 - 0.73	19.6	1	< 0.001	
Year	Plain	TBy	0.07	1.67	0.49	0.30	0.25 - 0.66	0.27	0.11 - 0.48	10.3	1	< 0.001	
	(n=186; ID=90)	TDy	0.03	0.43	0.12	0.09	0.05 - 0.17	0.20	0.03 - 0.41	4.67	1	0.02	

Table 2. Description of factors used to calculate individual trappability and trap-diversity indices. Data grouped by time-interval and habitat-type.

Time-interval	Session							Year						
Habitat-type		Alpine		Plain			Alpine			Plain				
Range of presence in the study sites	2–6 sessions			2–9 sessions			1–3 years			1–4 years				
	median	mean ± SE	range	median	mean ± SE	range	median	mean ± SE	range	median	mean ± SE	range		
n. captures	1	1.69 ± 0.07	1–4	2	2.15 ± 0.06	1–7	2	2.49 ± 0.15	1–8	4	5.22 ± 0.28	1–16		
n. different traps captured	1	1.57 ± 0.06	1–4	2	1.99 ± 0.05	1–6	2	1.94 ± 0.11	1–8	3	3.57 ± 0.17	1–11		
n. capture days	4	3.97 ± 0.05	3–6	4	4.20 ± 0.04	3–5	7	6.38 ± 0.17	3–9	9	11.68 ± 0.54	3–28		

Figure 1. Correlations (estimate \pm 95% credibility intervals) between the dependent variables derived from the MCMCglmm models per trapping session and per year, and for each habitat-type (alpine and plain). Significant results (0 not included in the 95% CIs).



Measuring personality traits in Eurasian red squirrels: a critical comparison of different methods

Santicchia Francesca, Van Dongen Stefan, Martinoli Adriano, Preatoni Damiano, Wauters Lucas Armand

Supporting Information

Table S1. Location of study sites in Lombardy and Piedmont, North Italy. Sample size refers to capture-mark-recaptures, number of different squirrels (ID) and sexes (M, F). Data are presented for each habitat-type (alpine or plain).

Site (size ha)	Coordinates	Sample size CMR (ID, M, F)	Sessions			N traps	Trap density (ha ⁻¹)	
			2016	2017	2018	2019		(114)
Alps								
Bormio (70 ha)	46°27′N, 10°30′E	84 (41, 33, 8)	june sept	june sept	june sept	june	20	0.29
Cancano (55 ha)	46°33′N, 10°15′E	103 (29, 17, 12)	june sept	june sept	may sept	june sept	18	0.33
Valfurva (70 ha)	46°27′N, 10°31′E	277 (87, 52, 35)	may sept	may sept	may sept	may	20	0.29
Plain								
Castelbarco (65 ha)	45°35′N, 9°31′E	551 (82, 45, 37)	jan apr sept oct	feb ¹ apr may oct dec	mar july	mar june	40	0.62
Vanzago (60 ha)	45°31′N, 8°58′E	287 (34, 20, 14)	jan mar may oct	feb june nov	mar nov	feb apr oct	28	0.47
Passatempo (20 ha)	45°00′N, 7°78′E	218 (30, 13, 17)	mar may oct	mar may oct dec	apr nov	mar apr dec	21	1.05

¹ two capture sessions were carried out in February 2017.

S1. Details on study sites

The alpine sites are mixed conifer forests dominated by either Norway spruce (*Picea abies*), Arolla pine (*Pinus cembra*) or mountain pine (*Pinus mugo*) (Wauters et al., 2008; Rodrigues et al., 2010). The lowland (plain) sites are mature mixed broadleaf-conifer woods dominated by oaks (*Quercus robur*, *Q. petraea*) and hornbeam (*Carpinus betulus*) with different proportions of conifers, and high proportions of strongly preferred tree seeds [hazel (*Corylus avellana*) and walnut (*Juglans regia*) in Passatempo; sweet chestnut (*Castanea sativa*), hazel and hornbeam in Castelbarco; hazel and hornbeam in Vanzago]. Based on the availability of preferred tree seeds (Wauters et al., 2001; Molinari et al., 2006; Rodrigues et al., 2010) and red squirrel densities, Valfurva, Bormio (alpine) and Castelbarco and Passatempo (plain) are considered high-quality habitats, while Cancano (alpine) and Vanzago (plain) are habitats of poorer quality.

S2. Details on arena test to measure personality

The arena is a white extruded polycarbonate box of $50 \times 51 \times 51$ cm; the floor of the arena consists of a panel with four blind holes (7 cm diameter × 4 cm deep), that allow to differentiate between exploration and activity behaviours (hole board test, Martin & Réale, 2008; Mazzamuto et al., 2019). In the lid of the arena (inside a 5 cm diameter hole) we fit a web camera (Drift, Professional HD Action Camera, model: FD9960, Ghost S) to record the animal's behaviour. We placed the arena on the ground near the trap where the squirrel was caught and started recording before we released the animal inside the arena (Mazzamuto et al., 2019; Wauters et al., 2019; Santicchia et al., 2020). After each experiment we cleaned the arena with 90% ethyl alcohol to eliminate urine and faecal pellets when present and to eliminate effects of squirrel's scent on behaviour of the next animal and to prevent transmission of infections. The protocol of the experiments and test duration validation are reported by Mazzamuto et al. (2019). Procedures to define the expert-based (EB) personality traits are explained in detail in previous papers (Mazzamuto et al., 2019; Wauters et al., 2019; Santicchia et al., 2020).

S3. Temporal difference between consecutive arena tests

Number of days from the previous arena test were included in models testing for repeatabilities of the OFT personality traits to account for the possible effect of temporal proximity between two tests. In details, in alpine sites 8 arena tests were conducted after 1 day from the previous test on the same individual, 7 arena tests after 2 days and 1 arena test after 3 days. Hence, 16 arena tests on a total of 273 were conducted in close temporal proximity (same capture session). In plain sites 14 arena tests were conducted after 1 day from the previous test on the same individual, 13 arena tests after 2 days and 7 arena tests after 3 days. Thus, 34 arena tests on a total of 309 were conducted in close temporal proximity (same capture session).

Table S2. Ethogram for the open field test (OFT). Description of the single behaviours and indication of the expert-based grouping into categories that represent personality traits (after Mazzamuto et al., 2019; Wauters et al., 2019; Santicchia et al., 2020).

Open Field Test

Behaviour	Behaviour description	Personality traits
Locomotion	Jump, walk	Activity
Rise	Rise up on hind legs	
Scan	Head moving	
Scratch	Scratch or chew floors/walls	Exploration
Sniff	Sniff the corner of arena	
Head dip	Put head in holes in the floor	
Hang	Hang on walls	Immobility
Immobile	No movement	

Table S3. Repeatabilities of OFT personality traits, by each habitat-type (alpine and plain), estimated with *rptR* function and relative linear mixed-effects models fitted by *lmer* function in *lmerTest* package.

Activity alpine sites

```
Repeatability estimation using the lmm method
Call = rpt(formula = act ~ SEX + order01 + AREA + YEAR + ndayprevtest + (1 | ID), grname =
c("ID"), data = dfalp, datatype = "Gaussian", CI = 0.95, nboot = 2000, npermut = 1000, rat
io = TRUE, adjusted = TRUE)
Data: 273 observations
______
ID (144 groups)
Repeatability estimation overview:
     R SE 2.5% 97.5% P permut LRT P
   0.47 0.071 0.335 0.622
                                   0.001
Bootstrapping and Permutation test:
          N Mean Median 2.5% 97.5%
2000 0.4909 0.4952 0.335 0.622
        1000 0.0396 0.0168 0.000 0.167
permut
Likelihood ratio test:
logLik full model = 168.9909
logLik red. model = 151.8655
D = 34.3, df = 1, P = 2.42e-09
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: act ~ SEX + order01 + AREA + YEAR + ndayprevtest + (1 | ID)
   Data: dfalp
REML criterion at convergence: -272.8
Scaled residuals:
     Min 1Q Median
                                   3Q
-2.83984 -0.54740 -0.02662 0.57639 2.04106
Random effects:
Groups Name Variance Std.Dev.
         (Intercept) 0.009596 0.09796
                      0.010813 0.10398
 Residual
Number of obs: 273, groups: ID, 144
Fixed effects:
               Estimate Std. Error
                                              df t value Pr(>|t|)
(Intercept) 4.169e-01 3.768e-02 2.229e+02 11.066 < 2e-16 ***
SEXM -1.232e-02 2.350e-02 1.296e+02 -0.524 0.60100 order011 1.687e-01 2.055e-02 1.705e+02 8.210 5.25e-14 ** AREAFRA 9.501e-02 3.304e-02 1.315e+02 2.876 0.00470 **
                                                    8.210 5.25e-14 ***
             4.097e-02 2.674e-02 1.427e+02 1.532 0.12766
AREAVAL
YEAR2017
              3.350e-02 2.046e-02 2.490e+02 1.637 0.10282
YEAR2017 3.350e-02 2.046e-02 2.490e+02 1.637 0.10282

YEAR2018 -7.464e-02 2.514e-02 2.635e+02 -2.969 0.00326 **

YEAR2019 -3.335e-02 2.874e-02 2.567e+02 -1.160 0.24702
YEAR2019 -3.335e-02 2.874e-02 2.567e+02 -1.160 0.24702 ndayprevtest 2.412e-04 7.966e-05 1.719e+02 3.028 0.00284 **
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Immobility alpine sites

Repeatability estimation using the 1mm method

```
Call = rpt(formula = immob ~ SEX + order01 + AREA + YEAR + ndayprevtest + (1 | ID), grname
= c("ID"), data = dfalp, datatype = "Gaussian", CI = 0.95, nboot = 2000, npermut = 1000, r
atio = TRUE, adjusted = TRUE)
Data: 273 observations
______
ID (144 groups)
Repeatability estimation overview:
    R SE 2.5% 97.5% P_permut LRT_P
  0.464 0.0699 0.344 0.612 0.001
Bootstrapping and Permutation test:
          N Mean Median 2.5% 97.5%
         2000 0.4852 0.4872 0.344 0.612
       1000 0.0414 0.0136 0.000 0.194
Likelihood ratio test:
logLik full model = 148.8642
logLik red. model = 137.154
D = 23.4, df = 1, P = 6.51e-07
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: immob ~ SEX + order01 + AREA + YEAR + ndayprevtest + (1 | ID)
   Data: dfalp
REML criterion at convergence: -233.8
Scaled residuals:
                         3Q
Min 1Q Median 3Q Max -3.3138 -0.3390 0.0550 0.5414 2.2229
Random effects:
Groups Name Variance Std.Dev.
         (Intercept) 0.01094 0.1046 0.01262 0.1123
Residual
Number of obs: 273, groups: ID, 144
Fixed effects:
              Estimate Std. Error
                                          df t value Pr(>|t|)
             8.944e-01 4.050e-02 2.133e+02 22.084 < 2e-16 *** 3.305e-03 2.522e-02 1.126e+02 0.131 0.89597
(Intercept)
SEXM
           -1.730e-01 2.217e-02 1.553e+02 -7.803 8.31e-13 ***
order011
           -8.358e-02 3.545e-02 1.145e+02 -2.358 0.02008 *
            -3.661e-02 2.870e-02 1.257e+02 -1.276 0.20441
AREAVAL
                                    2.455e+02 -1.435 0.15247
2.633e+02 1.989 0.04768
YEAR2017
            -3.164e-02 2.204e-02
YEAR2018 5.384e-02 2.706e-02 2.633e+02 1.989 0.04768
YEAR2019 5.437e-02 3.092e-02 2.540e+02 1.758 0.07992
                                                       0.04768 *
ndayprevtest -2.499e-04 8.597e-05 1.566e+02 -2.907 0.00418 **
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Exploration alpine sites

Repeatability estimation using the lmm method

```
Call = rpt(formula = expl ~ SEX + order01 + AREA + YEAR + ndayprevtest + (1 | ID), grname
= c("ID"), data = dfalp, datatype = "Gaussian", CI = 0.95, nboot = 2000, npermut = 1000, r
atio = TRUE, adjusted = TRUE)
Data: 273 observations
______
ID (144 groups)
Repeatability estimation overview:
      R SE 2.5% 97.5% P_permut LRT_P
  0.182 0.0834 0.0396 0.372 0.019 0.011
Bootstrapping and Permutation test:
           N Mean Median 2.5% 97.5%
         2000 0.2072 0.2080 0.0396 0.372
       1000 0.0378 0.0144 0.0000 0.172
Likelihood ratio test:
logLik full model = 272.9636
logLik red. model = 270.3625
D = 5.2, df = 1, P = 0.0113
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: expl ~ SEX + order01 + AREA + YEAR + ndayprevtest + (1 | ID)
   Data: dfalp
REML criterion at convergence: -473
Scaled residuals:
    Min 1Q Median
-2.32728 -0.54581 -0.06242 0.55428 2.94454
Random effects:
Groups Name Variance Std.Dev.
          (Intercept) 0.001530 0.03911
Residual
                     0.006866 0.08286
Number of obs: 273, groups: ID, 144
Fixed effects:
               Estimate Std. Error
                                            df t value Pr(>|t|)
             1.381e-01 2.420e-02 2.224e+02 5.706 3.66e-08 ***
(Intercept)
          -5.248e-03 1.372e-02 1.168e+02 -0.383 0.702721
1.030e-01 1.544e-02 2.131e+02 6.667 2.20e-10 ***
-8.037e-03 1.935e-02 1.206e+02 -0.415 0.678604
SEXM
order011
AREAFRA
AREAVAL
            -3.261e-02 1.590e-02 1.356e+02 -2.051 0.042145 *
YEAR2017
             3.448e-02 1.435e-02 2.620e+02 2.403 0.016947 *
YEAR2018 2.241e-02 1.685e-02 2.508e+02 1.330 0.184706
YEAR2019 -6.362e-02 1.881e-02 2.233e+02 -3.383 0.000848 ***
ndayprevtest 2.338e-04 5.986e-05 2.134e+02 3.906 0.000126 ***
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Activity plain sites

Repeatability estimation using the 1mm method

```
Call = rpt(formula = act \sim SEX + order01 + AREA + YEAR + ndayprevtest + (1 | ID), grname =
c("ID"), data = dfpla, datatype = "Gaussian", CI = 0.95, nboot = 2000, npermut = 1000, rat
io = TRUE, adjusted = TRUE)
Data: 309 observations
______
ID (120 groups)
Repeatability estimation overview:
    R SE 2.5% 97.5% P_permut LRT_P
  0.345 0.0689 0.218 0.482 0.001
Bootstrapping and Permutation test:
          N Mean Median 2.5% 97.5%
         2000 0.3549 0.3554 0.218 0.482
       1000 0.0289 0.0102 0.000 0.124
Likelihood ratio test:
logLik full model = 197.9881
logLik red. model = 179.7631
D = 36.5, df = 1, P = 7.83e-10
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: act ~ SEX + order01 + AREA + YEAR + ndayprevtest + (1 | ID)
   Data: dfpla
REML criterion at convergence: -329.5
Scaled residuals:
    Min 1Q Median 3Q
-3.13805 -0.55426 -0.01489 0.56940 2.61264
Random effects:
Groups Name Variance Std.Dev.
         (Intercept) 0.006498 0.08061
Residual
                    0.012329 0.11104
Number of obs: 309, groups: ID, 120
Fixed effects:
                Estimate Std. Error
                                            df t value Pr(>|t|)
              4.047e-01 2.687e-02 2.176e+02 15.058 < 2e-16 ***
(Intercept)
SEXM
               -1.594e-02 2.080e-02 1.120e+02 -0.766 0.4452
order011 1.594e-01 1.861e-02 2.478e+02 8.569 1.14e-15 ***
AREAC06-04 1.259e-01 2.543e-02 1.022e+02 4.951 2.93e-06 ***
AREASal-Passat 5.206e-02 2.684e-02 1.088e+02 1.940 0.0550 .
               4.685e-02 2.196e-02 2.999e+02 2.133 0.0337 *
YEAR2017
              -1.051e-01 2.409e-02 2.993e+02 -4.365 1.75e-05 ***
YEAR2018
             2.643e-01 2.547e-02 2.545e+02 10.378 < 2e-16 *** 1.719e-04 7.236e-05 2.458e+02 2.375 0.0183 *
YEAR2019
ndayprevtest
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Immobility plain sites

Repeatability estimation using the lmm method

```
Call = rpt(formula = immob ~ SEX + order01 + AREA + YEAR + ndayprevtest + (1 | ID), grname
= c("ID"), data = dfpla, datatype = "Gaussian", CI = 0.95, nboot = 2000, npermut = 1000, r
atio = TRUE, adjusted = TRUE)
Data: 309 observations
______
ID (120 groups)
Repeatability estimation overview:
      R SE 2.5% 97.5% P_permut LRT_P
  0.309 0.0721 0.18 0.462 0.001
Bootstrapping and Permutation test:
           N Mean Median 2.5% 97.5%
         2000 0.3244 0.3254 0.18 0.462
permut 1000 0.0284 0.0103 0.00 0.121
Likelihood ratio test:
logLik full model = 117.9232
logLik red. model = 105.3577
D = 25.1, df = 1, P = 2.68e-07
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: immob ~ SEX + order01 + AREA + YEAR + ndayprevtest + (1 | ID)
   Data: dfpla
REML criterion at convergence: -173.9
Scaled residuals:
Min 1Q Median 3Q Max -2.98194 -0.42839 0.04519 0.50227 3.13872
                                          Max
Random effects:
                       Variance Std.Dev.
Groups Name
 TD
         (Intercept) 0.00956 0.09777
Residual
                       0.02137 0.14619
Number of obs: 309, groups: ID, 120
Fixed effects:
                 Estimate Std. Error
                                               df t value Pr(>|t|)
               8.356e-01 3.437e-02 2.092e+02 24.310 < 2e-16 ***
(Intercept)
               1.715e-02 2.622e-02 1.020e+02 0.654 0.514515
-1.491e-01 2.435e-02 2.458e+02 -6.124 3.59e-09 ***
SEXM
order011
              -1.184e-01 3.198e-02 9.129e+01 -3.703 0.000365 ***
AREAC06-04
AREASal-Passat -4.227e-02 3.380e-02 9.881e+01 -1.251 0.214064
YEAR2017 4.315e-02 2.845e-02 2.996e+02 1.517 0.130405
YEAR2018 1.278e-01 3.118e-02 2.982e+02 4.100 5.33e-05 ***
YEAR2018 1.278e-01 3.118e-02 2.982e+02 4.100 5.33e-05 ***
YEAR2019 -3.374e-01 3.269e-02 2.411e+02 -10.321 < 2e-16 ***
ndayprevtest -2.504e-04 9.472e-05 2.439e+02 -2.643 0.008748 **
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 '' 1
```

Exploration plain sites

```
Repeatability estimation using the lmm method
Call = rpt(formula = expl ~ SEX + order01 + AREA + YEAR + ndayprevtest + (1 | ID), grname
= c("ID"), data = dfpla, datatype = "Gaussian", CI = 0.95, nboot = 2000, npermut = 1000, r
atio = TRUE, adjusted = TRUE)
Data: 309 observations
______
ID (120 groups)
Repeatability estimation overview:
     R SE 2.5% 97.5% P_permut LRT_P
 0.102 0.0637 1.19e-16 0.245
                              0.052 0.071
Bootstrapping and Permutation test:
         N Mean Median 2.5% 97.5%
        2000 0.1160 0.11337 1.19e-16 0.245
      1000 0.0273 0.00797 0.00e+00 0.124
Likelihood ratio test:
logLik full model = 237.4557
logLik red. model = 236.382
D = 2.15, df = 1, P = 0.0714
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: expl ~ SEX + order01 + AREA + YEAR + ndayprevtest + (1 | ID)
  Data: dfpla
REML criterion at convergence: -404.7
Scaled residuals:
                             3Q
    Min 10
                 Median
-2.93072 -0.57473 -0.09505 0.50439 3.09174
Random effects:
Groups Name
                    Variance Std.Dev.
         (Intercept) 0.001343 0.03664
ID
Residual
                   0.011791 0.10859
Number of obs: 309, groups: ID, 120
Fixed effects:
               Estimate Std. Error
                                         df t value Pr(>|t|)
             2.701e-01 2.161e-02 2.009e+02 12.499 < 2e-16 ***
(Intercept)
            -1.205e-02 1.504e-02 8.801e+01 -0.801 0.4251
SEXM
order011
             3.738e-02 1.738e-02 2.694e+02 2.150 0.0324 *
          -4.726e-05 1.794e-02 6.750e+01 -0.003 0.9979
AREAC06-04
                        1.931e-02 8.525e+01 -1.691 0.0944 .
1.915e-02 2.937e+02 -6.757 7.57e-11 ***
AREASal-Passat -3.267e-02
YEAR2017
             -1.294e-01
             -1.090e-01 2.085e-02 2.864e+02 -5.226 3.34e-07 ***
YEAR2018
YEAR2019
             4.696e-02 2.069e-02 1.907e+02 2.270 0.0243 *
ndayprevtest 7.339e-05 6.767e-05 2.692e+02 1.085 0.2791
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Table S4. Repeatabilities of trappability (TB) and trap-diversity (TD), per session and year, by each habitattype (alpine and plain), estimated with *rptR* function and relative linear mixed-effects models fitted by *lmer* function in *lmerTest* package.

Trappability/session (TBs) alpine sites

```
Repeatability estimation using the lmm method
Call = rpt(formula = trappsesstrans ~ SEX + AREA + YEAR + (1 | ID), grname = c("ID"), data
= dfalprep, datatype = "Gaussian", CI = 0.95, nboot = 2000, npermut = 1000, ratio = TRUE,
adjusted = TRUE)
Data: 203 observations
______
ID (70 groups)
Repeatability estimation overview:
     R SE 2.5% 97.5% P permut LRT P
  0.33 0.0839 0.174 0.503
                             0.001
Bootstrapping and Permutation test:
         N Mean Median 2.5% 97.5%
        2000 0.3442 0.3475 0.174 0.503
permut 1000 0.0361 0.0117 0.000 0.168
Likelihood ratio test:
logLik full model = 87.1323
logLik red. model = 76.92647
D = 20.4, df = 1, P = 3.12e-06
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: trappsesstrans ~ SEX + AREA + YEAR + (1 | ID)
  Data: dfalprep
REML criterion at convergence: -137.7
Scaled residuals:
   Min 1Q Median
                         3Q
-2.0532 -0.6750 -0.1793 0.5910 2.5208
Random effects:
Groups Name Variance Std.Dev.
        (Intercept) 0.009413 0.09702
Residual
                   0.019081 0.13813
Number of obs: 203, groups: ID, 70
Fixed effects:
          Estimate Std. Error
                                    df t value Pr(>|t|)
(Intercept) 0.55547 0.04664 86.09489 11.911 <2e-16 ***
                                               0.1390
                      0.03327
                                        1.497
SEXM
            0.04981
                               69.03769
           AREAFRA
AREAVAL
           0.04459 0.04037 69.66446 1.105
           -0.01561 0.02740 179.77209 -0.570
                                               0.5697
YEAR2017
           -0.01380
YEAR2018 -0.01380
YEAR2019 0.01863
                      0.03185 195.59112 -0.433
0.04395 186.71480 0.424
                                                0.6652
                                                0.6721
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 '' 1
```

Trap-diversity/session (TDs) alpine sites

```
Repeatability estimation using the lmm method
Call = rpt(formula = trapdivsesstrans \sim SEX + AREA + YEAR + (1 | ID), grname = c("ID"), da
ta = dfalprep, datatype = "Gaussian", CI = 0.95, nboot = 2000, npermut = 1000, ratio = TRU
E, adjusted = TRUE)
Data: 203 observations
______
ID (70 groups)
Repeatability estimation overview:
     R SE 2.5% 97.5% P_permut LRT_P
  0.406 0.0798 0.254 0.572
                             0.001
Bootstrapping and Permutation test:
          N Mean Median 2.5% 97.5%
        2000 0.4189 0.42141 0.254 0.572
permut 1000 0.0337 0.00776 0.000 0.147
Likelihood ratio test:
logLik full model = 285.942
logLik red. model = 271.6149
D = 28.7, df = 1, P = 4.33e-08
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: trapdivsesstrans ~ SEX + AREA + YEAR + (1 | ID)
  Data: dfalprep
REML criterion at convergence: -522.1
Scaled residuals:
                         3Q
   Min 1Q Median
-1.9608 -0.5562 -0.1835 0.6364 3.0624
Random effects:
Groups Name Variance Std.Dev.
ID (Intercept) 0.001717 0.04143
Residual 0.002514 0.05014
Number of obs: 203, groups: ID, 70
Fixed effects:
             Estimate Std. Error
                                       df t value Pr(>|t|)
             (Intercept)
                      0.013312 65.895916 1.273 0.207550
            0.016944
SEXM
            AREAFRA
AREAVAL
            0.002125 0.016146 66.260461 0.132 0.895672
_AK2017
YEAR2018
YEAR201
YEAR2017 -0.026690 0.010124 173.698173 -2.636 0.009142 **
YEAR2018 -0.015633 0.011901 193.195578 -1.314 0.190536
YEAR2019 -0.004567 0.016290 180.756499 -0.280 0.779539
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 '' 1
```

Trappability/session (TBs) plain sites

Repeatability estimation using the lmm method

```
Call = rpt(formula = trappsesstrans ~ SEX + AREA + YEAR + (1 | ID), grname = c("ID"), data
= dfplarep, datatype = "Gaussian", CI = 0.95, nboot = 2000, npermut = 1000, ratio = TRUE,
adjusted = TRUE)
Data: 452 observations
______
ID (90 groups)
Repeatability estimation overview:
     R SE 2.5% 97.5% P_permut LRT_P
 0.169 0.0498 0.0799 0.273
                            0.001
Bootstrapping and Permutation test:
         N Mean Median 2.5% 97.5%
        2000 0.1727 1.72e-01 0.0799 0.2730
      1000 0.0126 1.98e-09 0.0000 0.0658
Likelihood ratio test:
logLik full model = 123.4903
logLik red. model = 112.38
D = 22.2, df = 1, P = 1.22e-06
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: trappsesstrans ~ SEX + AREA + YEAR + (1 | ID)
  Data: dfplarep
REML criterion at convergence: -207.3
Scaled residuals:
                      3Q
   Min 1Q Median
-2.1737 -0.7740 -0.0105 0.7155 2.8621
Random effects:
Groups Name Variance Std.Dev.
        (Intercept) 0.006118 0.07822
Residual
                   0.030129 0.17358
Number of obs: 452, groups: ID, 90
Fixed effects:
              Estimate Std. Error df t value Pr(>|t|)
              0.57422 0.02562 141.84278 22.411 < 2e-16 *** 0.03673 0.02438 86.43539 1.507 0.1355
(Intercept)
SEXM
              AREAC06-04
AREASal-Passat 0.18042 0.03109 94.87407 5.802 8.60e-08 ***
YEAR2017
             0.02344 0.02100 444.72538 1.116 0.2650
                                          0.666
                                                  0.5058
YEAR2018
               0.01973
                         0.02962 444.99273
YEAR2019
               0.07327
                         0.03247 365.29382
                                           2.257
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Trap-diversity/session (TDs) plain sites

Repeatability estimation using the lmm method

```
Call = rpt(formula = trapdivsesstrans ~ SEX + AREA + YEAR + (1 | ID), grname = c("ID"), da
ta = dfplarep, datatype = "Gaussian", CI = 0.95, nboot = 2000, npermut = 1000, ratio = TRU
E, adjusted = TRUE)
Data: 452 observations
______
ID (90 groups)
Repeatability estimation overview:
     R SE 2.5% 97.5% P_permut LRT_P
 0.175 0.0497 0.0829 0.278
                              0.001
Bootstrapping and Permutation test:
          N Mean Median 2.5% 97.5%
        2000 0.1792 1.78e-01 0.0829 0.278
       1000 0.0133 2.52e-19 0.0000 0.070
Likelihood ratio test:
logLik full model = 602.0758
logLik red. model = 590.2882
D = 23.6, df = 1, P = 6.01e-07
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: trapdivsesstrans ~ SEX + AREA + YEAR + (1 | ID)
  Data: dfplarep
REML criterion at convergence: -1149.7
Scaled residuals:
                        3Q
   Min 1Q Median
                                  Max
-2.2213 -0.6636 -0.1184 0.5961 3.0755
Random effects:
Groups Name Variance Std.Dev.
        (Intercept) 0.0007679 0.02771
Residual
                    0.0036089 0.06007
Number of obs: 452, groups: ID, 90
Fixed effects:
               Estimate Std. Error df t value Pr(>|t|)
           1.831e-01 8.949e-03 1.404e+02 20.460 < 2e-16 ***
1.693e-02 8.539e-03 8.607e+01 1.983 0.0506 .
7.134e-02 1.041e-02 9.371e+01 6.851 7.62e-10 ***
(Intercept)
AREAC06-04
AREASal-Passat 1.180e-01 1.088e-02 9.425e+01 10.842 < 2e-16 ***
YEAR2017 8.618e-03 7.283e-03 4.446e+02 1.183 0.2374
YEAR2018
              1.301e-02 1.027e-02 4.450e+02 1.267
                                                      0.2060
YEAR2019
              1.491e-02 1.129e-02 3.665e+02
                                              1.321
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Trappability/year (TBy) alpine sites

```
Repeatability estimation using the lmm method
Call = rpt(formula = trappyeartrans ~ SEX + AREA + YEAR + (1 | ID), grname = c("ID"), data
= dfalprepy, datatype = "Gaussian", CI = 0.95, nboot = 2000, npermut = 1000, ratio = TRUE,
adjusted = TRUE)
Data: 138 observations
______
ID (70 groups)
Repeatability estimation overview:
    R SE 2.5% 97.5% P_permut LRT_P
  0.33 0.109 0.141 0.564 0.008 0.002
Bootstrapping and Permutation test:
         N Mean Median 2.5% 97.5%
        2000 0.3619 0.3641 0.141 0.564
      1000 0.0675 0.0357 0.000 0.272
Likelihood ratio test:
logLik full model = 57.73423
logLik red. model = 53.59558
D = 8.28, df = 1, P = 0.00201
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: trappyeartrans ~ SEX + AREA + YEAR + (1 | ID)
  Data: dfalprepy
REML criterion at convergence: -80.5
Scaled residuals:
                       3Q
   Min 1Q Median
-1.8961 -0.6418 -0.1019 0.6242 2.6627
Random effects:
Groups Name Variance Std.Dev.
        (Intercept) 0.009407 0.09699
Residual
                    0.019110 0.13824
Number of obs: 138, groups: ID, 70
Fixed effects:
           Estimate Std. Error df t value Pr(>|t|)
0.50369 0.05333 91.98205 9.445 3.37e-15 ***
0.05395 0.03648 66.68717 1.479 0.14384
(Intercept)
SEXM
           AREAFRA
AREAVAL
           0.02495 0.04583 76.52664 0.544 0.58771
         0.01477
0.01685
0.09017
YEAR2017
                     0.03281 91.51174 0.450 0.65356
YEAR2018
                       0.03761 113.51521
                                          0.448 0.65504
YEAR2019
            0.09017
                       0.04752 108.59805
                                         1.897 0.06043 .
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 '' 1
```

Trap-diversity/year (TDy) alpine sites

```
Repeatability estimation using the lmm method
Call = rpt(formula = trapdivyeartrans ~ SEX + AREA + YEAR + (1 | ID), grname = c("ID"), da
ta = dfalprepy, datatype = "Gaussian", CI = 0.95, nboot = 2000, npermut = 1000, ratio = TR
UE, adjusted = TRUE)
Data: 138 observations
______
ID (70 groups)
Repeatability estimation overview:
     R SE 2.5% 97.5% P_permut LRT_P
 0.548 0.086 0.39 0.721
                            0.001
Bootstrapping and Permutation test:
         N Mean Median 2.5% 97.5%
        2000 0.5756 0.5841 0.39 0.721
permut 1000 0.0635 0.0255 0.00 0.276
Likelihood ratio test:
logLik full model = 157.6368
logLik red. model = 147.8494
D = 19.6, df = 1, P = 4.84e-06
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: trapdivyeartrans ~ SEX + AREA + YEAR + (1 | ID)
  Data: dfalprepy
REML criterion at convergence: -270.7
Scaled residuals:
                      3Q
   Min 1Q Median
-1.9838 -0.5315 -0.0547 0.5573 3.9264
Random effects:
Groups Name Variance Std.Dev.
        (Intercept) 0.004174 0.06461
Residual
                   0.003446 0.05870
Number of obs: 138, groups: ID, 70
Fixed effects:
         Estimate Std. Error
                               df t value Pr(>|t|)
(Intercept) 0.31341 0.02829 81.47352 11.079 < 2e-16 *** SEXM 0.01160 0.02012 62.17859 0.577 0.566331
SEXM
AREAFRA
          0.10426
                    0.02984 69.55651 3.493 0.000834 ***
AREAVAL
         YEAR2017
         YEAR2018
          -0.02282
                    0.01709 97.03169 -1.335 0.184875
         -0.02402
YEAR2019
                     0.02138 89.64081 -1.123 0.264246
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 '' 1
```

Trappability/year (TBy) plain sites

```
Repeatability estimation using the lmm method
Call = rpt(formula = trappyeartrans ~ SEX + AREA + YEAR + (1 | ID), grname = c("ID"), data
= dfplarepy, datatype = "Gaussian", CI = 0.95, nboot = 2000, npermut = 1000, ratio = TRUE,
adjusted = TRUE)
Data: 186 observations
______
ID (90 groups)
Repeatability estimation overview:
     R SE 2.5% 97.5% P_permut LRT_P
 0.271 0.0928 0.106 0.471 0.004 0.001
Bootstrapping and Permutation test:
         N Mean Median 2.5% 97.5%
        2000 0.2947 0.2981 0.106 0.471
permut 1000 0.0487 0.0218 0.000 0.213
Likelihood ratio test:
logLik full model = 69.06984
logLik red. model = 63.94264
D = 10.3, df = 1, P = 0.000682
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: trappyeartrans ~ SEX + AREA + YEAR + (1 | ID)
  Data: dfplarepy
REML criterion at convergence: -101.2
Scaled residuals:
Min 1Q Median 3Q Max -2.38693 -0.64732 0.02389 0.54025 2.75486
                             3Q
                                     Max
Random effects:
Groups Name
                   Variance Std.Dev.
        (Intercept) 0.00825 0.09083
TD
Residual
                   0.02216 0.14885
Number of obs: 186, groups: ID, 90
Fixed effects:
               Estimate Std. Error
                                        df t value Pr(>|t|)
               0.525746 0.031191 129.478160 16.855 < 2e-16 ***
(Intercept)
               0.042769 0.030220 88.655131 1.415 0.16050 0.197763 0.036487 89.022331 5.420 5.04e-07 ***
SEXM
AREAC06-04
                        0.038187 94.003182 5.599 2.13e-07 ***
AREASal-Passat 0.213801
YEAR2017 -0.005114 0.028406 133.002423 -0.180 0.85741
YEAR2018
               0.056819 0.032854 150.725656 1.729 0.08578 .
YEAR2019
               Signif. codes: 0 '***' 0.001 '**' 0.05 '.' 0.1 ' ' 1
```

Trap-diversity/year (TDy) plain sites

```
Repeatability estimation using the lmm method
Call = rpt(formula = trapdivyeartrans ~ SEX + AREA + YEAR + (1 | ID), grname = c("ID"), da
ta = dfplarepy, datatype = "Gaussian", CI = 0.95, nboot = 2000, npermut = 1000, ratio = TR
UE, adjusted = TRUE)
Data: 186 observations
______
ID (90 groups)
Repeatability estimation overview:
     R SE 2.5% 97.5% P_permut LRT_P
 0.198 0.095 0.0279 0.4 0.041 0.015
Bootstrapping and Permutation test:
          N Mean Median 2.5% 97.5%
        2000 0.2195 0.2190 0.0279 0.400
permut 1000 0.0492 0.0162 0.0000 0.217
Likelihood ratio test:
logLik full model = 168.3561
logLik red. model = 166.019
D = 4.67, df = 1, P = 0.0153
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: trapdivyeartrans ~ SEX + AREA + YEAR + (1 | ID)
  Data: dfplarepy
REML criterion at convergence: -292.1
Scaled residuals:
                           3Q
    Min 1Q Median
-2.30036 -0.60114 -0.09387 0.58574 2.07227
Random effects:
Groups Name Variance Std.Dev.
        (Intercept) 0.002024 0.04499
                    0.008197 0.09054
Number of obs: 186, groups: ID, 90
Fixed effects:
                Estimate Std. Error
                                          df t value Pr(>|t|)
                0.247890 0.017816 129.200567 13.914 < 2e-16 *** 0.034807 0.016950 83.436832 2.054 0.0432 *
(Intercept)
SEXM
AREAC06-04 0.098376 0.020464 82.820790 4.807 6.75e-06 ***
AREASal-Passat 0.146058 0.021482 90.394891 6.799 1.10e-09 ***
YEAR2017
              0.027251 0.017098 132.767764 1.594 0.1134
                          0.019633 153.223521 -2.542
0.023462 170.242499 0.152
YEAR2018
               -0.049914
                                                       0.0120 *
YEAR2019
               0.003565
                          0.023462 170.242499
                                                        0.8794
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Table S5. Multivariate MCMCglmm model for alpine sites: prior, model parameters and outputs. immob = centered and scaled immobility score, expl = centered and scaled exploration score, act = centered and scaled activity score, TBstd = trappability per session, standardized within study site; TDstd = trap-diversity per session, standardized within study site, BMs = centered and scaled body mass value, AREA = study site (FRA = Cancano; VAL = Valfurva; BOR = Bormio). (sex, year, season, order: as described in methods).

```
burnin <- 50000
iterations <- 1050000
thinning <- 400
prior2 < -list(R = list(V = diag(5), nu = 0.002),
               G = list(G1 = list(V = diag(5), nu = 5, alpha.mu = rep(0,5), alpha.V = diag(25^2,5,5)))
formula = cbind (immob,expl,act,TBstd,TDstd) ~ trait-1 +
                     trait:SEX + trait:BMs + trait:YEAR +
                     at.level(trait, c(4,5)):season + at.level(trait, c(1,2,3)):order + at.level(trait, c(1,2,3)):AREA
mcmc3 <- MCMCglmm(fixed=formula,</pre>
                  random = ~ us(trait):ID,
                  rcov = ~ us(trait):units,
                  data=alp,
                  family=c(rep('gaussian',5)),
                  prior=prior2,
                  nitt=iterations,
                  burnin=burnin,
                  thin=thinning,
                  verbose=TRUE)
Iterations = 50001:1049601
 Thinning interval = 400
 Sample size = 2500
 DIC: 1798.701
 G-structure: ~us(trait):ID (among-individual variance covariance)
                         post.mean 1-95% CI u-95% CI eff.samp
                               0.18942 1.353e-05 0.386799
traitimmob:traitimmob.ID
                                                               2500
traitexpl:traitimmob.ID
                         -0.06842 -1.941e-01 0.013269
                                                             2500
```

```
traitact:traitimmob.ID
                            -0.18171 -3.743e-01 0.003539
                                                             2754
traitTBstd:traitimmob.ID
                                                             2027
                             0.08673 -3.330e-02 0.213871
traitTDstd:traitimmob.ID
                             0.11604 -1.155e-02 0.253555
                                                             2500
traitexpl:traitexpl.ID
                           0.06227 2.684e-07 0.166140
                                                           2500
traitact:traitexpl.ID
                          0.06200 -2.895e-02 0.178326
                                                           2500
                         -0.04237 -1.314e-01 0.024799
                                                           2500
traitTBstd:traitexpl.ID
traitTDstd:traitexpl.ID
                         -0.05432 -1.526e-01 0.025805
                                                           2500
traitact:traitact.ID
                          0.22424 2.629e-02 0.423729
                                                           2500
traitTBstd:traitact.ID
                          -0.08177 -2.053e-01 0.041613
                                                           1919
traitTDstd:traitact.ID
                         -0.11180 -2.493e-01 0.021920
                                                           2500
traitTBstd:traitTBstd.ID 0.13017 5.981e-07 0.309363
                                                           2254
traitTDstd:traitTBstd.ID
                         0.13909 -4.523e-03 0.326151
                                                           2281
traitTDstd:traitTDstd.ID
                         0.18067 1.946e-07 0.386222
                                                           2358
```

R-structure: ~us(trait):units (within-individual variance covariance)

```
post.mean 1-95% CI u-95% CI eff.samp
traitimmob:traitimmob.units
                                 0.64535 0.45269 0.84923
                                                               2500
traitexpl:traitimmob.units
                              -0.38612 -0.54863 -0.24053
                                                             2500
                              -0.56929 -0.75609 -0.38306
                                                             2500
traitact:traitimmob.units
traitTBstd:traitimmob.units
                              -0.10784 -0.26589 0.04799
                                                             2080
traitTDstd:traitimmob.units
                              -0.13553 -0.28576 0.04025
                                                             1949
traitexpl:traitexpl.units
                             0.77477 0.59367 0.97224
                                                           2500
                             0.30847 0.17134 0.46120
traitact:traitexpl.units
                                                           2500
traitTBstd:traitexpl.units
                             0.02316 -0.14874 0.17549
                                                           2500
traitTDstd:traitexpl.units
                             0.04514 -0.11276 0.20951
                                                           2500
traitact:traitact.units
                             0.60201 0.41988 0.80235
                                                           2500
traitTBstd:traitact.units
                             0.11260 -0.04494 0.25530
                                                           2207
traitTDstd:traitact.units
                             0.13897 -0.02536 0.28633
                                                           2125
traitTBstd:traitTBstd.units
                             0.84703 0.60480 1.09495
                                                           2500
traitTDstd:traitTBstd.units
                             0.72190 0.49658 0.98356
                                                           2335
traitTDstd:traitTDstd.units
                             0.85912 0.60859 1.14457
                                                           2311
```

Location effects: cbind(immob, expl, act, TBstd, TDstd) ~ trait - 1 + trait:SEX + trait:BMs + trait:YEAR + at.level(trait, c(4, 5)):season + at.level(trait, c(1, 2, 3)):order + at.level(trait, c(1, 2, 3)):AREA

```
post.mean 1-95% CI u-95% CI eff.samp pMCMC
traitimmob
                                      -0.417455 -0.893182 0.087909
                                                                        2226 0.0992 .
                                     0.314259 -0.158766 0.746419
traitexpl
                                                                      2500 0.1672
                                     0.443121 -0.050921 0.921020
                                                                      2350 0.0832 .
traitact
traitTBstd
                                     0.206456 -0.250473 0.609736
                                                                      2500 0.3384
                                                                      2500 0.7232
traitTDstd
                                     0.078458 -0.366507 0.499873
```

traitimmob:SEXM		-0.042501 -0.389003 0.318366	2500 0.8240
traitexpl:SEXM		0.011771 -0.304555 0.322435	2530 0.9592
traitact:SEXM		-0.084776 -0.447263 0.278113	2777 0.6544
traitTBstd:SEXM		0.434522 0.072597 0.792529	2500 0.0216 *
traitTDstd:SEXM		0.485710 0.105070 0.865130	2500 0.0168 *
traitimmob:BMs		-0.097352 -0.238474 0.053231	2500 0.2168
traitexpl:BMs		0.194407 0.047517 0.339730	2500 0.0136 *
traitact:BMs		0.082317 -0.077296 0.223312	2326 0.2784
traitTBstd:BMs		0.146982 -0.009056 0.306380	2500 0.0664 .
traitTDstd:BMs		0.185248 0.026405 0.342832	2500 0.0192 *
traitimmob:YEAR2017		-0.059443 -0.395990 0.262703	2180 0.7224
traitexpl:YEAR2017		0.453400 0.123514 0.805232	2500 0.0104 *
traitact:YEAR2017		0.098897 -0.238710 0.408398	2221 0.5472
traitTBstd:YEAR2017		-0.221272 -0.590141 0.107504	2355 0.1968
traitTDstd:YEAR2017		-0.523581 -0.911621 -0.191178	2500 0.0072 **
traitimmob:YEAR2018		0.444858 0.102738 0.867172	2500 0.0296 *
traitexpl:YEAR2018		0.345434 -0.076107 0.706482	2500 0.0856 .
traitact:YEAR2018		-0.594243 -0.975513 -0.231069	2500 0.0032 **
traitTBstd:YEAR2018		-0.290915 -0.698898 0.108008	2500 0.1504
traitTDstd:YEAR2018		-0.422033 -0.824803 -0.005656	2500 0.0472 *
traitimmob:YEAR2019		0.532624 -0.033646 1.059617	2500 0.0608 .
traitexpl:YEAR2019		-0.506106 -1.059647 0.079802	2377 0.0920 .
traitact:YEAR2019		-0.421933 -0.979537 0.111878	2531 0.1224
traitTBstd:YEAR2019		-0.421933 -0.979537 0.111878 -0.249522 -0.832611 0.331049	2500 0.4000
traitTDstd:YEAR2019		-0.258205 -0.864536 0.337672	2500 0.3960
at.level(trait, c(4,	5))1:seasonaut	-0.412240 -0.738706 -0.127629	2500 0.0136 *
at.level(trait, c(4,	5))2:seasonaut	0.054607 -0.242390 0.362141	2500 0.7120
at.level(trait, c(1,	2, 3))1:order0	0.801755 0.515731 1.077561	2500 <4e-04 ***
at.level(trait, c(1,	2, 3))2:order0	-0.720191 -1.005373 -0.413668	2328 <4e-04 ***
at.level(trait, c(1,	2, 3))3:order0	-0.731374 -1.012369 -0.459744	2500 <4e-04 ***
at.level(trait, c(1,	2, 3))1:AREAFRA	-0.330212 -0.873026 0.144594	2200 0.1920
at.level(trait, c(1,	2, 3))2:AREAFRA	0.119708 -0.338767 0.558285	2500 0.5808
		0.394465 -0.102318 0.909941	2500 0.1128
		-0.226737 -0.657508 0.176120	2282 0.2976
at.level(trait, c(1,			2213 0.3768
at.level(trait, c(1,	2, 3))3:AREAVAL	0.252343 -0.200062 0.664126	2259 0.2424

Description of fixed effects results

Males had higher trappability and trap-diversity than females. Red squirrels with a higher body mass were more explorative and had a higher trap-diversity than animals that weighed less. Trappability was lower in autumn than in spring, while there were no seasonal differences in trap-diversity. Immobility was expressed less strongly during the first arena test than subsequent ones, while exploration and activity were expressed more strongly during the first arena test than subsequent ones. There was no difference between study sites in the expression of OFT personality traits.

Table S6. Multivariate MCMCglmm model for plain sites: prior, model parameters and outputs. immob = centered and scaled immobility score, expl = centered and scaled exploration score, act = centered and scaled activity score, TBstd = trappability per session, standardized within study site; TDstd = trap-diversity per session, standardized within study site, BMs = centered and scaled body mass value, AREA = study site (C06-04 = Vanzago; Sal-Passat = Passatempo; C03-17 = Castelbarco). (sex, year, season, order: as described in methods).

```
burnin <- 50000
iterations <- 1050000
thinning <- 400
prior2 < -list(R = list(V = diag(5), nu = 0.002),
               G = list(G1 = list(V = diag(5), nu = 5, alpha.mu = rep(0,5), alpha.V = diag(25^2,5,5)))
formula = cbind (immob,expl,act,TBstd,TDstd) ~ trait-1 +
                     trait:SEX + trait:BMs + trait:YEAR +
                     at.level(trait, c(4,5)):season + at.level(trait, c(1,2,3)):order + at.level(trait, c(1,2,3)):AREA
mcmc4 <- MCMCglmm(fixed=formula,</pre>
                  random = ~ us(trait):ID,
                  rcov = ~ us(trait):units,
                  data=pla,
                  family=c(rep('gaussian',5)),
                  prior=prior2,
                  nitt=iterations,
                  burnin=burnin,
                  thin=thinning,
                  verbose=TRUE)
Iterations = 50001:1049601
 Thinning interval = 400
 Sample size = 2500
 DIC: 2157.401
 G-structure: ~us(trait):ID (among-individual variance covariance)
                          post.mean 1-95% CI u-95% CI eff.samp
traitimmob:traitimmob.ID
                              0.1151020 3.129e-02 0.20247
                                                                2500
                           -0.0146754 -6.771e-02 0.02900
traitexpl:traitimmob.ID
                                                              2532
traitact:traitimmob.ID
                        -0.1156960 -2.033e-01 -0.03142
                                                              2500
```

```
0.0034595 -3.988e-02 0.05037
                                                            2500
traitTBstd:traitimmob.ID
traitTDstd:traitimmob.ID
                           0.0079466 - 3.295e - 02 0.05780
                                                            2500
traitexpl:traitexpl.ID
                         0.0241233 4.106e-11 0.08133
                                                          2500
traitact:traitexpl.ID
                         0.0166267 -3.222e-02 0.07171
                                                          2500
traitTBstd:traitexpl.ID -0.0007762 -1.703e-02 0.01620
                                                          2500
traitTDstd:traitexpl.ID -0.0014897 -1.968e-02 0.01319
                                                          2500
traitact:traitact.ID
                        0.1365980 5.212e-02 0.24511
                                                          2500
traitTBstd:traitact.ID -0.0038198 -5.342e-02 0.04414
                                                          2500
traitTDstd:traitact.ID -0.0071402 -6.359e-02 0.03443
                                                          2500
traitTBstd:traitTBstd.ID 0.0109458 4.190e-09 0.04348
                                                          2500
traitTDstd:traitTBstd.ID 0.0071596 -3.120e-03 0.03676
                                                          2500
traitTDstd:traitTDstd.ID 0.0108689 2.168e-09 0.04425
                                                          2500
```

R-structure: ~us(trait):units (within-individual variance covariance)

```
post.mean 1-95% CI u-95% CI eff.samp
traitimmob:traitimmob.units
                                 0.35671 0.270500 0.44232
                                                               2500
traitexpl:traitimmob.units
                              -0.18905 -0.274385 -0.11415
                                                             2500
traitact:traitimmob.units
                              -0.27872 -0.363574 -0.20411
                                                             2500
traitTBstd:traitimmob.units
                              0.04321 -0.046231 0.12696
                                                             2500
traitTDstd:traitimmob.units
                               0.05446 -0.034889 0.13972
                                                             2500
                             0.65161 0.528639 0.77715
traitexpl:traitexpl.units
                                                           2500
traitact:traitexpl.units
                             0.08034 0.006163 0.15557
                                                           2040
traitTBstd:traitexpl.units -0.01308 -0.112908 0.09278
                                                           2500
traitTDstd:traitexpl.units
                           -0.02548 -0.136697 0.07369
                                                           2500
traitact:traitact.units
                            0.34419 0.265703 0.43787
                                                           2500
traitTBstd:traitact.units
                            -0.01094 -0.094743 0.08571
                                                           2500
traitTDstd:traitact.units
                            -0.03022 -0.121767 0.05857
                                                           2500
traitTBstd:traitTBstd.units 0.86874 0.707000 1.04903
                                                           2500
traitTDstd:traitTBstd.units 0.80802 0.645627 0.97385
                                                           2500
traitTDstd:traitTDstd.units 0.90043 0.731700 1.07644
                                                           2500
```

Location effects: cbind(immob, expl, act, TBstd, TDstd) \sim trait - 1 + trait:SEX + trait:BMs + trait:YEAR + at.level(trait, c(4, 5)):season + at.level(trait, c(1, 2, 3)):order + at.level(trait, c(1, 2, 3)):AREA

```
post.mean 1-95% CI u-95% CI eff.samp pMCMC
                                                                            2500 0.4704
traitimmob
                                           -0.091664 -0.334449 0.158610
traitexpl
                                          0.579951 0.298069 0.869187
                                                                          2500 <4e-04 ***
traitact
                                          0.059693 -0.199177 0.324811
                                                                          2500 0.6496
traitTBstd
                                         -0.635819 -1.263882 -0.011034
                                                                          2500 0.0520 .
traitTDstd
                                         -0.559435 -1.205549 0.070755
                                                                          2500 0.0888 .
traitimmob:SEXM
                                            0.198036 -0.023876 0.421227
                                                                            2645 0.0840 .
traitexpl:SEXM
                                              -0.112003 -0.333757 0.140796
                                                                                  2500 0.3312
traitact:SEXM
                                              -0.199143 -0.416391 0.034510
                                                                                  2500 0.0896 .
traitTBstd:SEXM
                                               0.271701 0.018920 0.514033
                                                                                  2500 0.0328 *
traitTDstd:SEXM
                                               0.292362 0.018189 0.528057
                                                                                  2500 0.0224 *
```

```
traitimmob: BMs
                                              0.054622 -0.043629 0.149946
                                                                               2500 0.2672
traitexpl:BMs
                                            -0.097362 -0.216694 0.015088
                                                                              2657 0.0952 .
                                            -0.033497 -0.132160 0.060389
                                                                              2500 0.4720
traitact:BMs
                                            0.065181 -0.062902 0.187636
traitTBstd:BMs
                                                                              2500 0.3064
traitTDstd:BMs
                                            0.075068 -0.056066 0.201390
                                                                              2434 0.2464
                                              0.091042 -0.143202 0.306840
                                                                               2359 0.4216
traitimmob:YEAR2017
traitexpl:YEAR2017
                                            -0.949750 -1.223902 -0.686813
                                                                             2365 <4e-04 ***
traitact:YEAR2017
                                            0.322678 0.082209 0.534106
                                                                             2295 0.0040 **
                                            0.213724 -0.145730 0.562653
traitTBstd:YEAR2017
                                                                              2500 0.2408
traitTDstd:YEAR2017
                                            0.293716 -0.051419 0.652372
                                                                              2140 0.1104
traitimmob: YEAR2018
                                              0.512266 0.233353 0.785308
                                                                               2500 0.0008 ***
                                           -0.888342 -1.235651 -0.585222
                                                                              2500 <4e-04 ***
traitexpl:YEAR2018
                                                                             2500 0.0008 ***
traitact:YEAR2018
                                           -0.528897 -0.812584 -0.249426
traitTBstd:YEAR2018
                                           -0.107126 -0.446921 0.275174
                                                                             2591 0.5520
                                           -0.008724 -0.384843 0.337620
traitTDstd:YEAR2018
                                                                              2500 0.9536
                                             -1.686343 -2.016665 -1.396611
traitimmob: YEAR2019
                                                                               2500 <4e-04 ***
traitexpl:YEAR2019
                                            0.620515 0.231049 0.976946
                                                                              2500 0.0008 ***
traitact:YEAR2019
                                            1.500674 1.191365 1.826204
                                                                              2500 <4e-04 ***
                                                                              2500 0.1920
traitTBstd:YEAR2019
                                            0.273116 -0.147319 0.681338
traitTDstd:YEAR2019
                                            0.134879 -0.276191 0.547680
                                                                             2500 0.5168
                                            0.475000 -0.215121 1.230820
                                                                              2500 0.2040
at.level(trait, c(4, 5))1:seasonaut
at.level(trait, c(4, 5))2:seasonaut
                                            0.647048 -0.063734 1.401226
                                                                              2500 0.0824
                                            0.554503 -0.130543 1.184975
                                                                              2500 0.1056
at.level(trait, c(4, 5))1:seasonspr-sum
at.level(trait, c(4, 5))2:seasonspr-sum
                                            0.377767 -0.318705 1.015214
                                                                              2500 0.2600
at.level(trait, c(1, 2, 3))1:order0
                                            0.369707 0.177240 0.565452
                                                                             1749 0.0008 ***
at.level(trait, c(1, 2, 3))2:order0
                                           -0.012487 -0.258807 0.232415
                                                                              2500 0.9232
at.level(trait, c(1, 2, 3))3:order0
                                                                             2500 <4e-04 ***
                                           -0.635534 -0.832405 -0.448026
at.level(trait, c(1, 2, 3))1:AREAC06-04
                                           -0.427858 -0.712765 -0.170090
                                                                              2500 <4e-04 ***
at.level(trait, c(1, 2, 3))2:AREAC06-04
                                           -0.049143 -0.335657 0.204281
                                                                              2788 0.7312
at.level(trait, c(1, 2, 3))3:AREAC06-04
                                            0.629534 0.349477 0.899524
                                                                             2999 <4e-04 ***
at.level(trait, c(1, 2, 3))1:AREASal-Passat -0.207497 -0.484789 0.067026
                                                                              2036 0.1528
at.level(trait, c(1, 2, 3))2:AREASal-Passat -0.233719 -0.531522 0.019624
                                                                              2750 0.0896
at.level(trait, c(1, 2, 3))3:AREASal-Passat 0.333089 0.051728 0.604527
                                                                              2004 0.0232 *
```

Description of fixed effects results

Male red squirrels had higher trappability and trap-diversity than females. In the plain habitat-type, we found no relationship of body mass with immobility, exploration, activity or trappability and trap-diversity. There was no difference in trappability or trap diversity between the seasons. Immobility was expressed less strongly during the first arena test than subsequent ones, while activity was expressed more strongly during the first arena test than subsequent ones. The amount of exploration, which was always low, did not vary with arena test order. We found differences in the OFT personality traits among study sites: squirrels had lower immobility in Vanzago than in Castelbarco, while, in contrast, activity expression was higher. Squirrels had also higher activity in Passatempo than in Castelbarco.

Table S7. Multivariate MCMCglmm model for alpine sites: prior, model parameters and outputs. immob = centered and scaled immobility score, expl = centered and scaled exploration score, act = centered and scaled activity score; TBstdy = trappability per year, standardized within study site; TDstdy = trap-diversity per year, standardized within study site, BMs = centered and scaled body mass value, AREA = study site (FRA = Cancano; VAL = Valfurva; BOR = Bormio). (sex, year, order: as described in methods).

```
burnin <- 50000
iterations <- 1050000
thinning <- 400
prior2 < -list(R = list(V = diag(5), nu = 0.002),
               G = list(G1 = list(V = diag(5), nu = 5, alpha.mu = rep(0,5), alpha.V = diag(25^2,5,5)))
formula2 = cbind (immob, expl, act, TBstdy, TDstdy) ~ trait-1 +
                     trait:SEX + trait:BMs + trait:YEAR +
                     at.level(trait, c(1,2,3)):order + at.level(trait, c(1,2,3)):AREA
mcmc3a <- MCMCglmm(fixed=formula2,</pre>
                  random = \sim us(trait):ID,
                  rcov = ~ us(trait):units,
                  data=alpy,
                  family=c(rep('gaussian',5)),
                  prior=prior2,
                  nitt=iterations,
                  burnin=burnin,
                  thin=thinning,
                  verbose=TRUE)
Iterations = 50001:1049601
 Thinning interval = 400
 Sample size = 2500
 DIC: 1313.824
 G-structure: ~us(trait):ID (among-individual variance covariance)
                            post.mean 1-95% CI u-95% CI eff.samp
traitimmob:traitimmob.ID
                                0.2955177 2.368e-07 0.72111
                                                                   2500
traitexpl:traitimmob.ID
                             -0.1536869 -4.349e-01 0.03127
                                                                 2500
```

```
traitact:traitimmob.ID
                            -0.2467083 -6.250e-01 0.01868
                                                              2341
traitTBstdy:traitimmob.ID
                                                              2500
                             0.0063634 -1.522e-01 0.17922
traitTDstdy:traitimmob.ID
                             0.0406356 -1.265e-01 0.21424
                                                              2500
traitexpl:traitexpl.ID
                           0.1896397 5.424e-07 0.44947
                                                             2500
traitact:traitexpl.ID
                           0.1200155 -6.983e-02 0.35921
                                                             2500
traitTBstdy:traitexpl.ID
                          -0.0202183 -1.567e-01 0.07755
                                                             2500
traitTDstdy:traitexpl.ID
                          -0.0422554 -1.887e-01 0.06889
                                                             2500
traitact:traitact.ID
                          0.2711169 5.035e-07 0.60801
                                                             2312
traitTBstdy:traitact.ID
                          -0.0001003 -1.450e-01 0.14961
                                                             2500
traitTDstdy:traitact.ID
                          -0.0261500 -1.853e-01 0.12773
                                                             2500
traitTBstdy:traitTBstdy.ID 0.0754674 4.043e-09 0.29389
                                                             2500
traitTDstdy:traitTBstdy.ID 0.0632689 -1.378e-02 0.28591
                                                            1600
traitTDstdy:traitTDstdy.ID 0.1016116 3.365e-08 0.35326
                                                             2500
```

R-structure: ~us(trait):units (within-individual variance covariance)

```
post.mean 1-95% CI u-95% CI eff.samp
traitimmob:traitimmob.units
                                  0.748946 0.38268 1.15319
                                                                 2500
traitexpl:traitimmob.units
                               -0.351362 -0.64238 -0.09931
                                                               2500
                                                               2355
traitact:traitimmob.units
                               -0.622226 -0.99076 -0.30890
traitTBstdy:traitimmob.units
                               -0.031586 -0.24341 0.19651
                                                               2261
traitTDstdy:traitimmob.units
                               0.055190 -0.16589 0.28825
                                                               2500
traitexpl:traitexpl.units
                              0.726119 0.46066 1.02390
                                                             2500
traitact:traitexpl.units
                              0.219411 -0.01499 0.45671
                                                             2500
traitTBstdy:traitexpl.units
                              0.136826 -0.04734 0.32331
                                                             2500
traitTDstdy:traitexpl.units
                              0.055579 -0.14644 0.25610
                                                             2500
traitact:traitact.units
                                                             2310
                              0.611125 0.31372 0.93488
traitTBstdy:traitact.units
                              0.006056 -0.18821 0.20431
                                                             2312
traitTDstdy:traitact.units
                             -0.020486 -0.22341 0.18601
                                                             2500
traitTBstdy:traitTBstdy.units 0.942931 0.61863 1.24200
                                                             2500
traitTDstdy:traitTBstdy.units 0.730565 0.44186 1.03304
                                                             2500
traitTDstdy:traitTDstdy.units 0.894159 0.54856 1.20597
                                                             2500
```

Location effects: cbind(immob, expl, act, TBstdy, TDstdy) ~ trait - 1 + trait:SEX + trait:BMs + trait:YEAR + at.level(trait, c(1, 2, 3)):order + at.level(trait, c(1, 2, 3)):AREA

```
post.mean 1-95% CI u-95% CI eff.samp pMCMC
traitimmob
                                      -0.452812 -1.060580 0.220345
                                                                       2500 0.1760
traitexpl
                                     0.411724 -0.185252 0.996589
                                                                     2500 0.1816
                                     0.495802 -0.142438 1.069808
                                                                     2500 0.1192
traitact
traitTBstdv
                                    -0.358417 -0.828821 0.084862
                                                                     2320 0.1032
traitTDstdv
                                     0.120878 -0.334245 0.574454
                                                                     2291 0.5880
```

traitimmob:SEXM		-0.073720 -0.503704 0.383542 2335 0.7	
traitexpl:SEXM		-0.026043 -0.431059 0.420398 2500 0.917	
traitact:SEXM		-0.060571 -0.464081 0.374081 2500 0.786	
traitTBstdy:SEXM		0.490190 0.092677 0.857622 2500 0.016	
traitTDstdy:SEXM		0.300582 -0.104819 0.706558 2500 0.147	
traitimmob:BMs		-0.039382 -0.245579 0.145409 2672 0.6	896
traitexpl:BMs		0.129765 -0.058695 0.293132 2500 0.156	8
traitact:BMs		0.003903 -0.176389 0.181266 2652 0.952	0
traitTBstdy:BMs		0.069181 -0.113791 0.249549 2500 0.444	. 0
traitTDstdy:BMs		0.064000 -0.117028 0.242631 2991 0.481	. 6
traitimmob:YEAR2017		-0.048479 -0.555261 0.408987 2679 0.8	472
traitexpl:YEAR2017		0.626639 0.149485 1.053826 2500 0.008	0 **
traitact:YEAR2017		0.038504 -0.384711 0.500389 2631 0.864	8
traitTBstdy:YEAR2017		0.023727 -0.411505 0.493412 2500 0.901	. 6
traitTDstdy:YEAR2017		-0.434004 -0.887352 -0.011657 2500 0.052	0.
traitimmob:YEAR2018		0.447028 -0.149922 1.051973 2681 0.1	520
traitexpl:YEAR2018		0.537805 0.006631 1.080540 2500 0.051	2.
traitact:YEAR2018		-0.567169 -1.105758 -0.005505 2660 0.049	6 *
traitTBstdy:YEAR2018		-0.021273 -0.502243 0.479670 2937 0.922	4
traitTDstdy:YEAR2018		-0.376224 -0.835631 0.107218 2500 0.116	8
traitimmob:YEAR2019		0.680271 -0.134944 1.482008 2500 0.0	992
traitexpl:YEAR2019		-0.573717 -1.383572 0.148655 2500 0.138	4
traitact:YEAR2019		-0.592778 -1.300615 0.184131 2500 0.120	0
traitTBstdy:YEAR2019		0.331401 -0.229845 1.043843 2305 0.312	0
traitTDstdy:YEAR2019		-0.527690 -1.191160 0.113903 2028 0.111	.2
at.level(trait, $c(1, 2,$	3))1:order0	0.489631 0.027376 0.975773 2500 0.047	2 *
at.level(trait, c(1, 2,	3))2:order0	-0.423077 -0.863644 0.020121 2308 0.063	2 .
at.level(trait, c(1, 2,			4 .
at.level(trait, c(1, 2,			2
at.level(trait, c(1, 2,			0
at.level(trait, c(1, 2,	3))3:AREAFRA	0.294984 -0.289701 0.884237 2500 0.339	2
at.level(trait, c(1, 2,			8
at.level(trait, c(1, 2,			0
at.level(trait, c(1, 2,			8

Description of fixed effects results

Males had higher trappability than females. There was no effect of sex on trap-diversity or on any of the OFT personality traits. Also a squirrel's body mass was not related with any of the dependent variables. Immobility was expressed less strongly during the first arena test than subsequent ones. The difference in amount of exploration or activity was slightly higher in first arena test, but 95% CI overlapped 0 (p = 0.063 and 0.086, respectively). There was no difference between study sites in the expression of OFT personality traits.

Table S8. Multivariate MCMCglmm model for plain sites: prior, model parameters and outputs. immob = centered and scaled immobility score, expl = centered and scaled exploration score, act = centered and scaled activity score; TBstdy = trappability per year, standardized within study site; TDstdy = trap-diversity per year, standardized within study site, BMs = centered and scaled body mass value, AREA = study site (C06-04 = Vanzago; Sal-Passat = Passatempo; C03-17 = Castelbarco). (sex, year, order: as described in methods).

```
burnin <- 50000
iterations <- 1050000
thinning <- 400
prior2 < -list(R = list(V = diag(5), nu = 0.002),
               G = list(G1 = list(V = diag(5), nu = 5, alpha.mu = rep(0,5), alpha.V = diag(25^2,5,5)))
formula2 = cbind (immob, expl, act, TBstdy, TDstdy) ~ trait-1 +
                     trait:SEX + trait:BMs + trait:YEAR +
                     at.level(trait, c(1,2,3)):order + at.level(trait, c(1,2,3)):AREA
mcmc4a <- MCMCglmm(fixed=formula2,</pre>
                  random = ~ us(trait):ID,
                  rcov = ~ us(trait):units,
                  data=play,
                  family=c(rep('gaussian',5)),
                  prior=prior2,
                  nitt=iterations,
                  burnin=burnin,
                  thin=thinning,
                  verbose=TRUE)
Iterations = 50001:1049601
 Thinning interval = 400
 Sample size = 2500
 DIC: 1665.632
 G-structure: ~us(trait):ID (among-individual variance covariance)
                           post.mean 1-95% CI u-95% CI eff.samp
traitimmob:traitimmob.ID
                                0.011622 3.743e-09 0.04487
                                                                  2500
```

```
traitexpl:traitimmob.ID
                            -0.003296 -3.234e-02 0.01974
                                                              2500
traitact:traitimmob.ID
                            -0.005011 -2.944e-02 0.00450
                                                              2280
traitTBstdy:traitimmob.ID
                            -0.002302 -4.759e-02 0.04512
                                                              2500
traitTDstdv:traitimmob.ID
                             0.000556 -3.403e-02 0.03061
                                                              2500
traitexpl:traitexpl.ID
                           0.063772 3.965e-08 0.17579
                                                            2500
                                                            2315
traitact:traitexpl.ID
                           0.002680 -1.872e-02 0.02735
traitTBstdy:traitexpl.ID
                           0.013615 -6.524e-02 0.09522
                                                            2500
traitTDstdy:traitexpl.ID
                           0.012517 -4.211e-02 0.07894
                                                            2500
traitact:traitact.ID
                           0.009135 5.142e-09 0.03566
                                                            2500
traitTBstdv:traitact.ID
                           0.001260 -4.181e-02 0.04421
                                                            2500
traitTDstdy:traitact.ID
                           0.001740 -2.654e-02 0.03326
                                                            2500
traitTBstdy:traitTBstdy.ID 0.184765 1.053e-04 0.38179
                                                            2621
traitTDstdy:traitTBstdy.ID 0.075304 -1.856e-02 0.22306
                                                            2500
traitTDstdy:traitTDstdy.ID 0.074941 9.832e-09 0.21693
                                                            2500
```

R-structure: ~us(trait):units (within-individual variance covariance)

```
post.mean 1-95% CI u-95% CI eff.samp
traitimmob:traitimmob.units
                                   0.47632 0.36925 0.60399
                                                                 2500
                                -0.20804 -0.31729 -0.10934
                                                               2500
traitexpl:traitimmob.units
traitact:traitimmob.units
                                -0.40519 -0.51497 -0.30143
                                                               2500
traitTBstdv:traitimmob.units
                                 0.05971 -0.04797 0.18175
                                                               2500
traitTDstdv:traitimmob.units
                                 0.04697 -0.06938 0.15478
                                                               2682
traitexpl:traitexpl.units
                               0.66376 0.48291 0.83325
                                                             2500
traitact:traitexpl.units
                               0.11419 0.01266 0.21208
                                                             2500
traitTBstdy:traitexpl.units
                               0.03879 -0.10873 0.17314
                                                             2500
traitTDstdy:traitexpl.units
                               0.10623 -0.02573 0.24025
                                                             2500
traitact:traitact.units
                               0.48228 0.36875 0.59515
                                                             2500
traitTBstdy:traitact.units
                              -0.05808 -0.16623 0.06344
                                                             2500
traitTDstdy:traitact.units
                              -0.09397 -0.21051 0.01020
                                                             2500
traitTBstdy:traitTBstdy.units
                               0.76905 0.52696 1.01898
                                                             2500
traitTDstdy:traitTBstdy.units
                               0.56886 0.36424 0.77365
                                                             2282
traitTDstdy:traitTDstdy.units
                               0.79877 0.58787 1.02791
                                                             2253
```

Location effects: cbind(immob, expl, act, TBstdy, TDstdy) \sim trait - 1 + trait:SEX + trait:BMs + trait:YEAR + at.level(trait, c(1, 2, 3)):order + at.level(trait, c(1, 2, 3)):AREA

```
post.mean 1-95% CI u-95% CI eff.samp pMCMC
traitimmob
traitexpl
traitact
0.416012 0.073907 0.770748 2500 0.0200 *
traitact
0.039249 -0.251684 0.316235 2500 0.7816
traitTBstdy
-0.341597 -0.720294 -0.022806 2500 0.0504 .
```

1100 11	0.004705 0.001000 0.006000	0500 0 0006
traitTDstdy	-0.034705 -0.381028 0.306382	2500 0.8296
traitimmob:SEXM	0.182442 -0.035301 0.413970	2500 0.1088
traitexpl:SEXM	-0.047145 -0.322596 0.257278	2500 0.7544
traitact:SEXM	-0.158753 -0.382033 0.074498	2648 0.1824
traitTBstdy:SEXM	0.383944 0.002525 0.701124	2500 0.0336 *
traitTDstdy:SEXM	0.419926 0.105644 0.767188	2334 0.0128 *
traitimmob:BMs	0.031770 -0.078661 0.154137	2330 0.5832
traitexpl:BMs	-0.054316 -0.194583 0.084086	2500 0.4424
traitact:BMs	-0.019007 -0.143522 0.094450	2403 0.7408
traitTBstdy:BMs	0.038985 -0.103535 0.193385	2500 0.5952
traitTDstdy:BMs	0.069315 -0.070904 0.208599	2500 0.3384
traitimmob:YEAR2017	0.159022 -0.158964 0.468797	2500 0.3216
traitexpl:YEAR2017	-0.752672 -1.146213 -0.381388	2645 <4e-04 ***
traitact:YEAR2017	0.234352 -0.064823 0.543055	2500 0.1336
traitTBstdy:YEAR2017	-0.092952 -0.468268 0.275746	2498 0.6240
traitTDstdy:YEAR2017	0.063898 -0.293056 0.435708	2500 0.7096
traitimmob:YEAR2018	0.562989 0.181700 0.960957	2500 0.0056 **
traitexpl:YEAR2018	-0.580922 -1.089140 -0.118400	2830 0.0208 *
traitact:YEAR2018	-0.565525 -0.930647 -0.158819	2500 0.0040 **
traitTBstdy:YEAR2018	0.182313 -0.196246 0.626397	2500 0.3784
traitTDstdy:YEAR2018	-0.861104 -1.289866 -0.476146	2500 <4e-04 ***
traitimmob:YEAR2019	-1.561646 -1.993471 -1.147556	2500 <4e-04 ***
traitexpl:YEAR2019	0.696541 0.201999 1.209853	2652 0.0072 **
traitact:YEAR2019	1.495922 1.042524 1.892902	2500 <4e-04 ***
traitTBstdy:YEAR2019	0.596203 0.083887 1.054142	2500 0.0224 *
traitTDstdy:YEAR2019	-0.269199 -0.732464 0.163840	2500 0.2440
at.level(trait, c(1, 2, 3))1:order0	0.344356 0.022922 0.646887	2795 0.0328 *
at.level(trait, c(1, 2, 3))2:order0	-0.293097 -0.649403 0.065852	2500 0.1104
at.level(trait, c(1, 2, 3))3:order0	-0.607272 -0.901893 -0.272259	3230 0.0008 ***
at.level(trait, c(1, 2, 3))1:AREAC06-04	-0.596911 -0.860847 -0.325350	2500 <4e-04 ***
at.level(trait, c(1, 2, 3))2:AREAC06-04	0.146638 -0.177590 0.492197	2500 0.3936
at.level(trait, c(1, 2, 3))3:AREAC06-04	0.680817 0.415682 0.957268	2500 <4e-04 ***
at.level(trait, c(1, 2, 3))1:AREASal-Passat		2500 0.0912 .
at.level(trait, c(1, 2, 3))2:AREASal-Passat		2500 0.2224
at.level(trait, c(1, 2, 3))3:AREASal-Passat		2500 0.0216 *
	0.0010.2 0.007000 0.001001	2000 0.0210

Description of fixed effects results

Males had higher trappability and trap-diversity than females. There was no relationship of body mass with any of the dependent variables. Squirrels had lower values for immobility during the first than subsequent arena tests, while activity was expressed more strongly during the first arena test than in subsequent ones. There was no difference in exploration in relation to arena test order. Squirrels were less immobile and more active in Vanzago than in Castelbarco, and also the individuals from Passatempo had higher activity than those from Castelbarco. Hence, patterns analysed at annual level were similar to those from the session-based model.

Table S9. Correlations (95% credibility intervals between brackets) between the dependent variables derived from the MCMCglmm models per trapping session and per year, as well as for both habitat-types (alpine and plain; Figure 1). Estimates of the between-individual and within-individual variances for the three OFT personality traits, trappability and trap-diversity per session and per year in alpine and plain sites are detailed in the Supporting Information (Table S5, S6, S7 and S8). Significant results (0 not included in the 95% CIs) in bold.

Session			Year			
Variables	Alpine sites	Plain sites	Variables	Alpine sites	Plain sites	
immob - expl	-0.60 (-0.99 – 0.20)	-0.25 (-0.99 – 0.78)	immob - expl	-0.54 (-0.99 – 0.39)	-0.07 (-0.83 – 0.79)	
immob – act	-0.85 (-0.98 – -0.62)	-0.92 (-0.99 – -0.81)	immob - act	-0.72 (-0.99 – 0.12)	-0.24 (-0.96 – 0.62)	
immob-TBs	0.62 (-0.30 – 0.99)	0.07 (-0.91 – 0.97)	immob - TBy	0.03 (-0.92 – 0.95)	-0.05 (-0.87 – 0.79)	
immob - TDs	0.71 (0.09 – 0.99)	0.19 (-0.89 – 0.99)	immob - TDy	0.24 (-0.79 – 0.99)	0.02 (-0.89 – 0.83)	
expl – act	0.50 (-0.29 – 0.99)	0.27 (-0.76 – 0.99)	expl - act	0.42 (-0.47 – 0.98)	0.07 (-0.75 – 0.88)	
expl - TBs	-0.51 (-0.99 – 0.46)	-0.03 (-0.90 – 0.84)	expl - TBy	-0.15 (-0.97 – 0.80)	0.11 (-0.69 – 0.88)	
expl - TDs	-0.56 (-0.99 – 0.33)	-0.05 (-0.95 – 0.83)	expl - TDy	-0.30 (-0.99 – 0.66)	0.15 (-0.69 – 0.91)	
act – TBs	-0.54 (-0.99 – 0.36)	-0.08 (-0.98 – 0.90)	act - TBy	0.008 (-0.95 – 0.90)	0.009 (-0.84 – 0.86)	
act - TDs	-0.63 (-0.99 – 0.02)	-0.16 (-0.97 – 0.92)	act - TDy	-0.16 (-0.97 – 0.81)	0.05 (-0.82 – 0.90)	
TBs -TDs	0.82 (0.13 – 0.99)	0.34 (-0.61 – 0.99)	TBy -TDy	0.45 (-0.55 – 0.99)	0.51 (-0.34 – 0.98)	

References

- Martin, J. G. A., & Réale, D. (2008). Temperament, risk assessment and habituation to novelty in eastern chipmunks, *Tamias striatus*. *Animal Behaviour*, 75, 309–318. doi:10.1016/j.anbehav.2007.05.026
- Mazzamuto, M. V., Cremonesi, G., Santicchia, F., Preatoni, D. G., Martinoli, A., & Wauters, L. A. (2019).

 Rodents in the arena: a critical evaluation of methods measuring personality traits. *Ethology, Ecology and Evolution*, *31*, 38–58. doi:10.1080/03949370.2018.1488768
- Molinari, A., Wauters, L. A., Airoldi, G., Cerinotti, F., Martinoli, A., & Tosi, G. (2006). Cone selection by Eurasian red squirrels in mixed conifer forests in the Italian Alps. *Acta Oecologica*, *30*, 1–10. doi:10.1016/j.actao.2005.11.004
- Rodrigues, D., Wauters, L. A., Romeo, C., Mari, V., Preatoni, D., Mathias, M. L., Tosi, G., & Martinoli, A. (2010). Living on the edge: can Eurasian red squirrels (*Sciurus vulgaris*) persist in extreme high-elevation habitats? *Arctic, Antarctic, and Alpine Research*, 42, 106–112. doi:10.1657/1938-4246-42.1.106
- Santicchia, F., Wauters, L. A., Piscitelli, A. P., Van Dongen, S., Martinoli, A., Preatoni, D., Romeo, C., & Ferrari, N. (2020). Spillover of an alien parasite reduces expression of costly behaviour in native host species. *Journal of Animal Ecology*, 89, 1559–1569. doi:10.1111/1365-2656.13219
- Wauters, L. A., Gurnell, J., Martinoli, A., & Tosi, G. (2001). Does interspecific competition with introduced grey squirrels affect foraging and food choice of Eurasian red squirrels? *Animal Behaviour*, 61, 1079–1091. doi:10.1006/anbe.2001.1703
- Wauters, L. A., Githiru, M., Bertolino, S., Molinari, A., Tosi, G., & Lens, L. (2008). Demography of alpine red squirrel populations in relation to fluctuations in seed-crop size. *Ecography*, *31*, 104–114. doi:10.1111/j.2007.0906-7590.05251.x
- Wauters, L. A., Mazzamuto, M. V., Santicchia, F., Van Dongen, S., Preatoni, D. G., & Martinoli, A. (2019). Interspecific competition affects the expression of personality-traits in natural populations. *Scientific Reports*, 9, 11189. doi:10.1038/s41598-019-47694-4