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(Article begins on next page)

1 **Personality traits, sex and food abundance shape space use in an arboreal mammal**

2

3 Lucas A. Wauters<sup>a, b, †</sup>; Maria Vittoria Mazzamuto<sup>a, c, †</sup>, Francesca Santicchia<sup>a\*</sup>, Adriano Martinoli<sup>a</sup>,  
4 Damiano G. Preatoni<sup>a</sup>, Peter W.W. Lurz<sup>d</sup>, Sandro Bertolino<sup>e</sup>, Claudia Romeof<sup>f</sup>

5

6 <sup>a</sup>Environment Analysis and Management Unit - Guido Tosi Research Group - Department of  
7 Theoretical and Applied Sciences, Università degli Studi dell'Insubria, Varese, Italy; <sup>b</sup> Department  
8 of Biology, University of Antwerp, Wilrijk, Belgium; <sup>c</sup> School of Natural Resources and the  
9 Environment, University of Arizona, Tucson, USA; <sup>d</sup> The Royal (Dick) School of Veterinary  
10 Studies and the Roslin Institute, University of Edinburgh, Roslin, UK; <sup>e</sup> Department of Life  
11 Sciences and Systems Biology, Università degli Studi di Torino, Italy; <sup>f</sup> Department of Veterinary  
12 Medicine, Università degli Studi di Milano, Italy.

13

14 \*Corresponding author (Francesca Santicchia): Environment Analysis and Management Unit -  
15 Guido Tosi Research Group - Department of Theoretical and Applied Sciences, Università degli  
16 Studi dell'Insubria, via J.H. Dunant, 3, 21100 Varese, Italy. tel +39 0332 421538, email:  
17 [f.santicchia@uninsubria.it](mailto:f.santicchia@uninsubria.it)

18

19 **Declaration of authorship.** LAW and AM originally formulated the idea, DGP and FS developed  
20 data-analyses software and were responsible for data management; LAW, PWWL, and SB  
21 conducted fieldwork; MVM and CR performed statistical analyses and LAW, MVM and CR wrote  
22 the manuscript and all other authors provided editorial advice. <sup>†</sup>Lucas A. Wauters and Maria  
23 Vittoria Mazzamuto contributed equally.

24

25 **Abstract**

26 Animal space use is affected by spatio-temporal variation in food availability and/or population  
27 density and varies among individuals. This inter-individual variation in spacing behaviour can be  
28 further influenced by sex, body condition, social dominance, and by the animal's personality. We  
29 used capture-mark-recapture and radio-tracking to examine the relationship between space use and  
30 personality in Eurasian red squirrels (*Sciurus vulgaris*) in three conifer forests in the Italian Alps.  
31 We further explored to what extent this was influenced by changes in food abundance and/or  
32 population density. Measures of an individual's trappability and trap diversity had a high  
33 repeatability and were used in a Principal Component Analysis to obtain a single personality score  
34 representing a boldness-exploration tendency. Males increased home-range size with low food  
35 abundance and low female density, independent of their personality. However, bolder males used  
36 larger core-areas that overlapped less with other males than shy ones, suggesting different resource  
37 (food, partners) utilization strategies among personality types. For females, space use-personality  
38 relationships varied with food abundance, and bolder females used larger home ranges than shy  
39 ones at low female density, but the trend was opposite at high female density. Females' intrasexual  
40 core-area overlap was negatively related to body mass, with no effect of personality. We conclude  
41 that relationships between personality traits and space use in free-ranging squirrels varied with sex,  
42 and were further influenced by spatio-temporal fluctuations in food availability. Moreover, different  
43 personality types (bold-explorative vs shy) seemed to adopt different space-use strategies to  
44 increase access to food and/or partners.

45

46 **Keywords:** core-area; home-range size; *Sciurus vulgaris*; seed-crop size; trappability

47

48

49 **Introduction**

50 Animals need to travel in search of resources such as food, refuge, nesting site or mates, making  
51 movement and space use key aspects of their behaviour, survival and reproductive success (Burt  
52 1943; Moorcroft 2012). Spatial dynamics therefore have important consequences in ecological  
53 issues like gene flow (through dispersal), species distribution, population and community dynamics,  
54 and, therefore, are relevant for conservation (Nathan et al. 2008; Cote et al. 2010; Kays et al. 2015).  
55 A species' movement ecology determines how individuals will interact with their conspecifics, with  
56 other species and their environment, ultimately shaping the spatial structure of communities and  
57 ecosystems (van Beest et al. 2011; Tamburello et al. 2015).

58 Animal movement patterns can vary between and within species, and the size, shape or structure of  
59 the space utilised can be affected by both extrinsic and intrinsic factors, which have been widely  
60 studied for many species (McLoughlin and Ferguson 2000; Tucker et al. 2014). At the population  
61 level, extrinsic factors such as habitat quality and heterogeneity are relevant in shaping animal  
62 space use (Wauters et al. 2001). For example, abundant food resources often lead to smaller home-  
63 range size (e.g. Šálek et al. 2015), which in turn may lead to changes in the intensity of inter- and  
64 intraspecific interactions and, sometimes, social organisation (Joshi et al. 1995; Jetz et al. 2004).

65 Space use has been widely demonstrated to vary also within populations and this inter-individual  
66 variation in animal movement and home-range size has led to the concept of individual niche  
67 specialization (Schirmer et al. 2019). For instance, an animal's home range can be affected by  
68 intrinsic factors such as its age, sex or body size (e.g. Wauters and Dhondt 1992; Lurz et al. 2000;  
69 Frafjord 2016). However, a substantial part of this intraspecific, individual variation in home-range  
70 size and movement patterns remains unexplained (van Overveld and Matthysen 2010; Moorcroft  
71 2012; Cote et al. 2014). A growing number of studies has acknowledged that consistent individual  
72 variation in space use is related to differences in personality (Cote et al. 2014; Spiegel et al. 2017;  
73 Schirmer et al. 2019), defined as among-individual differences in behaviour that persist through  
74 time and under different ecological contexts (Biro and Stamps 2008; Carter et al. 2013).

75 In many species, personality traits are measured using the movement response of an individual to  
76 stimuli. An exploratory individual is one who, exposed to a new environment and/or object (e.g.  
77 open field test), will explore longer and/or faster; a bold individual is one who will move more into  
78 riskier environments (more implicit concept of movement) (Walsh and Cummins 1976; Spiegel et  
79 al. 2017; Mazzamuto et al. 2019). Hence, since personality traits affect how individuals perceive  
80 and interact with their environment, they are likely to influence the way individuals adapt their  
81 space use to fluctuating environmental conditions (Haughland and Larsen 2004). Such relationships  
82 between personality and space use, with differences in personality affecting movement, settlement  
83 and home-range size, have been documented for several vertebrate species (Spiegel et al. 2015,  
84 2017; Merrick and Koprowski 2017; Cooper 2017; Villegas - Ríos et al. 2018; Schirmer et al. 2019;  
85 Wat et al. 2019).

86 Moreover, since the existence of personality types implies that animals may respond differently to  
87 constraints, the effects of variation in personality on an individual's space use should be more  
88 pronounced when it experiences marked changes in environmental conditions, such as reduced  
89 resource availability and/or increased population density (Sih et al. 2018). Although this is  
90 theoretically well established, few studies have considered the potential interactions between  
91 personality, the animal's sex and fluctuating environmental conditions in affecting spacing  
92 behaviour. We used multi-year and multi-site data, covering a wide range in fluctuating  
93 environmental conditions (food availability and sex-specific population density), to explore how the  
94 animal's sex and changes in extrinsic factors interact with the complex relationships between space  
95 use and personality, using an arboreal rodent as study species.

96 Researchers who want to study personality-dependent spatial ecology in wild animals can adopt two  
97 approaches. One is to use animal spatial data to assess whether repeatable, between-individual  
98 differences in space use exist (Boon et al. 2008; Harrison et al. 2015; Hertel et al. 2019). However,  
99 individual differences in personality and behavioural plasticity to environmental conditions both

100 contribute to observed behavioural differences. Caution must therefore be exercised when trying to  
101 disentangle these factors (Hertel et al. 2020). The second approach is the use of a two-step method  
102 where the animal is first captured and tested in a novel, standard, and controlled environment to  
103 determine behavioural responses. The animal is then released to relate the test to natural behaviours  
104 measured in the wild (e.g. Merrick & Koprowski 2017). This second approach is not always  
105 applicable, because of the difficulties related to creating a standard, repeatable controlled test in the  
106 wild; and/or when large species are involved that are difficult to manage. Moreover, interpretation  
107 of the correlations between behaviours displayed in an artificial environment and in the wild must  
108 be made carefully (Niemelä and Dingemanse 2014).

109 In this study, we aimed to investigate how the animal's sex and differences in the environmental  
110 context (variation in food abundance, population density) can shape the relationship between space  
111 use of adult Eurasian red squirrels (*Sciurus vulgaris*) and their personality along a bold, more  
112 explorative – shy, less explorative continuum. Earlier studies showed that spacing behaviour differs  
113 between male and female squirrels, and that red squirrels tend to increase their home ranges in  
114 response to poor food availability and/or when densities are low (Wauters and Dhondt 1992; Lurz et  
115 al. 2000; Romeo et al. 2010; Di Pierro et al. 2011). The novelty of this study is that we incorporate  
116 temporal fluctuations in food availability and population density to explore how an animal's  
117 personality affects individual variation in space use within a given habitat (or population), and  
118 whether these associations vary with the squirrel's sex.

119 We radio-tracked squirrels to determine home-range and core-area (i.e. the most intensively used  
120 part of the entire home range) size and inter-individual core-area overlap (Wauters et al. 2007; Di  
121 Pierro et al. 2008). We also calculated the core-area/home-range ratio as a proxy of home range  
122 structure. For each of these radio-tracked individuals, we used a capture-mark-recapture derived  
123 trappability index (as measure of boldness) and trap diversity index (as measure of exploration)  
124 (Boyer et al. 2010; Santicchia et al. 2018, 2020). We predict that: 1) Bolder, more explorative

125 individuals of both sexes will have larger home ranges than shy-less explorative ones, due to  
126 frequent excursions further away from the core-area and to react faster to changing environmental  
127 situations; moreover, they might also have larger core-areas to increase the areas of intensive  
128 foraging; 2) bolder, more explorative individuals will have higher core-area/ home range ratio,  
129 meaning that they will intensively use a larger proportion of their home range; 3) as a consequence  
130 of predictions 1 and 2, core-area overlap of bolder, more explorative squirrels should be higher than  
131 for shyer, less explorative ones. Finally, since extrinsic factors such as food availability and density  
132 of conspecifics are known to greatly affect space use of squirrels (Wauters and Dhondt 1992;  
133 Wauters et al. 2005; Romeo et al. 2010; Di Pierro et al. 2011), we expect that the relationships  
134 between personality traits and spatial behaviour of squirrels could be enhanced by fluctuating  
135 environmental and/or social conditions. In particular, we predict that 4) while male home ranges  
136 will vary inversely in size with food availability and with the density of females, the personality-  
137 space use relationship in females will be mainly affected by food availability to sustain energy  
138 requirements of lactation and thus enhance reproductive success (female space use is more strongly  
139 food-dependent than for males; Wauters and Dhondt 1992, 1995; Di Pierro et al. 2011).

140

## 141 **Materials and Methods**

### 142 *Study species*

143 In the Alps, the Eurasian red squirrel (henceforth referred to as red squirrel) mostly feeds on conifer  
144 seeds in the tree canopy from late summer to early next spring, and, in some forest types, recovers  
145 scatter-hoarded cones in late spring when no new cones are available in the trees. Some buds,  
146 shoots, and flowers of conifers, fungi and berries can also be consumed in late spring and summer  
147 (Romeo et al. 2010; Di Pierro et al. 2011).

148 Red squirrels have overlapping home ranges, with more intensively used core-areas. Home-range  
149 and core-area size differ markedly among habitat types, based on overall habitat quality (food

150 resource availability) and squirrel density, and home-range size can fluctuate seasonally (Wauters  
151 and Dhondt 1992; Lurz et al. 2000; Wauters et al. 2001, 2005; Romeo et al. 2010; Di Pierro et al.  
152 2011). In most habitats, male squirrels have larger home ranges than females and overlap with  
153 several females to increase their probability of mating. In stable habitats, females tend to defend  
154 exclusive core-areas against other females and have smaller core areas than males (Wauters and  
155 Dhondt 1992; Lurz et al. 2000; Wauters et al., 2001; Di Pierro et al. 2008, 2011; Romeo et al.  
156 2010). Hence, male and female red squirrels have different space use patterns. Females may  
157 copulate with more than one male, but the majority only mates with a dominant male of high body  
158 mass (Wauters et al. 1990). They can produce 1 to 2 litters/year, and reproductive success depends  
159 mainly on body condition and food availability (Wauters and Dhondt 1995; Wauters et al. 2007;  
160 Rodrigues et al. 2010).

161

#### 162 *Study area and food availability*

163 We studied red squirrels and counted cones produced yearly in three study areas in the Italian Alps  
164 in Northern Italy (Oga = OGA; Cedrasco = CED; Val di Rhêmes = RHE; Santicchia et al. 2018;  
165 details in ESM, Table ESM1). Annual estimates of conifer seed-crop size and the number of red  
166 squirrels used to estimate personality traits and space use are reported in ESM, Table ESM2. In this  
167 paper, we only used a categorical index of food abundance for each period in which squirrel home-  
168 range sizes were estimated: poor seed-crop versus medium-high seed-crop (Table ESM2).

169

#### 170 *Trapping and handling*

171 We trapped squirrels in three periods per year (April–May, June–July, September–October): from  
172 April 2000 to October 2006 in OGA, from April 2000 to April 2009 in CED and RHE. We used 25  
173 (CED), 23 (OGA), or 30 (RHE) ground-placed Tomahawk traps (models 201 and 202, Tomahawk  
174 Live Trap Co., Hazelhurst, WI, USA), homogeneously distributed over the study areas (distance



175 between traps 100–130 m; trap density 0.7–0.8 traps ha<sup>-1</sup>). Details on study area boundaries and  
176 edge effects are given in Santicchia et al. (2018). We pre-baited traps 4 times over a 30-day period  
177 using hazelnuts, then baited and activated for 6–10 days (Wauters et al. 2008). We checked traps  
178 three times per day. We marked each trapped squirrel using unique numbered metal ear-tags and  
179 weighed them using a spring-balance ( $\pm 5$  g, Pesola AG, Baar, Switzerland). We determined sex  
180 and age class based on external genitalia and body mass (juveniles < 250 g; Wauters and Dhondt  
181 1995; Wauters et al. 2007). See *Ethical note* for further details.

182 As in previous studies on tree squirrels (e.g. Kenward et al. 1998; Wauters et al. 2004, 2008; Boutin  
183 et al. 2006), we estimated population density, in each trapping period, using the minimum number  
184 of animals known to be alive (MNA) from CMR, radio-tracking and observations. Because of sex-  
185 specific space use and demographic processes, we calculated density for each sex separately  
186 (Wauters et al. 2004; Di Pierro et al. 2011).

187

### 188 *Radio-tracking*

189 To study space use, since we aimed to estimate core-area overlap among squirrels, we radio-  
190 collared as many individuals as possible (no sample size restrictions). We radio-collared 36 adult  
191 red squirrels (22 males and 14 females) at CED, 22 adults (12 males, 10 females) at OGA, and 42  
192 squirrels (23 males, 19 females) at RHE with species-specific collars. We used either PD-2C  
193 transmitters (8 g, < 4% of an individual's body mass, Holohil Systems Ltd., Carp, Ontario, Canada)  
194 or TW-4 transmitters (12 g, < 5% of an individual's body mass, Biotrack Ltd., Wareham, Dorset,  
195 UK) with adjustable necklace size. In all study areas we took one or two locations per day (one  
196 during the morning activity bout, the second in the afternoon). The interval between consecutive  
197 radio-tracking days was irregular avoiding autocorrelation in location data. Of the 100 squirrels, 9  
198 were predated (9%, below the average 20% of 6-month mortality-rate; from Wauters et al. 2004,  
199 2008) and for 86 of the remaining 91 (95%) collars were removed.

200 We estimated locations (fixes) to the nearest 10 by 10 m by homing-in to the radio-signal (Wauters  
201 and Dhondt, 1992; Wauters et al., 2001) and to estimate home-range and core-area size we used  
202 only squirrels for which we had between 23 and 45 fixes each. For each year, we estimated home  
203 ranges on a seasonal basis: spring-summer (April-July) and autumn (September-November). Since  
204 space use of several individuals was monitored in different seasons and/or years, we had a total of  
205 121 home-range and core-area size estimates of 64 different squirrels for which we also had  
206 personality data (males 73 estimates of 40 individuals, females 48 estimates of 24 individuals). We  
207 used the 95% fixed kernel probability density estimator with adjusted bandwidth  $h$  ( $KDE_{adj}$ ,  
208 Wauters et al. 2007, hereinafter KDE) to produced reliable estimates of home-range size (Di Pierro  
209 et al. 2008, 2011; Romeo et al. 2010). We estimated core-area size using the 85% Incremental  
210 Cluster Polygon (hereinafter core-area; see also Lurz et al. 2000; Wauters et al. 2005; Di Pierro et  
211 al. 2008, 2011) because the utilization distribution curve of core-area size on percentage of fixes  
212 used showed a clear inflection point between the 85 and 90% isopleths. Core-area overlap data were  
213 obtained from previous studies (Wauters et al. 2005; Romeo et al. 2010; Di Pierro et al. 2011). In  
214 summary, overlap of an individual's core-area was calculated as the total % of overlap with the  
215 core-areas of all other radio-tracked squirrels. We calculated it for each sex separately rendering  
216 four combinations: a male by other males, a male by females, a female by males and a female by  
217 other females. Not all squirrels present in a given period were radio-collared (CED 80-100% of  
218 residents, OGA 75-77% of residents, RHE 60-87% of residents; from Wauters et al. 2005; Romeo  
219 et al. 2010; Di Pierro et al. 2011), resulting in a slight underestimation of core-area overlap inherent  
220 to most radio-telemetry studies. Radio-tracking data and home range analyses were described in Di  
221 Pierro et al. (2011) for CED, in Romeo et al. (2010) for OGA and in Wauters et al. (2005) for RHE.  
222 Since space use, population density and body size (foot length and body mass) of squirrels differed  
223 among study areas (see also Wauters et al. 2005, 2007; Romeo et al. 2010), all continuous  
224 explanatory variables were standardised  $[x_i - \text{mean } x]/SD x$  within each study area before using

225 them in the LMM models that explored variation in space use determined by the animal's  
226 personality, other intrinsic variables and environmental variables (see *Space use – personality*  
227 *models*).

228

#### 229 *Ethical note*

230 Our procedures of trapping, handling, marking and radio-tracking squirrels complied with the  
231 Guidelines for the treatment of animals in behavioural research and teaching (Animal Behaviour,  
232 2020, 159, I-XI; <https://doi.org/10.1016/j.anbehav.2019.11.002>). We partly covered the Tomahawk  
233 Live Traps with dark plastic bag to provide animals with shelter and checked traps three times/day  
234 to minimize time in trap. Before handling, we completely covered the trap with a cloth to reduce  
235 stress. We flushed the trapped animal in a zipper-tube handling bag to reduce direct contact with the  
236 operator. At first capture, we marked each squirrel with a Monel 1005 1L1 ear-tag (size 2.3 – 10  
237 mm, 0.2 g or less than 0.1% of squirrel's body mass; National Band & Tag Co. Newport, KY,  
238 USA), putting the tag near the base of the ear to reduce risk of injury. There is no evidence that ear-  
239 tags affect grooming behaviour or occurrence of ectoparasite around the ear region. To reduce  
240 stress, only trained researchers handled the squirrels, and handling time was kept as short as  
241 possible (< 5 minutes). The animals were released at the trap site immediately after handling. Since  
242 the study also aimed at estimating population size based on CMR, all animals captured were marked  
243 (no sample size restrictions).

244 Trapping and handling squirrels complied with the current laws on animal research in Italy and  
245 were carried out under permission of the authorities for wildlife research and management of  
246 Lombardy Region and Gran Paradiso National Park. Legal requirements according to the Italian  
247 Wildlife Protection and Hunting Law L.N. 157 from 1992 and fieldwork was approved by  
248 authorization decrees n. 855 of 17/01/2000, n. 7489 of 29/04/2002, n. 10816 of 10/06/2002 and  
249 n.1861 of 16/02/2004 from Direzione Generale Agricoltura, Regione Lombardia, Italy; and the  
250 permission (DGE25–2000) from the Gran Paradiso National Park, Italy.

251

252 *Personality: trappability and trap diversity indices*

253 For each individual, we used the indices of trappability (number of captures /number of capture  
254 days from the first to the last trapping session an animal was present in the study area) and trap  
255 diversity (number of different traps in which an individual was captured/number of available traps  
256 in the study area). Trappability measures an animal's tendency to take risks (boldness), while trap  
257 diversity measures willingness to explore novel environments (Boon et al. 2008; Boyer et al. 2010).  
258 Because the number of traps available and capture histories differed among study areas, the  
259 trappability and trap diversity indices were standardised within each area.

260 Since we analysed all space use – personality models for each sex separately and the repeatability of  
261 behaviours (i.e. within-individual consistency) may also vary in a sex-specific manner (Schuett and  
262 Dall 2009), we estimated the repeatability of trappability and trap diversity per sex on a subset of 44  
263 males and 30 females trapped in more than one year. Since in this subset, length of capture period  
264 and number of available traps were constant over both years, we estimated the repeatability (R) in  
265 the number of captures per year and in trap diversity per year with a Linear Mixed Models (LMM)  
266 (Nakagawa and Schielzeth 2010). We used the R software (version 3.6.0) package rptR v 0.9.22 to  
267 estimate R and its 95% CIs (number of parametric bootstraps for interval estimation = 5000,  
268 number of permutations used when calculating asymptotic  $P$  values = 1000; see also Santicchia et  
269 al. 2018). We ln-transformed number of captures and square root transformed trap diversity  
270 (number of different traps) to meet assumptions of normality (Shapiro-Wilk's test on transformed  
271 data, all  $W \geq 0.94$ ). We included study area, and year and their interactions as fixed effects and  
272 squirrel identity as random factor.

273 Finally, because standardised trappability and trap diversity were highly correlated ( $r = 0.82$ ;  $N =$   
274  $121$ ;  $P < 0.0001$ ), we used a Principal Component Analysis (PCA) to derive new non-correlated  
275 variables (see also Boyer et al. 2010; Santicchia et al. 2018, 2019). The loadings were PC1 =

276  $0.707*\text{trappability} + 0.707*\text{trap diversity}$ ;  $\text{PC2} = 0.707*\text{trap diversity} - 0.707*\text{trappability}$   
277 (Eigenvalues  $\text{PC1} = 1.820$ ,  $\text{PC2} = 0.180$ ). Since the first component explained 91% of total variance  
278 in the PCA, we used only PC1 in our mixed models (see below). PC1 had a high score for bold  
279 squirrels with a strong exploration tendency, and a low score for shy, less explorative animals.

280 Trappability and trap diversity indices derived from standardised Capture-Mark-Recapture (CMR)  
281 studies have a moderate to good repeatability and represent reliable measures of the personality  
282 traits boldness and exploration in the habitat where the animal settled (Boon et al. 2008; Boyer et al.  
283 2010; LeCoeur et al. 2015; Santicchia et al. 2018, 2019, 2020). We further refer to the *Discussion*  
284 regarding possible potential caveats related to the use of these indices.

285

#### 286 *Space use – personality models*

287 Models that described broad patterns of variation in home-range and core-area size, and in the ratio  
288 of core-area/home-range are presented in the ESM (ESM3 and Table ESM3). Since, as mentioned  
289 above, male and female red squirrels have different space use patterns (e.g. Wauters and Dhondt  
290 1992; Lurz et al. 2000; Romeo et al. 2010), we analysed effects of personality on space use for each  
291 sex separately (Santicchia et al. 2018).

292 We explored variation in space use using a LMM with standardised home-range or core-area size as  
293 the dependent variable, adding individual as a repeated measure to account for pseudoreplication  
294 (Verbeke and Molenberghs 2000). In the full model we used PC1 as explanatory variable, and  
295 further included the squirrel's body mass, density of animals of the same sex, density of animals of  
296 the other sex as continuous variable, and season and a food abundance index (low vs medium-high)  
297 as categorical fixed effects. We tested whether space use – personality relationships were affected  
298 by changes in food abundance and/or population density (our predictions 4 and 5), by including the  
299 interactions of these variables with PC1. We did not use number of fixes in the models because our  
300 earlier studies in these areas showed that variation in the number of fixes did not affect the space-

301 use estimates after a threshold of 22 fixes was reached (Wauters et al. 2005; Romeo et al. 2010; Di  
302 Pierro et al. 2011).

303 We investigated which of three different correlation structures of the residual correlation matrix  
304 best fitted the data using the Schwarz's Bayesian Information Criterion (BIC), where lower values  
305 indicate better fit (Verbeke and Molenberghs 2000). We compared simple (no correlation between  
306 repeated measures on an individual), compound symmetry (CS; assuming a correlation between two  
307 measures on the same individual that does not vary over time) and first order autoregression  
308 correlation structures (assuming that the correlation between two measures on the same individual  
309 is a function of the time-interval between them). We used a stepwise backward model selection  
310 based on partial p-values eliminating non-significant interactions and fixed effects to produce  
311 selected models. Degrees of freedom and standard errors of F- and t-tests were obtained using  
312 Kenward-Rogers method (Verbeke and Molenberghs 2000). Model residuals did not deviate from a  
313 normal distribution (based on QQ-plots and Shapiro-Wilk's statistic). The same LMM modelling  
314 was also used with the standardised ratio of core-area/home-range size as dependent variable.

315 Finally, we investigated the effects of personality on the patterns of core-area overlap, using the  
316 within study area standardised values of % core-area overlap as dependent variables. We modelled  
317 four different response variables: males overlap by other males, males overlap by females, females  
318 overlap by males and females overlap by other females (Wauters and Dhondt 1992; Romeo et al.  
319 2010; Di Pierro et al. 2011). We tested the same fixed effects as in the models above, but we only  
320 considered density of the overlapping sex as the biologically relevant density measure; thus we  
321 included male density when overlap with males was modelled, female density when overlap with  
322 females was modelled. Model selection was carried out as described above.

323 All tests of significance are two-tailed and the significance level was set at 0.05. All the statistical  
324 analyses, except estimates of repeatability, were done using SAS/STAT 9.4 software (Copyright ©  
325 2011, SAS Institute Inc., Cary, NC, USA).

326

## 327 **Results**

### 328 *Space use patterns*

329 Individual variation in home-range and core-area size of red squirrels was large ( $N = 121$ ; mean  $\pm$   
330 SD: KDE  $23.45 \pm 32.33$  ha, range 1.26 - 194.20 ha; core-area  $7.47 \pm 10.13$  ha, range 0.56 - 98.53  
331 ha). The two space use estimators were positively correlated ( $r = 0.65$ ;  $N = 121$ ;  $P < 0.0001$ ). Raw  
332 data of home-range and core-area size (in ha) per study area and sex are given in Table 1. Details on  
333 statistical analyses and differences between areas and the sexes can be found in ESM3 and Table  
334 ESM3.

335

### 336 *Repeatability of trapping indices*

337 Trappability and trap diversity indices were consistent through time and had a high repeatability ( $R$ )  
338 in both sexes (44 males: trappability  $R = 0.70$ , 95% CI = 0.54 – 0.84; trap diversity  $R = 0.64$ , 95%  
339 CI = 0.46– 0.81; 30 females: trappability  $R = 0.65$ , 95% CI = 0.43 – 0.84; trap diversity  $R = 0.62$ ,  
340 95% CI = 0.39– 0.83; all likelihood ratio test  $P < 0.001$ ). Therefore, we consider them as suitable  
341 measures of, respectively, boldness and exploration in red squirrels. As explained above, because of  
342 their strong correlation, we performed a PCA on trappability and trap diversity and used the scores  
343 along the first axis (PC1 scores) as our final measure of personality in the space use models.

344

### 345 *Space use and personality*

346 Full LMMs testing the effects of PC1 on each of the space use estimators (dependent variable) are  
347 given in the Appendix 1 (Table ESM4 for males, Table ESM5 for females). An individual's body  
348 mass and PC1 score were not correlated (males,  $r = 0.16$ ;  $N = 73$ ;  $P = 0.16$ ; females  $r = 0.24$ ;  $N =$   
349 48;  $P = 0.09$ ).

350 Home-range and core-area size of male ( $N = 73$  of 40 different animals) and female red squirrels ( $N$   
351 = 48 of 24 different animals) were not affected by variation in personality (PC1) (Tables ESM4,

352 ESM5). However, other factors affected their size. In males, home range size increased when food  
353 abundance was low (estimate low vs medium-high food =  $0.69 \pm 0.26$ ;  $t_{70} = 2.68$ ;  $P = 0.009$ ), and  
354 decreased at high female density (estimate  $-0.31 \pm 0.16$ ;  $t_{70} = 1.96$ ;  $P = 0.054$ ; Table ESM4a), while  
355 variation in core-area size was not affected by any of the fixed effects (Table ESM4b). In females,  
356 home-range size also tended to increase when female density decreased (Selected model: female  
357 density effect estimate  $-0.40 \pm 0.14$ ;  $t_{42} = 2.80$ ;  $P = 0.008$ ), and, as in males, variation in core-area  
358 size was not affected by any of the fixed effects (Table ESM5b).

359 We found a positive relationship of the standardised ratio of core-area/home-range with PC1 among  
360 male red squirrels ( $0.23 \pm 0.08$ ;  $t_{70} = 2.92$ ;  $P = 0.0047$ ), but not females. Thus, bolder and more  
361 explorative males (high PC1 score) used relatively larger core-areas within their home range than  
362 shy ones (Fig. 1). None of the other explanatory variables significantly affected variation in the  
363 standardised core-area/home-range ratio of males or females (Tables ESM4c, ESM5c).

364 Overlap of a male's core-area with those of other males was higher in spring than in autumn (season  
365 effect  $0.49 \pm 0.21$ ;  $t_{70} = 2.32$ ;  $P = 0.023$ ) and decreased with PC1 ( $-0.16 \pm 0.07$ ;  $t_{70} = 2.21$ ;  $P = 0.03$ ;  
366 Fig. 2); hence bolder, more explorative males had less core-area overlap with other males than shy,  
367 less explorative ones (Table ESM6a). In the model of males overlapped by females, only food  
368 abundance had a significant effect: core-area overlap between a male and female squirrels increased  
369 at low food availability (food effect  $0.64 \pm 0.24$ ;  $t_{71} = 2.69$ ;  $P = 0.009$ ; Table ESM6b). A female's  
370 core-area overlap with males was not related to its personality and there was no effect of male  
371 density or food abundance on individual variation in female by male core-area overlap (Table  
372 ESM7a). The selected model of a female's overlap by other females showed a significant effect of  
373 body mass ( $-0.25 \pm 0.12$ ;  $t_{46} = 2.10$ ;  $P = 0.041$ ); heavier females had less intrasexual core-area  
374 overlap than those of lower body mass. A female's personality did not affect the amount of intra-  
375 sexual overlap (Table ESM7b).

376  
377 *Food- or density related associations between personality and space use*



378 We did not find any relationships between personality traits and spatial behaviour of male squirrels  
379 when environmental and/or social conditions fluctuated. Among female red squirrels the effect of  
380 personality (PC1) on home-range size differed with food availability (Fig. 3), and was negatively  
381 related with home-range size during poor seed-crops, but not so during periods with medium-high  
382 seed-crops (PC1\*food interaction  $-0.61 \pm 0.23$ ;  $t_{42} = 2.71$ ;  $P = 0.0098$ ; table ESM5a). Hence, there  
383 were no differences in home-range size between bold and shy females in years with medium to rich  
384 seed-crops, while bolder, more explorative females used smaller home ranges than shy, less  
385 explorative ones at low food availability (Fig. 3). We also found a nearly significant interaction of  
386 PC1 with female density (PC1\*Nfemales estimate  $-0.30 \pm 0.15$ ;  $t_{42} = 1.97$ ;  $P = 0.055$ ). In response  
387 to fluctuations in female density, bolder females used larger home ranges than shy ones at low  
388 density, at medium densities there was no effect of personality on home-range size, while at high  
389 female densities, bolder and more explorative animals tended to use smaller home ranges than shy,  
390 less explorative ones.

391

## 392 **Discussion**

393 Consistent differences in behaviour among individuals, hence animal personality, is a key candidate  
394 to determine inter-individual variation in space use and movements (Minderman et al. 2010; Spiegel  
395 et al. 2017; Schirmer et al. 2019; Wat et al. 2019). Moreover, the personality traits that influence  
396 space use might differ between male and female vertebrates in relation to sex-biased strategies to  
397 maximize reproductive success (e.g. LeCoeur et al. 2015; Wat et al. 2019). Moreover, since spatio-  
398 temporal fluctuations in environmental variables, in particular food availability and density of  
399 conspecifics, will influence movement patterns, they are key candidates to interact with  
400 personality–spacing behaviour relationships. Whilst this is well established theoretically, we are  
401 among the first to have used multi-year and multi-site data to explore how the animal's sex and  
402 changes in environmental factors interact with the complex relationships between space use and  
403 personality. Here, we found evidence for sex-specific effects of personality on home range size and

404 space use patterns in populations of Eurasian red squirrels occupying different montane and  
405 subalpine conifer forests. Moreover, we showed that complex interactions of personality with seed-  
406 crop size and/or with sex-specific density influence a squirrels' space use. In this study, we did not  
407 use standardized behavioural tests (e.g. arena tests), but adopted spatial capture-recapture data to  
408 assess whether repeatable, between-individual differences in behaviour exist. We analysed two  
409 indices of personality: trappability and trap diversity; however, since they were strongly correlated  
410 (see also Boyer et al. 2010; Santicchia et al. 2018, 2019), we used PCA to derive a single  
411 personality score. Hereinafter we shall refer to animals with high values along the first PCA axis  
412 (high PC1 score) as bolder squirrels that also tended to be the more explorative ones.

413

#### 414 *Personality and space use: home range and core-area size*

415 Contrary to our first prediction, personality traits were not directly related to absolute home-range  
416 or core-area size of male or female squirrels. Bolder, more explorative squirrels did not have larger  
417 home ranges or larger core-areas than shyer, less explorative ones. Variation in home-range size  
418 was mainly determined by access to limited resources, independent from the animal's personality.  
419 Males increased their home range when food abundance and density of females (partners) were low,  
420 partly in agreement with our fourth prediction. Females increased their home-range size when  
421 female density decreased, confirming earlier studies showing that that in this sex, intrasexual  
422 competition for space is the main driver of fluctuations in home-range size (Wauters and Dhondt  
423 1992; Romeo et al. 2010)

424

#### 425 *Personality and space structure: core-area/home-range ratio and core-area overlap*

426 Personality influenced how males used the habitat inside their home range: bolder, more explorative  
427 males had a larger core-area/home-range ratio, and spatially their core-areas overlapped less with

428 those of other males than for shy, less explorative ones. Hence, bolder and more explorative males  
429 intensively used a relatively large part of their total home range from which they are more prone to  
430 exclude other males, in agreement with our second and third prediction. This behaviour could result  
431 in an advantage to bolder males by increasing their access to limited food resources inside their  
432 core-areas. Similarly, bolder bank voles (*Myodes glareolus*) had smaller core-area overlap than  
433 shyer individuals. However, in contrast to male red squirrels, bolder voles also had larger home  
434 ranges and core-areas (Schirmer et al. 2019). In sleepy lizards (*Tiliqua rugosa*), core-area overlap  
435 was higher for unaggressive animals than for aggressive ones, while home-range size was positively  
436 associated with the behavioural trait boldness (Spiegel et al. 2015). The differences in male  
437 squirrels' personality may also result in two different reproductive strategies. Bolder, more  
438 explorative males used relatively larger core-areas within their home range (core area/home range  
439 ratio) to increase access to food while shy, less explorative ones used relatively smaller core-areas.  
440 The latter suggests they might move over multinuclear core-areas that consist of several small but  
441 intensively used patches, a behaviour that could favour them when conifer seed availability is  
442 strongly reduced and alternative resources must be sought (Wauters et al. 2005). Finally, when  
443 female density was low, male squirrels used larger home ranges than at high female density,  
444 independently of their boldness-exploration level. Hence, all male red squirrels responded to  
445 fluctuations in the density of potential partners, which also explained higher overlap among males  
446 in spring-summer, when matings occur, compared to the autumn.

447         Contrary to males, females' space use within their home ranges (i.e. core-area/home-range  
448 ratio or overlap ) did not vary with personality as predicted (prediction 2 and 3). However,  
449 intrasexual core-area overlap was inversely related to a female's body mass, confirming the pattern  
450 of intrasexual territoriality among adult, dominant females of high body mass which is consistent  
451 over a wide range of habitats and densities (Wauters and Dhondt 1992; Lurz et al. 2000; Wauters et

452 al. 2001; Romeo et al. 2010; Di Pierro et al. 2011). Hence, female red squirrels typically have low  
453 overlap with other females, independent from their personality.

454

455 *Personality, space use and changes in resources: food and squirrel density*

456 Overall, both male and female red squirrels tended to increase their home-range size when food  
457 abundance was low and when female density in the population decreased; a pattern typical for this  
458 species (e.g. Wauters et al. 2001, 2005; Romeo et al. 2010; Di Pierro et al. 2011). Contrary to our  
459 first prediction, personality traits were not directly related to absolute home-range or core-area size  
460 of squirrels, however, in agreement with prediction 4, the relationship between individual  
461 personality and space use became relevant at specific extrinsic conditions, at least for females, with  
462 food availability being the most influential factor.

463 Among females, personality had no effect on home-range size at high food availability, but when  
464 food was scarce, bold-explorative females reduced home-range size whereas shy, less explorative  
465 individuals increased it. This counter-intuitive behaviour could be a reflection of habitat quality in  
466 that bold-explorative females have a better knowledge of and select high quality patches that  
467 contained still sufficient food resources during low tree-seed availability. With medium-high seed-  
468 crops, female space use was more stable and independent from boldness-exploration tendency. This  
469 pattern suggests that bold, explorative females are more aware of their surroundings and the  
470 distribution and availability of food resources than shy, less explorative ones. Spatial knowledge  
471 about the changing distribution of food resources is key, and these females are therefore quicker to  
472 respond to periods of poor-seed-crops by shifting their home range to the few high-quality habitat  
473 patches that allow a relatively high daily energy-intake, resulting in smaller ranges. In contrast, shy  
474 and less explorative individuals will be forced to increase the size of their foraging grounds to meet  
475 their energy requirements. This is likely an adaptive strategy, as our study areas were characterised

476 by high spatio-temporal variation in the abundance of conifer seeds, the squirrels' main food supply  
477 (Wauters et al. 2005; Romeo et al. 2010; Di Pierro et al. 2011; and Table ESM2). Food availability  
478 did not only fluctuate annually, but there was considerable spatial variation, which was more  
479 extreme in years of poor seed-crops (coefficient of variation of seed-crop estimates over the 20  
480 sampling plots: poor food years 91 to 221%, average 150%; medium-high food years 38 to 105%,  
481 average 68%; from table ESM2). Thus, when food availability is medium-high, most trees produce  
482 cones and spatial distribution of food resources is more homogeneous than with low food.

483 A similar sex-specific pattern was found in common brushtail possum (*Trichosurus vulpecula*)  
484 where less explorative females, yet high explorative males, had larger home ranges (Wat et al.  
485 2019). Also, in a study with juvenile great tits (*Parus major*) fast explorers rapidly shifted to  
486 different foraging areas, but did not show a larger increase in home-range size than slow explorers  
487 when the food supply was experimentally reduced (van Overveld and Matthysen 2010). These  
488 authors suggested that slow and fast explorers differed in how they used the information collected  
489 on temporal changes in food availability, but not in the extent of space used for foraging (van  
490 Overveld and Matthysen 2010). In contrast in starlings (*Sturnus vulgaris*), the relationship between  
491 an exploration score and home-range size was positive, but it also became more evident when local  
492 density (flock size) was high and habitat quality low (Minderman et al. 2010).

493 Finally, we found a weak, and not-significant tendency for an interaction of PC1 with female  
494 density on fluctuations in home-range size. Shy and less explorative females (low PC1 score) did  
495 not vary their home-range size with fluctuating female densities, while bolder and more explorative  
496 females tended to use larger ranges than shy, less explorative ones at low densities, while at high  
497 densities the trend was opposite. Tentatively, this suggests that bolder, more explorative females  
498 seemed to be more flexible in response to intra-sexual competition, which could enhance their  
499 access to higher-quality foraging patches (e.g. Patrick and Weimerskirch 2014).

500

501 *Potential caveats of the study methods*

502 The reliability of trappability and trap diversity indices as proxies of, respectively, boldness and  
503 exploration in red squirrels have been discussed by Santicchia et al (2018). Nevertheless, one might  
504 argue that trap diversity, which we used as our measure of adult squirrels' exploration in a known  
505 environment, is a proxy of home-range or core-area size rather than a personality index, since  
506 home-range size affects how many traps the owner can potentially visit. We are convinced this is  
507 not the case because: (1) trap diversity had a high repeatability, suggesting it indeed measures a  
508 personality trait; and more importantly; (2) there was no positive correlation between home-range  
509 (Pearson correlation test  $r = -0.13$ ) or core area size ( $r = -0.11$ ) and trap diversity; (3) as described in  
510 the methods, the periods over which trappability and trap diversity were estimated did not overlap  
511 strongly with the (generally shorter) periods of radio-tracking. Most animals were trapped both  
512 before, during and after space use parameters were determined and some traps in which they were  
513 caught were outside the estimated home range area (Santicchia et al. 2018). Moreover, we are  
514 confident that our standardised methods of pre-baiting traps and seasonally spaced multiple days  
515 CMR sessions strongly reduced any potential bias in trappability [see also Michelangeli et al. 2016  
516 in delicate skink (*Lampropholis delicata*); Jolly et al. 2019 in grassland melomys (*Melomys*  
517 *burtoni*)] as discussed in detail in previous studies on red squirrels (Wauters et al. 2008; Santicchia  
518 et al. 2018, 2020). Future research with the use of GPS-collars, which provide continuous animals'  
519 locations and complete movements recordings (e.g. Melovski et al. 2020; Pisanu et al. 2020), will  
520 allow corroborating these assumptions.

521

522 *Conclusions*

523 Male and female red squirrels adapted their space use in different ways to fluctuations in squirrel  
524 density and/or food abundance. Moreover, inter-individual variation in red squirrel space use was,

525 to some extent, influenced by their personality, but these relationships were highly context-driven  
526 (see also Mindermann et al. 2010; Dingemanse and Wolf 2010) and differed with sex. For example,  
527 in males there was a direct effect of boldness, exploration tendency on home-range use (measured  
528 with core-area/home-range ratio), while among females, bolder, more explorative females reduced  
529 their home ranges when food availability was low, but there was no effect of personality on home-  
530 range size at medium-high seed-crops. Hence, the capacity to acquire information about changing  
531 environmental variables (e.g. food resources, competitors, partners) is likely to differ between the  
532 various personality types, which will feedback to their movement and space use decisions (Spiegel  
533 and Crofoot 2016). Thus, different space use strategies between the sexes to maximize access to  
534 limited, and seasonally changing resources (food resources for females, partners and food resources  
535 for males), linked to differences in personality, resulted in individual variation in home-range size  
536 and space use in populations. Variation in spacing behaviour and changing fitness advantages (e.g.  
537 Le Coeur et al. 2015; Santicchia et al. 2018) of animals with different personalities will further  
538 enhance the possibility that at least part of the population will respond successfully to strong  
539 fluctuations in resource abundance in boom and bust production-consumer systems, guaranteeing  
540 the long-term persistence of the populations.

541

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548

549

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556

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559

#### 560 **Ethics approval: Animal Welfare Statement**

561 All applicable institutional and/or national guidelines for the care and use of animals were followed.  
562 Trapping and handling squirrels complied with the current laws on animal research in Italy and  
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570

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572

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575

576 **Electronic Supplementary Material.** The online version of this article contains 2 files with  
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578

579 **Data availability:** The datafile is added in Electronic Supplementary Material 2 (ESM2: Wauters-  
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581

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583

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586 conducted fieldwork; MVM and CR performed statistical analyses and LAW, MVM and CR wrote  
587 the manuscript and all other authors provided editorial advice. †Lucas A. Wauters and Maria  
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589

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769 **Table 1.** Red squirrel home-range size (mean  $\pm$  SD) and core-area size (mean  $\pm$  SD) variation

770 between the sexes and among study areas. Core-area overlap estimates (mean  $\pm$  SD): Male ovl by =

771 average % overlap for a male by other males and by females (column Sex) in each study area; and

772 Female ovl by = average % overlap for a female by males and by other females (column Sex) in

773 each study area.

Study area	Sex ( <i>N</i> )	95% KDE (ha)	Core area (ha)	Male ovl by (%)	Female ovl by (%)
CED	Males (27)	9.92 $\pm$ 12.72	4.30 $\pm$ 3.22	38 $\pm$ 45	26 $\pm$ 29
CED	Females (18)	6.11 $\pm$ 7.76	2.97 $\pm$ 3.66	61 $\pm$ 44	12 $\pm$ 21
OGA	Males (15)	9.83 $\pm$ 11.17	5.66 $\pm$ 5.17	42 $\pm$ 46	25 $\pm$ 32
OGA	Females (10)	3.88 $\pm$ 0.96	2.75 $\pm$ 0.66	51 $\pm$ 63	11 $\pm$ 14
RHE	Males (31)	44.54 $\pm$ 40.17	10.05 $\pm$ 6.18	50 $\pm$ 38	58 $\pm$ 48
RHE	Females (20)	40.61 $\pm$ 39.93	15.48 $\pm$ 20.38	49 $\pm$ 46	52 $\pm$ 66

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783 **Figure Headings**

784 **Figure 1.** Relationship between core-area/home-range ratio and PC1 (standardised values) in male red  
785 squirrels (at density of females=-0.5). The solid line represents the predicted relationship, shaded areas  
786 represent the 95% confidence interval, symbols represent observed values.

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788 **Figure 2.** Relationship between core-area overlap among male red squirrels and PC1 (standardised values);  
789 season effect kept constant at spring season. The lines represent the predicted relationship, shaded areas  
790 represent the 95% confidence intervals and symbols represent observed values.

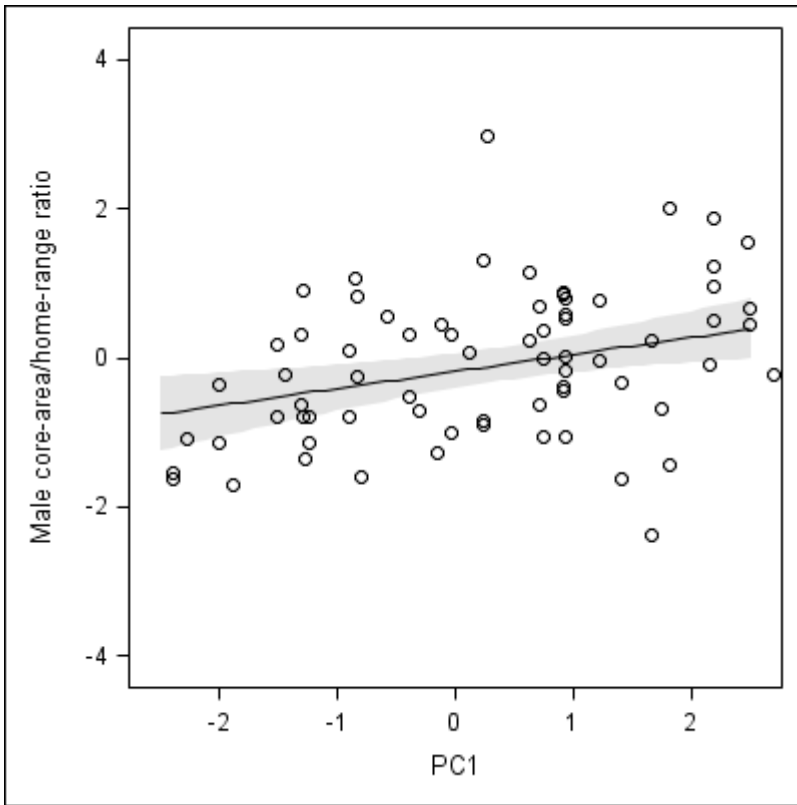
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792 **Figure 3.** Relationship between home-range size and PC1 (standardised values) in female red squirrels at  
793 low (solid line, triangles) and medium-high (dashed line, circles) food availability (at density of females=-  
794 0.66). The lines represent the predicted relationships, shaded areas represent the 95% confidence intervals,  
795 symbols represent observed values.

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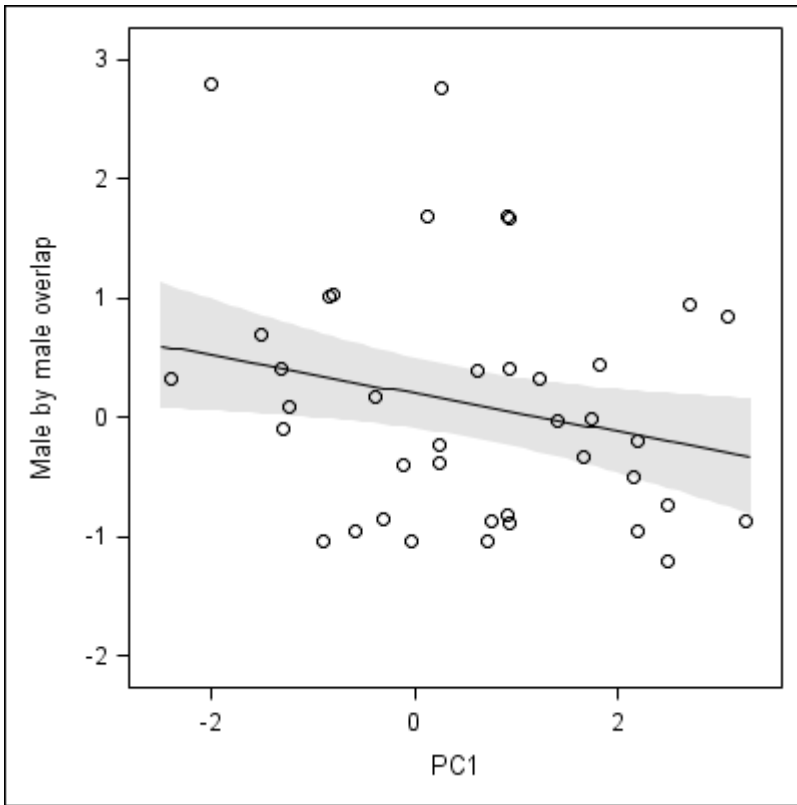
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