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1 **Linking Personality and Health to Use of Space in the Gray Partridge: Perspectives for Management**

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23 **ABSTRACT**

24 Behavioral adjustments are of critical importance for the survival of animals when exposed to risk and resource
25 variations in their environment. Moving to safer habitats allows prey to reduce the risk of mortality triggered by
26 predation. This response has been well studied at the population level to assist in identifying key habitat
27 components for wildlife conservation. However, while individuals may differ in their response to risk and thus in
28 their survival expectancy, the determinants of individual adjustments in space and habitat use are largely
29 unknown in management and conservation studies. Using GPS monitoring, we investigated the relationship
30 between individual traits (morphometry, personality, health status) and adjustments in use of space relative to

31 risky features (hedgerows, roads/tracks, woodlands, built-up areas) with regard to predation risk. We used the
32 gray partridge (*Perdix perdix*) as a study model (captive-reared birds released into the farmlands). During the
33 diel cycle, predation risk mainly occurs by carnivores at night whereas human hunting pressure occurs during the
34 day. We found that personality and health status had an effect on adjustments in use of space as response to risky
35 features. At night, when carnivore activity is expected to be high, bolder individuals were farther from
36 hedgerows relative to the day. Similarly, individuals in good health were located farther from hedgerows,
37 roads/tracks, and woodland at night relative to the day. We discuss the need for better consideration of individual
38 traits in management and conservation programs, with a particular focus on recovery programs that rely on
39 translocation of captive-reared individuals.

40 **KEYWORDS:** Behavioral adjustment, Gray partridge, Health status, Personality, Space use, Wildlife
41 management

42

43 **DECLARATIONS**

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52 **Code availability:** The authors agree to archive the code associated with this manuscript should the manuscript
53 be accepted. The code will be added to the same repository as the data.

54 **Ethics approval:** Field studies did not involve endangered or protected species. Permission to handle the study
55 birds was given by the authority Préfecture Départementale des Deux-Sèvres (Number 2017/1). All applicable
56 French guidelines for the ethical use of animals in research were followed.

57

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68 **INTRODUCTION**

69 Animals adjust their behavior in response to the spatial and temporal variations in resource availability and
70 predation risk (Lima and Dill 1990; Johnson et al. 1992; Lima and Bednekoff 1999). Adjustments in space and
71 habitat use are among the most commonly studied responses that allow prey to reduce their immediate mortality
72 risk from predators, by moving toward safer areas or habitats (Laundré et al. 2001; Fortin et al. 2005; Tolon et al.
73 2009; Lone et al. 2015). However, these responses may become particularly complex in human-dominated
74 landscapes, where human disturbance may conflict with risks imposed by non-human predators (Lone et al.
75 2014, 2017; Bonnot et al. 2020). For example, some prey living in heterogeneous landscapes, such as the
76 European rabbit (*Oryctolagus cuniculus*) and the roe deer (*Capreolus capreolus*), shift their behavior patterns
77 during the day and night in response to variation in risk. They use open habitats that offer better detection and
78 escape from nocturnal carnivores at night, and shift to the opposite more vegetated habitats during the day,
79 which provide shelter from human disturbance and/or diurnal predators (Moreno et al. 1996; Bonnot et al. 2014;
80 Lone et al. 2017). Similar patterns have also been found in gamebirds, such as the gray partridge (Harmange et
81 al. 2021).

82 Individuals within a population may however show significant variation in their perception of, and
83 response to dangerous situations, depending on their phenotypes (Sih and Del Giudice 2012; Bonnot et al. 2014).
84 This may result in between-individual differences in survival (Ciuti et al. 2012; Lone et al. 2015). However,
85 little is known about the between-individual differences in how space is used and what determines these
86 differences. Individual traits may influence the movement-related decision-making of individuals or their ability
87 to move, thus affecting the use of space by several mechanisms (Nathan et al. 2008). First, the internal state of
88 animals (i.e., the physiological and neurological states that affect motivation and readiness to move, Nathan et al.
89 2008) depends on personality traits that influence their propensity to take risks, and then their fitness (Both et al.
90 2005; Réale et al. 2007; Smith and Blumstein 2008; Sih et al. 2012). Personality has been defined as correlated
91 behavioral traits within individuals, usually related to boldness, aggressiveness, activity and exploratory
92 tendency, and is commonly expressed as a bold/shy gradient (Sih and Del Giudice 2012). Bolder individuals are
93 often more aggressive and often engage in risk-taking behaviors, such as exploring novel environments or
94 returning to disturbed areas faster than shy individuals (Verbeek et al. 1994; Van Oers et al. 2004a, b), thereby
95 increasing their mortality risk (Van Oers et al. 2004a; Smith and Blumstein 2008). Secondly, morphometric
96 traits may constrain motion capacity (i.e., the biomechanical properties that affect the ability to execute
97 movement, Nathan et al. 2008). For instance, increased wing loading (or body mass) in birds impairs flight

98 abilities such as maneuverability (Dietz et al. 2007; van den Hout et al. 2010), as well as take-off velocity and
99 angle (Kullberg et al. 1996), which alters escape behavior (Gosler et al. 1995; Lindström et al. 2003; Møller
100 2015). Thirdly, health status may interfere with navigation capacity (i.e., the ability to orient and select where
101 and/or when to move, Nathan et al. 2008). Illness and increased allocation of energy to immune function in
102 infected individuals, may reduce the locomotion abilities (Moore 2002; Lindström et al. 2003). Despite calls to
103 integrate such individual variability into conservation and management schemes (Watters and Meehan 2007;
104 Smith and Blumstein 2008; Caro and Sherman 2012; Berger-Tal and Saltz 2014), this has been seldom
105 incorporated to date (see Merrick and Koprowski 2017).

106 It is of particular interest to address these issues in game species, for which management strategies often rely
107 on the translocation of captive-reared animals (Griffith et al. 1989; Laikre et al. 2006; Sokos et al. 2008;
108 Champagnon et al. 2012a). Animals raised in captivity usually show low survival expectancy after release,
109 which is mainly ascribed to predation. Indeed, mortality rates one month after release can be as high as 81% in
110 *Phasianus colchicus* (Hessler et al. 1970), 63-94% in *Alectoris rufa* (Gortázar et al. 2000), 63-95% in *Alectoris*
111 *graeca* (Dessi-Fulgheri et al. 2001), or 73-90% in *Perdix perdix* (Rymesova et al. 2013). The captive-reared
112 origin of individuals has been viewed as a major cause of failures in restoring self-sustainable populations in
113 game species (Griffith et al. 1989; Sokos et al. 2008), because such animals often undergo multiple alterations in
114 traits related to anti-predator behavior, such as morphology and/or physiology, which affect their ability to
115 escape from predators (Putala and Hissa 1995; Putala et al. 1997; van Heezik et al. 1999; Rantanen et al. 2010;
116 Champagnon et al. 2012b).

117 The gray partridge (*Perdix perdix*) is an iconic gamebird living in farmland landscape in Europe. However,
118 agricultural intensification has resulted in reduced reproductive success for this species (Potts 1986; Kuijper et
119 al. 2009; Gée et al. 2018). Populations have now reached such a low abundance in many areas and even gone
120 locally extinct (Aebischer and Kavanagh 1997; Chamberlain and Fuller 2000; Comolet-Tirman et al. 2015;
121 Harmange et al. 2019), that population persistence relies on releasing millions of captive-reared birds per year
122 (e.g. 2 million individuals per year in France in Bro 2016; see also Buner et al. 2011; Bro and Crosnier 2012). In
123 most cases, these programs have failed to help population recovery (Bro and Mayot 2006; Buner 2009; Jenny
124 2015; Harmange et al. 2019). Increased predation and shooting pressure have been identified as two of the main
125 proximal causes for the decline of partridges over the last decades (Kuijper et al. 2009; Aebischer and Ewald
126 2012). However, these act in contrasting ways: predation mainly occurs at night on birds located closer to roads
127 or tracks, while birds that are killed by hunters during the day are located in areas farther from hedgerows (i.e.,

128 in more open areas) during daytime (Harmange et al. 2021). Such contrasting pressures should result in a
129 partitioning in the use of space between day and night (Moreno et al. 1996; Monterroso et al. 2013, 2014; Lone
130 et al. 2014, 2017), but whether, and how individual traits may affect behavioral adjustments remains unknown in
131 the context of management (see Merrick and Koprowski 2017).

132 In this study, we investigated the relationship between individual traits (morphometry, personality, and
133 health status) and individual response to risk across the diel cycle. We did this by monitoring released partridges
134 equipped with GPS devices, allowing to correlate individual traits to use of space. Although naïve at release, we
135 already showed that captive-reared partridges are able to adjust to some extent their use of space in ways
136 consistent with a reduction of risk from nocturnal carnivores at night, and of human-induced disturbance and/or
137 raptor predation risk during daytime (Harmange et al. 2021). In particular, landscape features such as woodlands
138 and built-up areas, which are predator reservoirs, and hedgerows and roads, which are predator corridors (Pereira
139 and Rodríguez 2010; Krauze-Gryz et al. 2012; Bischof et al. 2019; Pita et al. 2020), present a high risk to
140 partridges. We therefore assume that distance to risky landscape features may be a reasonable proxy of risk-
141 taking behavior, and used these distances to estimate to what extent individual partridges adjust their use of
142 space in response to the spatial variation in risks between day and night. We thus contrasted the average distance
143 to risk-related features between the night and day by calculating difference in the mean nocturnal less the mean
144 diurnal distances (following Harmange et al. 2021). A positive difference would indicate high levels of
145 behavioral adjustment, that is avoidance of features with high risk at night, and greater proximity to shelter
146 during daytime, in response to human disturbance and diurnal birds of prey (Moreno et al. 1996; Lone et al.
147 2017), or food-rich habitats (e.g. roadside habitats: Hopwood 2008; von der Lippe et al. 2013). We predicted that
148 bolder individuals would adjust better to such contrasting environmental pressures because of their capacity for
149 rapid exploration (Verbeek et al. 1994; Van Oers et al. 2004a; Fucikova et al. 2009), their fast decision-making
150 ability in a risky situation (Burns and Rodd 2008; Sih and Del Giudice 2012), their ability to return faster to a
151 place after a disturbance (Van Oers et al. 2004a, b; Quinn and Cresswell 2005), and their ability to adopt routine
152 behaviors (Groothuis and Carere 2005). Boldness was measured through behaviors indicative of birds
153 fearfulness when handled (Edelaar et al. 2012; Garcia-Longoria et al. 2014). Because high investment in the
154 immune function is often associated with reduction in the locomotion abilities, birds with low health conditions
155 were expected to be less mobile and thus to adjust their use of space less than healthy birds. Finally, individuals
156 with low wing loading were expected to adjust better because of their better flying ability. As the gray partridge

157 is a gregarious species in winter (Beani and Dessi-Fulgheri 1986), we did not expect a strong difference in
158 spatial adjustment between sexes.

159

160 **MATERIAL AND METHODS**

161 **Study area**

162 The study was conducted on the Long-Term Socio-Ecological Research (LTSER) platform “Zone Atelier Plaine
163 & Val de Sèvre”, *Département des Deux-Sèvres*, in Western France. Study area covers 435 km², which is
164 characterized by intensive cereal production. Land-cover use has been surveyed annually since 1994, and is
165 represented by winter cereals (41.5%, mean value calculated over the years 2009–2016), sunflower (10.4%),
166 corn (9.6%), rape (8.3%), meadows (13.5%), woodlands (2.9%) and built-up areas (9.8%) (Bretagnolle et al.
167 2018). The densities of hedgerows and roads/tracks are respectively 34 m/ha and 50 m/ha. In the study area, the
168 main predators of partridges are mammalian carnivores including the red fox *Vulpes vulpes*, mustelids and the
169 domestic cat *Felis catus*, and to a lesser extent, raptors mainly represented by the hen harrier *Circus cyaneus*.

170 The population density of gray partridge was very low during the years in which the study was conducted
171 (Harmange et al. 2019). Important annual releases of captive-reared birds are carried out by hunter associations
172 (around 250 birds per commune, see Harmange et al. 2019). Hunting activity occurs twice a week on Thursdays
173 and Sundays in the LTSER area (Casas et al. 2009), during daylight hours (from 1 hour before sunrise to 1 hour
174 after sunset). While the hunting season for partridges starts in mid-September and ends in mid-November,
175 disturbance from hunting extends for longer because of shooting of other game species such as the brown hare
176 (*Lepus europaeus*), and the common pheasant (*Phasianus colchicus*). Although shooting of the gray partridge
177 had been suspended for three years at the release site, shooting of the red-legged partridge and other game
178 species was still allowed.

179

180 **GPS Monitoring**

181 Five-month old captive-reared gray partridges were released into the area of the Communal Hunting Society of
182 Marigny. Released birds were raised in a commercial game farm following a standard game rearing method
183 (Sokos et al. 2008): the rearing farm receives 1-day-old chicks from an egg production farm (around 30
184 generations bred in captivity). Chicks are then artificially reared using brooders, without parents. Three session
185 of releases were carried out (mid-December 2016, mid-September 2017, and late October 2017; see Table 1),
186 following the same protocol: partridges were transported by car from the rearing farm to the release sites

187 (transportation time of ca. 40 minutes), in cardboard boxes of 8 individuals, separating the males and females.
188 Flocks of 12–16 individuals were then released (with the same proportion of each sex), 6–8 of whom were
189 equipped with a GPS device. The birds were left in acclimation pens of approximately 5 m² for five days. Prior
190 to placement in acclimation pens, birds were weighed using a spring scale (Pesola 500 g, accuracy: ± 5 g),
191 measured (wing length, using a ruler, accuracy: ± 1 mm), sexed, ringed (with colored and numbered metal
192 gamebird rings), and fitted using GPS loggers (CatLog-S2, Catnip Technologies Ltd, Hong Kong). These
193 loggers were placed on the breast of the bird using a necklace. Other birds were fitted using better performing
194 but more expensive GPS devices allowing for remote data transmission (5 units of UvA-BiTS GPS-transmitters,
195 www.uva-bits.nl Bouten et al. 2013 in 2016 ; and 2 units of Milsar’s GsmRadioTag-S9, www.milsar.com, in
196 2017). These GPS transmitters were fitted onto the back using a Teflon harness (Table 1). The average handling
197 time was 3–4 minutes per bird. The GPS loggers (CatLog-S2) were turned on at release and locations recorded
198 as one fix every 15 minutes during daytime, and one fix per hour at night. GPS transmitters were initially
199 programmed to record one fix per 10 minutes during daytime and one fix every 30 minutes at night, and then
200 remotely reprogrammed to a finer temporal resolution (up to one fix every five minutes during daytime and one
201 fix every 15 minutes at night), when the battery charge allowed. Permission to handle the study birds was given
202 by the authority Préfecture Départementale des Deux-Sèvres (Number 2017/1). All applicable French guidelines
203 for the ethical use of animals in research were followed.

204

205 **Data Collection**

206 The birds were recaptured to allow for retrieval of the GPS loggers (CatLog-S2) for downloading of data (Table
207 1). We used cages (height 30 * width 40 * depth 30 cm) positioned near release sites and close to locations
208 where recent partridge presence was reported by stakeholders or fieldworkers. Recaptures began one month after
209 release and were carried out monthly for 3–5 days. The recaptured birds were handled and measured directly at
210 the capture site (no transport). Once the assessment of the measures described below was performed, birds were
211 refitted with a GPS device with a fully charged battery, and released. The total handling time at recapture was
212 12–13 minutes per bird.

213

214 **Individual Traits**

215 Morphometric traits were measured again on individuals recaptured in the cages (n = 16). The ratio of body mass
216 to wing length was determined as a proxy for *wing loading*. Then, we used the handling of the birds as an

217 experimental procedure allowing to measure their reaction to a stressful or risky situation, by assessing the
218 following seven personality traits indicative of birds fearfulness (Møller et al. 2011; Edelaar et al. 2012; Garcia-
219 Longoria et al. 2014): *flight initiation distance (FID)*, *wriggle score*, *feather loss*, *distress call*, *tonic immobility*,
220 *alarm call* and *escape flight distance* (see Online Resource 1, Table S1 for details). All traits were assessed by
221 the same operator to standardize the recapture protocol and limit any bias in measurements.

222 Finally, two proxies of health status were measured. The white cell composition (i.e., lymphocytes,
223 monocytes, eosinophils, heterophils) was assessed from blood smears (see Online Resource 2 for protocol
224 details; see also Hõrak et al. 2004; Biard et al. 2015). The red coloration of the carotenoid-based red skin
225 ornament located behind the eye of the gray partridge was analyzed from photographs (see Online Resource 3
226 for protocol details). Carotenoids are involved in a trade-off between investment in ornamental signaling color
227 and immune function (Møller et al. 2000; Hõrak et al. 2001). Coloration of the carotenoid-based ornaments has
228 thus been described as a reliable proxy of health status (Zuk et al. 1990; Hõrak et al. 2001, 2004; Svobodová et
229 al. 2013). Infected individuals are thus expected to have a less intensive red color because of an increased
230 allocation of carotenoids to the immune response (see Svobodová et al. 2013 for example in gray partridge).

231

232 **Statistical Analyses**

233 *Computation of personality and health status variables*

234 Two principal component analyses (PCA) were performed from the sixteen recaptured individuals: one on the
235 personality traits (flight initiation distance, wriggle score, feather loss, distress call, tonic immobility, alarm call
236 and escape flight distance) and a second on the health status variables (lymphocytes, monocytes, eosinophils,
237 heterophils, and red coloration), to obtain synthetic variables (i.e., the first two axes of each PCA). As only one
238 measure of the health status variables was available for each bird, the data did not account for intra-individual
239 variability. A single measure of personality was available for birds that were recaptured only once (4 of 16
240 individuals). Each personality trait was thus averaged prior to PCA for those birds that were caught several
241 times.

242

243 *Adjustment in use of space*

244 As GPS data often contains erroneous or inaccurate fixes (see Lewis et al. 2007; Bjørneraas et al. 2010), a filter
245 was applied to the data before analysis, that resulted in a reduction of approximately 4% of the dataset and a
246 mean GPS location error of 15 m after filtering (see Harmange et al. 2021). We calculated the distances between

247 each GPS fix (mean number of fixes per bird = 3322; min = 339; max = 11346) and the nearest hedgerow,
248 road/track, woodland, and building for the sixteen individuals. Then, for each individual, each monitoring day
249 (mean duration = 55 days \pm 32 SD), the mean distance between the bird and the four risky features were
250 calculated during the day- and night-time periods. Day- and night-time periods used to compute these distances
251 were defined as follows: from 75 minutes after dawn to 45 minutes before dusk, and from 75 minutes after dusk
252 to 45 minutes before dawn, respectively (see Harmange et al. 2021). The time deviations from dawn and dusk
253 were computed using the *suncalc* package (Agafonkin and Thieurmél 2018). To study the influence of individual
254 traits on the adjustments in use of space in response to risk variation, synthetic dependent variables capturing the
255 magnitude and the sense of the adjustment were needed. Diel adjustments in use of space were thus computed
256 for each individual as the difference in the mean night- less the mean day-time ($\Delta_{\text{night-day}}$) distances to each
257 risky feature, averaged over the days monitored in the study and thus resulting in one synthetic value per bird.

258 Then, we tested the relationship between individual traits (i.e., sex, morphometry, personality, and
259 health status) and the four dependent variables measuring the $\Delta_{\text{night-day}}$ mean distances to the four risky features,
260 using linear models with recaptured partridges as sampling units (n = 16). The independent variables used were
261 *sex*, *wing loading*, *personality* (the first two axes of the PCA represented personality traits), and *health status*
262 (the first two axes of the PCA represented immunity parameters and coloration of the red skin ornament).
263 Models were selected based on Akaike's information criterion corrected for a small sample size (AICc)
264 (Burnham and Anderson 2002). All candidate models derived from a full (including all independent variables) to
265 a null model were considered in the model selection. We calculated the Akaike model weights (ω_i) as support for
266 each model and contrasted weights of each competing model with the best model (i.e., the model with the lowest
267 AICc value) by calculating the evidence ratio (Burnham and Anderson 2002). Competing models with a
268 difference in AICc (ΔAICc) <2 were considered equivalent. As many candidate models were tested (i.e., 64
269 models for each of the four dependent variables), only the top four of the most competitive models (ΔAICc with
270 the best models <4) and the null models are shown in the results.

271 All analyses were performed using R software (R Core Team 2019).

272

273 **RESULTS**

274 **Correlation in Individual Traits**

275 The PCA synthesizing personality traits accounted for 55.6% of the behavioral variability of individuals in the
276 first two dimensions (Fig. 1a; see Table S2 in Online Resource 1 for contributions). The first dimension of the

277 PCA (PC1-personality, accounting for 33.9% of total variance; Table S2) was positively correlated with alarm
278 calls displayed at release (PCA correlation coefficient between axis and variable $r = 0.83$) and the wriggle score
279 ($r = 0.60$), and was negatively correlated with escape distance ($r = -0.71$), tonic immobility ($r = -0.59$) and flight
280 initiation distance ($r = -0.51$). These results suggest a gradient in boldness in individuals: the higher the PC1-
281 personality score, the bolder the behavior of the individual (Fig. 1a). PC2-personality (21.7% of total variance;
282 Table S2) was positively correlated with distress calls displayed when handled ($r = 0.77$) and escape distance (r
283 $= 0.60$).

284 The health status of birds was also assessed using a PCA that accounted for 77.4% of the inter-
285 individual variability in the first two dimensions (Fig. 1b, see Table S3 in Online Resource 1 for contributions).
286 PC1-health status (54.6% of total variance, Table S3) was positively correlated with the proportion of monocytes
287 ($r = 0.89$) and heterophils ($r = 0.85$), and negatively correlated with lymphocytes ($r = -0.85$) and eosinophils ($r =$
288 -0.69), hence representing a gradient of acute immune response (Fig. 1b). The PC2-health status (22.8% of the
289 total variance, Table S3) was positively correlated with the red coloration of carotenoid-based skin ornament ($r =$
290 0.94).

291 No correlation was detected between the principal components of personality traits (PC1 and PC2-
292 personality) and health status (PC1 and PC2-health status) (Table S4 in Online Resource 1).

293

294 **Individual Traits and Adjustments in Use of Space**

295 Model selection showed that individual traits affected the adjustments in use of space relative to risky features
296 (Table 2). Analyses showed that $\Delta_{\text{night-day}}$ distances to hedgerows were positively related to PC1-personality
297 (Table 3): bolder individuals (high PC1-personality score) showed significant greater $\Delta_{\text{night-day}}$ distances to risky
298 hedgerows (Fig. 2a), suggesting that the birds stayed farther from risky features at night than in the day. Based
299 on model estimates (Fig. 2a), bolder individuals moved 127 m (± 7 SE) farther from hedgerows at night than in
300 the day, while shyer individuals moved only 69 m (± 12) farther away. $\Delta_{\text{night-day}}$ distances to hedgerows,
301 roads/tracks, and woodlands were significantly related to PC1-health status (Table 3). Individuals in good health
302 moved at a distance of 124 m (± 8) farther from hedgerows, 173 m (± 32) farther from woodlands and 85 m (± 18)
303 farther from roads at night than during the day (Fig. 2b-d). In contrast, individuals with poorer health moved at
304 only 83 m (± 11) farther from hedgerows at night than during the day, did not change their distance from
305 woodlands day or night, and were closer to roads (by 50 to 110 m) at night than during the day (Fig. 2b-d).

306 No influence was detected for PC2- personality, PC2-health status, sex and wing loading (mean value =
307 2.44 g/mm \pm 0.14 SD) on adjustments in use of space, nor any effect of any individual traits on the adjustment in
308 distances to built-up areas.

309

310 **DISCUSSION**

311 We found inter-individual variability in personality and health status parameters, indicating that individuals in
312 our study population actually differed in their boldness traits and health conditions. Moreover, personality and
313 health status affected adjustments in the use of space in relation to risky habitat features.

314

315 **Inter-individual Variability in Personality and Health Status**

316 Personality traits were reliably identified using the PC1-personality values and varied along a boldness gradient:
317 some individuals appeared to be more aggressive or impulsive as suggested by their strong wriggle behavior
318 when handled, and by the alarm calls they displayed once released (Koolhaas et al. 2007). They also
319 demonstrated higher risk-taking behaviors (lower flight initiation and shorter escape flight distances), consistent
320 with their low tonic immobility, suggesting lower levels of fear and stress (Møller et al. 2011; Edelaar et al.
321 2012). Such associations between personality traits, shown to be repeatable and heritable both in wild-caught and
322 hand-reared birds (e.g. in the great tit [*Parus major*]: Verbeek et al. 1994, 1996; Van Oers et al. 2004a, b), are
323 commonly observed in birds (Sih and Del Giudice 2012; Hall et al. 2015), and may have implications for their
324 survival and reproduction (Smith and Blumstein 2008; Arroyo et al. 2017).

325 Individuals also vary in their immune parameters. Some individuals had higher proportions of
326 heterophils and monocytes, and a low proportion of lymphocytes, suggesting a poor health status. Heterophils
327 are the main granulated leukocytes involved in the acute inflammatory response in Galliformes (Harmon 1998),
328 and are known to increase after a coccidian infection in other birds, such as in the greenfinch (*Chloris chloris*)
329 (Hörak et al. 2004). In birds, their high proportion relative to lymphocytes is also indicative of a high level of
330 long-term stress (Müller et al. 2011; see also Svobodová et al. 2013 for gray partridge). These results are
331 consistent with high proportions of monocytes, which are mainly linked to acute inflammatory responses or
332 chronic diseases (e.g. from bacterial and parasitic infection; Weiss and Wardrop 2010). This suggests that the
333 PC1-health status reliably predicts the intensity of the immune response in these birds. Although a correlation
334 between health status and personality traits of birds may have been expected (Barber and Dingemanse 2010), no
335 such correlation was found here (see Klueen et al. 2014 for similar results in the blue tit *Cyanistes caeruleus*).

336

337

338 **Influence on Adjustments in Use of Space**

339 We showed that birds varied in their adjustment in use of space relative to risky features and that individual traits
340 (personality and health status) may play a role in determining these diel adjustments (see Dunn et al. 2011; and
341 Bonnot et al. 2014 for other examples on the influence of such individual traits on the use of space, in the great
342 tit and roe deer, respectively). Indeed, we found that individuals that were apparently bolder, were located farther
343 from hedgerows at night than during the day. This suggests that bold individuals adjust their use of space in a
344 pattern consistent with avoiding nocturnal carnivores near such habitats, and/or human activity in open areas
345 during the day. This has also been previously documented in several studies on prey species inhabiting
346 agricultural landscapes such as the European rabbit and the roe deer (Moreno et al. 1996; Lone et al. 2017). This
347 could result from the ability of bolder individuals to quickly return to an environment after a disturbance (Van
348 Oers et al. 2004b; Quinn and Cresswell 2005), and to develop routine behaviors (Groothuis and Carere 2005;
349 Carere et al. 2010), favoring greater adjustments in terms of the diel cycle. Overall, these results are supported
350 by Sih et al. (2004), who reported that highly aggressive animals actively cope with environmental challenges,
351 such as the contrasting risks imposed by predators and humans in agricultural landscapes (Moreno et al. 1996;
352 Lone et al. 2017). They are also consistent with the findings reported by Arroyo et al. (2017), who showed that
353 long-term human disturbance can affect the composition of populations of the Montagu's harrier *Circus*
354 *pygargus*, by increasing the proportion of bold individuals. However, it should be noted that the data were
355 collected in an area where the shooting of gray partridges had been suspended (though shooting on other game
356 species was allowed). Therefore, bold individuals might not have survived here without this shooting suspension.
357 Indeed, hunters are reported to harvest particularly bold individuals, as observed in the common pheasant and
358 other game species (Ciuti et al. 2012; Madden and Whiteside 2014), as a result of their escape strategy. Bold
359 individuals are more likely to attempt to escape by flying over hunters and are thus more likely to be shot than
360 shy birds adopting more discrete behaviors such as freezing, running, or flying low to the ground (Robertson et
361 al. 1993; Quinn and Cresswell 2005; Madden and Whiteside 2014).

362 Birds that appeared to be in good health conditions (with low levels of heterophils and monocytes) were
363 located farther from three of the four tested risky features (hedgerows, roads/tracks, and woodlands) at night than
364 during the day. This suggests that healthy individuals might be more inclined to avoid carnivore predation risk at
365 night and human activity in open areas during the day. The gray partridge achieves diel adjustments in use of

366 space by commuting flights between diurnal and nocturnal sites and habitats (Harmange et al. 2021). The
367 energetic cost of short flights is high (see Tatner and Bryant 1986; Nudds and Bryant 2000) and birds in poor
368 health may thus invest more energy in fighting infection, rather than in costly adjustments in use of space
369 (Lindström et al. 2003; Dunn et al. 2011; van Dijk et al. 2015). For example, Kollias et al. (2004) showed that,
370 within 4 days of an infection administered experimentally, the house finch (*Haemorhous mexicanus*)
371 demonstrated a 50% reduction in motor activity. The interplay between parasitism and personality or cognition
372 (Kortet et al. 2010; Ducatez et al. 2020) could also explain such behavior, since individuals with higher
373 exploratory behavior and boldness would be more exposed to parasites and subjected to infection (Wilson et al.
374 1993; Boyer et al. 2010). Despite the absence of a correlation between personality and health in the present
375 study, we cannot exclude the possibility that such interplay may operate over time (see Kortet et al. 2010; Barber
376 and Dingemanse 2010).

377 Our results are however based on 16 recaptured birds out of the 129 GPS-equipped birds. Of the
378 remaining 113 individuals, 91 disappeared few days after release, 7 were predated (fresh carcasses with predator
379 traces), 3 were shot inadvertently despite shooting suspension, 1 was hit by a vehicle, 4 died from an
380 undetermined cause, and 7 were recaptured but had missing data (e.g. unexploitable GPS data). The low
381 recapture rate is consistent with the high mortality rates commonly observed in gamebirds within the first month
382 after of release (Sokos et al. 2008; Rymesova et al. 2013; Madden et al. 2018). Therefore, individual traits were
383 measured on the birds that survived long enough to be recaptured. This implies that (1) our data did not allow us
384 to test or control for intra-individual variability as several individuals were recaptured only once; (2) the sample
385 population may already have been subjected to selection, thus reducing the inter-individual variability in the
386 individual traits and in the behavioral adjustments measured. Further research involving more individuals and
387 based on longitudinal monitoring and measurements of birds, including pre-release assessment of individual
388 traits, should confirm our findings and help to appropriately address the overall inter-individual variability within
389 the released populations and assess its influence on survival.

390

391 **Management Implications**

392 Particular attention should be paid to management and conservation programs that rely on the translocation of
393 captive-bred animals (McDougall et al. 2006; Smith and Blumstein 2008). Captive-bred animals often represent
394 the only opportunity to restore self-sustainable populations, e.g. in conservation reintroductions or restocking
395 game populations (Fischer and Lindenmayer 2000; Sokos et al. 2008; Jule et al. 2008), but the quality of such

396 individuals is in the same time the greatest challenge of translocation success (Griffith et al. 1989; Sokos et al.
397 2008; Champagnon et al. 2012a). Several generations of captivity and inbreeding may contribute to the
398 impoverishment of the variability of immunogenetics (Ewen et al. 2012; Keller et al. 2012) and heritable
399 personality traits, such as risk-taking and exploratory behaviors (Dingemanse et al. 2002; Van Oers et al. 2004b).
400 This jeopardizes the ability of individuals to adapt to novel environmental conditions, and risks the recovery of
401 these vulnerable populations (Ewen et al. 2012; Merrick and Koprowski 2017).

402 Our results emphasize the need for managers to examine and select founder populations meticulously,
403 promoting appropriate management of individual traits (see McDougall et al. 2006; Smith and Blumstein 2008),
404 particularly those related to health and behavior (see also WPA and IUCN 2009; IUCN 2013). This will help to
405 reduce the immunological and behavioral naivety of released individuals (Faria et al. 2010; Tetzlaff et al. 2019).
406 We suggest that effective population management through translocation requires focus on quality (i.e. by
407 favoring individual traits that improve response to risk and thus survival expectancy), rather than merely on the
408 quantity, of released individuals. This includes favoring the translocation of wild-caught individuals when
409 possible (Sokos et al. 2008), or alternatively captive-reared populations promoting parental care that reduces the
410 level of fear of animals compared to artificial rearing (Santilli and Bagliacca 2019), anti-predator training that
411 promotes elicitation of motor behaviors in response to predators (Gaudioso et al. 2011; Sánchez-García et al.
412 2016), minimal human contact increasing the escape and fear-related behaviors to humans (Zaccaroni et al.
413 2007), controlled pre-exposure to pathogens (Faria et al. 2010) and the maintenance of high diversity of
414 immunogenetics improving the response to infection within the captive population (Charpentier et al. 2008).

415

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698 **Figure captions**

699 **Fig. 1** Correlation circles of principal component analyses synthesizing the measures of the partridge personality
700 (a), and health status from immune parameters (b). The inertia of each dimension is reported on the axes.
701 Apparent gradients of boldness (a) and intensity of the immune response (b), suggested by the first axes of
702 PCAs, were added for clarity. Details about personality metrics (Table S1) and variable contributions (Tables S2,
703 S3) are available in Online resource 1

704

705 **Fig. 2** Effect of personality traits (a) and health status (b-d) on the diel adjustments in use of space by the gray
706 partridge, measured as the difference in distance to risky features (i.e., hedgerows, roads/tracks, and woodlands),
707 between night and day ($\Delta_{\text{night-day}}$). Predicted values (\pm SE) derived from linear models (see Table 3) are
708 represented with solid lines with gray envelopes. The apparent gradients of boldness (a) and intensity of the
709 immune response (b-d) suggested by the first axes of PCAs were added to improve clarity

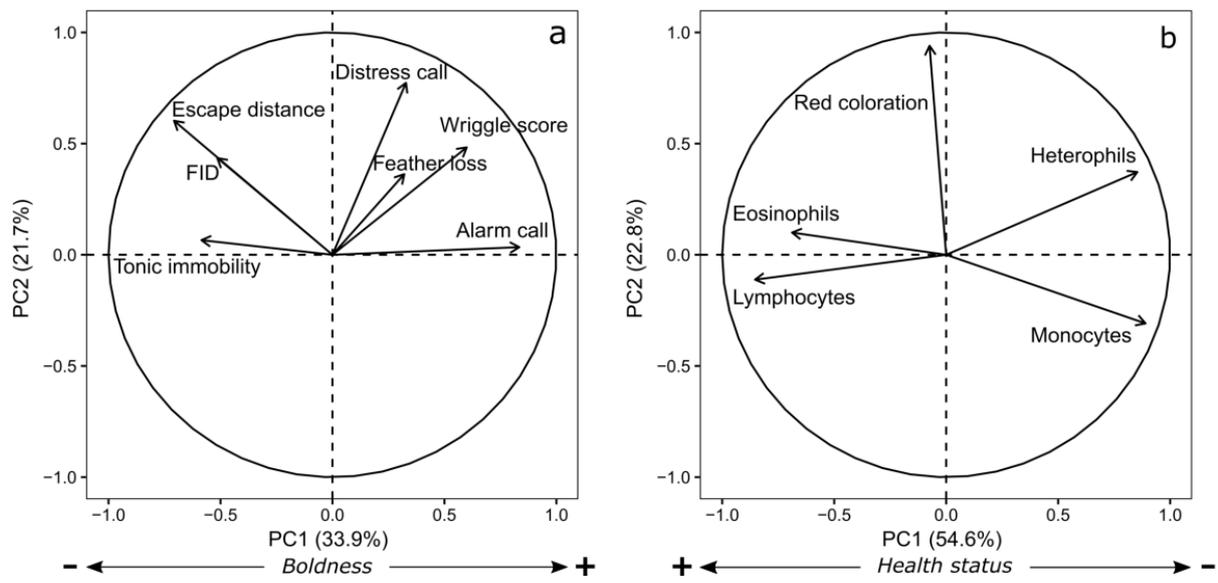


Fig. 1

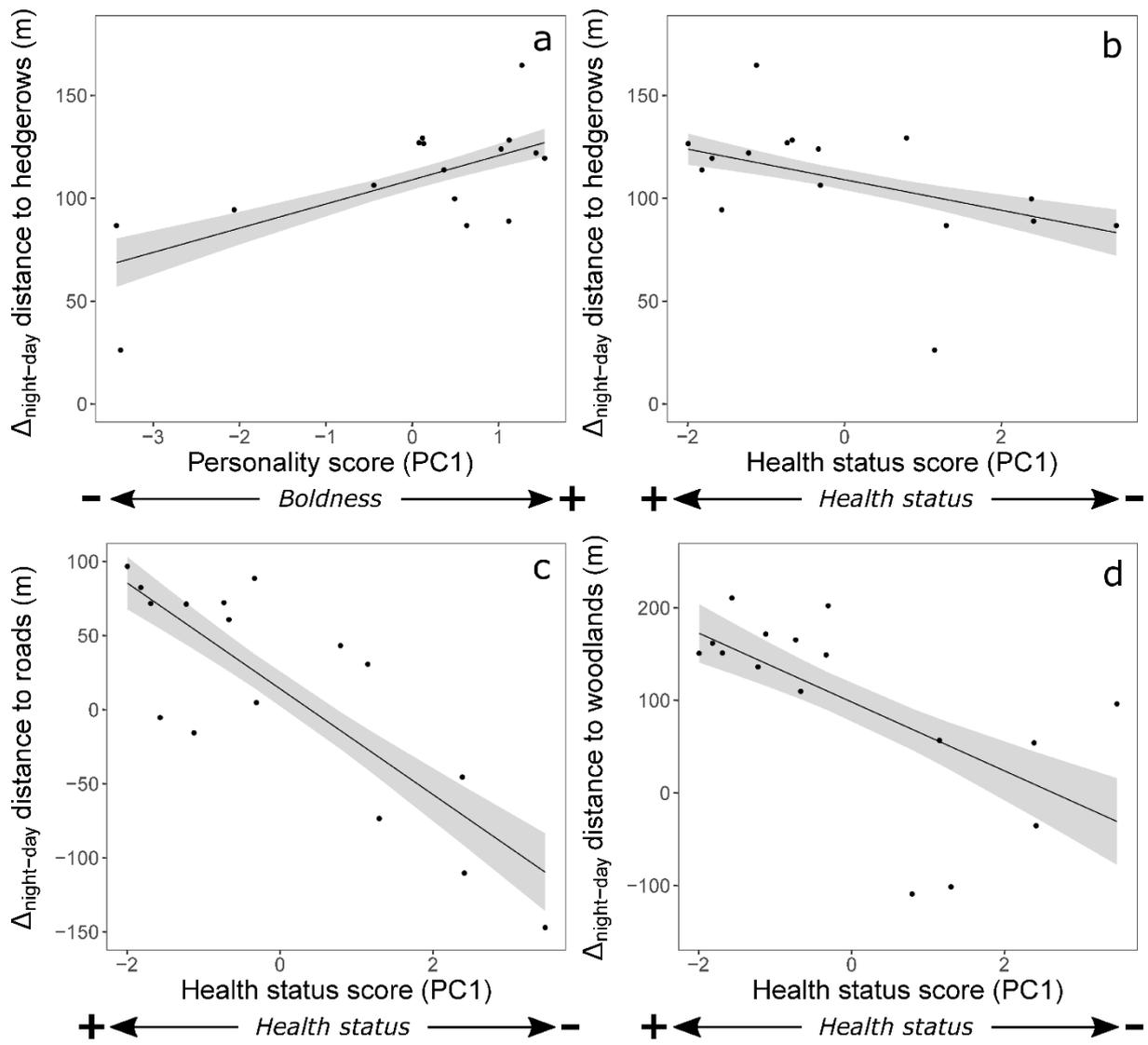


Fig. 2

Table 1 Summary of the total number of released birds, the number of GPS-equipped birds, and the number of recaptured GPS-equipped birds on which individual traits were measured, per release session. The total number of birds are given first, with number of males in brackets.

	Period of release			Total
	2016/12	2017/09	2017/10	
N of birds	131 (66)	98 (48)	81 (40)	310 (154)
N of GPS-equipped birds	63 (57)	36 (17)	30 (15)	129 (89)
N of GPS-equipped birds recaptured	6 (1)	0	10 (6)	16 (7)

Table 2 Statistical support for models testing the effects of individual traits (morphometry, personality (PC1), health status (PC1) and sex) on the adjustments in use of space in relation to risky features (hedgerows, roads / tracks, woodlands, built-up areas). The selection process was based on the Akaike's Information Criterion corrected for small sample size (AICc). The number of parameters (K) is presented together with model weights (ω_i), log likelihood values (LL) and differences in AICc (Δ AICc) in respect of the model with the highest statistical support. Personality (PC1- and PC2-perso) and health status (PC1- and PC2-health) correspond to the scores on the first two axes of the two principal component analyses previously performed. Models selected are represented in bold. Only the top four and the null models are shown (see Table 3 for estimates).

Dependent variables	Candidate models	K	AICc	Δ AICc	ω_i	LL	Evidence ratio
(a) Δ night – day distance to hedgerows	PC1-perso+PC1-health	4	148.18	0	0.35	-68.27	
	PC1-perso+PC1-health+PC2-health	5	150.44	2.27	0.11	-67.22	3.11
	Sex+PC1-perso+PC1-health	5	150.91	2.73	0.09	-67.46	3.92
	PC1-perso	3	150.94	2.77	0.09	-71.47	3.99
	NULL	2	158.25	10.07	0	-76.66	153.70
(b) Δ night – day distance to roads	PC1-health	3	173.22	0	0.46	-82.61	
	Sex+PC1-health	4	176.13	2.91	0.11	-82.25	4.28
	PC1-perso+PC1-health	4	176.74	3.52	0.08	-82.55	5.81
	PC1-health+PC2-perso	4	176.77	3.55	0.08	-82.57	5.90
	NULL	2	187.45	14.23	0	-91.26	1230.28
(c) Δ night – day distance to woodlands	PC1-health	3	191.73	0	0.28	-91.86	
	Wing load+PC1-health	4	192.91	1.18	0.15	-90.64	1.80
	PC1-health+PC2-health	4	193.66	1.93	0.10	-91.01	2.62
	PC1-perso+PC1-health	4	194.46	2.73	0.07	-91.41	3.92
	NULL	2	196.81	5.08	0.02	-95.94	12.68
(d) Δ night – day distance to buildings	PC1-health	3	205.36	0	0.16	-98.68	
	Wing load+PC1-health	4	206.10	0.75	0.11	-97.23	1.45
	NULL	2	206.43	1.07	0.10	-100.75	1.71
	PC1-health+PC2-perso	4	207.62	2.26	0.05	-97.99	3.10
	Sex	3	207.86	2.50	0.05	-99.93	3.49

Table 3 Estimates of the effect of individual traits on the adjustments in use of space in relation to risky features (a: hedgerows, b: roads / tracks, c: woodlands), from linear models previously selected (see Table 2).

Dependent variable	Independent variables	Estimate (\pm SE)	P value	Adj. R²
$\Delta_{\text{night-day}}$ distances to hedges	(intercept)	109.03 (4.79)	<0.01	0.60
	Health status	-7.43 (2.94)	0.03	
	Personality	11.77 (3.15)	<0.01	
$\Delta_{\text{night-day}}$ distances to roads	(intercept)	14.13 (11.30)	0.23	0.64
	Health status	-35.73 (6.84)	<0.01	
$\Delta_{\text{night-day}}$ distances to woodlands	(intercept)	98.25 (20.15)	<0.01	0.36
	Health status	-37.22 (12.19)	<0.01	

Online Resource 1. Additional information and results

Table S1 Behavioral metrics assessed as measures of bird personality (see Møller et al. 2011).

Behavioral metric	Assessment	Mechanism
Flight initiation distance (FID)	Distance at which a bird placed in a cage in an open area composed of bare ground near the capture site, reacted with a take-off attempt to a straight-line approach of the field operator (after 2-min of acclimation). All FID were assessed under clear weather conditions in daylight, by the same operator to standardize the approach speed, the operator dress, and thus limit the detectability bias.	Individuals with shorter FID (i.e., they escape when the predator is closer) are bolder and have a higher risk of being predated (Møller et al. 2008, 2010, Holtmann et al. 2017).
Wriggle score	This scored how much a bird moved during handling: 0 – no movement, 1 – moved rarely, 2 – regularly, 3 – continuously	Individuals that wriggle more are more likely to escape from a predator when captured (Møller et al. 2011).
Feather loss	This scored whether the bird lost feathers during handling (1), or not (0).	Feather loss can advantage a bird caught by a predator, as predator could lose their grip as a result (Møller et al. 2006).
Distress call	This scored whether the bird produced fear screams during handling (1), or not (0).	Birds emitting fear screams could increase their probability of escape once captured, attracting the attention of secondary predators (Møller and Nielsen 2010).
Tonic immobility	Before release, the bird was placed on its back in our flat hand, with a second hand restraining it until it was still. The time between when the second hand was removed, and the bird flew away was recorded. The trial was stopped after a delay of more than 30 s.	The longer the bird stays in the hand, the higher its level of fear (Møller et al. 2011, Edelaar et al. 2012)
Alarm call	This scored whether the bird emitted an alarm call leaving our hand after release (1), or not (0).	Alarm calls could play a role in distracting a predator, thereby decreasing the predation susceptibility of conspecifics, and are expected to be produced by bolder individuals, placing them in a greater immediate risk (Charnov and Krebs 1975, Platzen and Magrath 2004).
Escape flight distance	This is the flight distance achieved post-handling release.	Individuals with a shorter escape flight distance (also called distance fled) have a higher risk of being caught by a predator (Cooper and Blumstein 2015, Tätte et al. 2018).

Table S2 Contributions (%) of variables to the first three dimensions of the principal component analysis carried out on personality traits (see Fig. 1a). The eigen values and the percentage of total variance explained by each dimension is given in brackets.

Variable	Dimension 1 (2.37; 33.91%)	Dimension 2 (1.52; 21.73%)	Dimension 3 (1.28; 18.24%)
Flight initiation distance	11.13	12.45	16.40
Wriggle score	15.15	15.34	6.74
Feather loss	4.33	8.65	49.99
Distress call	4.54	39.31	1.40
Tonic immobility	14.42	0.29	10.15
Alarm call	29.34	0.08	7.66
Escape distance	21.08	23.89	7.67

Table S3 Contributions (%) of variables to the first three dimensions of the principal component analysis carried out on health status (immune parameters, see Fig. 1b). The eigen values and the

Variable	Dimension 1 (2.73; 54.58%)	Dimension 2 (1.14; 22.79%)	Dimension 3 (0.91; 18.12%)
Red coloration	0.20	77.52	8.97
Heterophils	26.70	12.16	6.05
Eosinophils	17.37	0.88	54.44
Monocytes	29.04	8.35	3.54
Lymphocytes	26.69	1.10	26.99

percentage of total variance explained by each dimension is given in brackets.

Table S4 Matrix of Spearman's correlation coefficients (p-values) between the first two axes of each principal component analysis carried out on personality (PC1- and PC2-perso) and health status (PC1 and PC2-health).

	PC1-perso	PC2-perso	PC1-health	PC2-health
PC1-perso	-	-	-	-
PC2-perso	0.121 (0.66)	-	-	-
PC1-health	-0.197 (0.46)	0.006 (0.99)	-	-
PC2-health	-0.253 (0.34)	0.003 (1.00)	0.006 (0.99)	-

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Online Resource 2. Protocol for the calculation of white cell proportions from gray partridge blood smears

A blood smear was collected from each recaptured bird, to determine the health status of the birds through white cell counts (Zuk et al. 1990, Hůrak et al. 2001, Svobodová et al. 2013, Biard et al. 2015). Birds were placed on their backs, with one wing spread, and a drop of blood was collected through a capillary from the brachial vein and deposited on a glass slide. Another slide was used as a spreader; it was placed at a 45° angle, pushed back towards the blood drop, and then pushed across the slide to spread the drop all along the slide.

Blood smears were fixed in the laboratory by submergence in a methanol bath for five to seven minutes. The smears were stained with a Giemsa solution diluted at 1/20 for 40 minutes. Finally, smear slices were rinsed several times with neutral pH water and left to air dry (Biard et al. 2010).

The white cell count was determined using immersion oil under a microscope with a 1000 × magnification. The number of leukocytes (distinguishing the heterophils, monocytes, lymphocytes, eosinophils, basophils; Campbell and Dein 1984, Weiss and Wardrop 2010) were reported, counted per reference number of 10000 erythrocytes. If the total number of leukocytes was lower than 100, the counting was continued until the number of leukocytes reached 100. The number of each cell type needed to reach this level of leukocyte count was also reported.

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Online Resource 3. Protocol for the colorimetry calculation of carotenoid-based red skin ornament behind the eye of gray partridge

Each recaptured bird was photographed (Fujifilm FinePix S4000) to assess the coloration of the carotenoid-based red skin ornament behind the eye, as an indicator of health status (Svobodová et al. 2013). Birds were placed outside, out of direct sun exposure, and their right-side profile was photographed from a distance of approximately 50 cm from the camera lens. The same gray standard reference was placed near birds in each picture (thus, in the same exposure and at the same distance from the lens), to standardize coloration measurements between pictures.

Pictures were analyzed using Adobe Photoshop© software, following the method of Lopez-Antia et al. (2013). An area of 0.20*0.20 cm was selected on the red skin ornament patch. The mean intensity values of red, green and blue (or RGB components) were calculated for all pixels contained within this area (Lopez-Antia et al. 2013). These values were corrected using the average RGB values from an area of the same dimension (0.20*0.20 cm) and in the same light exposure conditions on the gray reference to standardize color measurements between pictures (Lopez-Antia et al. 2013).

Lastly, the intensity of the carotenoid-based red skin ornament was calculated as the R value divided by the average values of R, G and B (see Lopez-Antia et al. 2013).

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