European Journal of Wildlife Research (2021) 67:81
https://doi.org/10.1007/s10344-021-01526-x

ORIGINAL ARTICLE

Linking personality and health to use of space in the gray partridge: perspectives for management

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Received: 23 March 2021 / Revised: 14 June 2021 / Accepted: 22 July 2021

Abstract

Behavioral adjustments are of critical importance for the survival of animals when exposed to risk and resource variations in their environment. Moving to safer habitats allows prey to reduce the risk of mortality triggered by predation. This response has been well studied at the population level to assist in identifying key habitat components for wildlife conservation. However, while individuals may differ in their response to risk and thus in their survival expectancy, the determinants of individual adjustments in space and habitat use are largely unknown in management and conservation studies. Using GPS monitoring, we investigated the relationship between individual traits (morphometry, personality, health status) and adjustments in the use of space relative to risky features (hedgerows, roads/tracks, woodlands, built-up areas) with regard to predation risk. We used the gray partridge (*Perdix perdix*) as a study model (captive-reared birds released into the farmlands). During the diel cycle, predation risk mainly occurs by carnivores at night, whereas human hunting pressure occurs during the day. We found that personality and health status had an effect on adjustments in the use of space as response to risky features. At night, when carnivore activity is expected to be high, bolder individuals were farther from hedgerows relative to the day. Similarly, individuals in good health were located farther from hedgerows, roads/tracks, and woodland at night relative to the day. We discuss the need for better consideration of individual traits in management and conservation programs, with a particular focus on recovery programs that rely on translocation of captive-reared individuals.

Keywords Behavioral adjustment · Gray partridge · Health status · Personality · Space use · Wildlife management

Introduction

Animals adjust their behavior in response to the spatial and temporal variations in resource availability and predation risk (Lima and Dill 1990; Johnson et al. 1992; Lima and Bednekoff 1999). Adjustments in space and habitat use are among the most commonly studied responses that allow prey to reduce their immediate mortality risk from predators, by moving toward safer areas or habitats (Laundré et al. 2001; Fortin et al. 2005; Tolon et al. 2009; Lone et al. 2015). However, these responses may become particularly complex in human-dominated landscapes, where human disturbance may conflict with risks imposed by non-human predators (Lone et al. 2014, 2017; Bonnot et al. 2020). For example, some prey living in heterogeneous landscapes, such as the European rabbit (*Oryctolagus cuniculus*) and the roe deer (*Capreolus capreolus*), shift their behavior patterns during the day and night in response to variation in risk. They use open habitats that offer better detection and escape from nocturnal carnivores at night and shift to the opposite more

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vegetated habitats during the day, which provide shelter from human disturbance and/or diurnal predators (Moreno et al. 1996; Bonnot et al. 2014; Lone et al. 2017). Similar patterns have also been found in gamebirds, such as the gray partridge (Harmange et al. 2021).

Individuals within a population may however show a significant variation in their perception of, and response to, dangerous situations, depending on their phenotypes (Sih and Del Giudice 2012; Bonnot et al. 2014). This may result in between-individual differences in survival (Ciuti et al. 2012; Lone et al. 2015). However, little is known about the between-individual differences in how space is used and what determines these differences. Individual traits may influence the movement-related decision-making of individuals or their ability to move, thus affecting the use of space by several mechanisms (Nathan et al. 2008). First, the internal state of animals (i.e., the physiological and neurological states that affect motivation and readiness to move, Nathan et al. 2008) depends on personality traits that influence their propensity to take risks and then their fitness (Both et al. 2005; Réale et al. 2007; Smith and Blumstein 2008; Sih et al. 2012). Personality has been defined as correlated behavioral traits within individuals, usually related to boldness, aggressiveness, activity and exploratory tendency and is commonly expressed as a bold/shy gradient (Sih and Del Giudice 2012). Bolder individuals are often more aggressive and often engage in risk-taking behaviors, such as exploring novel environments or returning to disturbed areas faster than shy individuals (Verbeek et al. 1994; Van Oers et al. 2004a, b), thereby increasing their mortality risk (Van Oers et al. 2004a; Smith and Blumstein 2008). Secondly, morphometric traits may constrain motion capacity (i.e., the biomechanical properties that affect the ability to execute movement, Nathan et al. 2008). For instance, increased wing loading (or body mass) in birds impairs flight abilities such as maneuverability (Dietz et al. 2007; van den Hout et al. 2010), as well as take-off velocity and angle (Kullberg et al. 1996), which alters escape behavior (Gosler et al. 1995; Lindström et al. 2003; Møller 2015). Thirdly, health status may interfere with navigation capacity (i.e., the ability to orient and select where and/or when to move, Nathan et al. 2008). Illness and increased allocation of energy to immune function in infected individuals may reduce the locomotion abilities (Moore 2002; Lindström et al. 2003). Despite calls to integrate such individual variability into conservation and management schemes (Watters and Meehan 2007; Smith and Blumstein 2008; Caro and Sherman 2012; Berger-Tal and Saltz 2014), this has been seldom incorporated to date (see Merrick and Koprowski 2017).

It is of particular interest to address these issues in game species, for which management strategies often rely on the translocation of captive-reared animals (Griffith et al. 1989; Laikre et al. 2006; Sokos et al. 2008; Champagnon et al. 2012a). Animals raised in captivity usually show low survival expectancy after release, which is mainly ascribed to predation. Indeed, mortality rates 1 month after release can be as high as 81% in *Phasianus colchicus* (Hessler et al. 1970), 63–94% in *Alectoris rufa* (Gortázar et al. 2000), 63–95% in *Alectoris graeca* (Dessì-Fulgheri et al. 2001), or 73–90% in *Perdix perdix* (Rymesova et al. 2013). The captive-reared origin of individuals has been viewed as a major cause of failures in restoring self-sustainable populations in game species (Griffith et al. 1989; Sokos et al. 2008), because such animals often undergo multiple alterations in traits related to anti-predator behavior, such as morphology and/or physiology, which affect their ability to escape from predators (Putaala and Hissa 1995; Putaala et al. 1997; van Heezik et al. 1999; Rantanen et al. 2010; Champagnon et al. 2012b).

The gray partridge (*Perdix perdix*) is an iconic gamebird living in farmland landscapes in Europe. However, agricultural intensification has resulted in reduced reproductive success for this species (Potts 1986; Kuijper et al. 2009; Gée et al. 2018). Populations have now reached such a low abundance in many areas and even gone locally extinct (Aebischer and Kavanagh 1997; Chamberlain and Fuller 2000; Comolet-Tirman et al. 2015; Harmange et al. 2019), that population persistence relies on releasing millions of captive-reared birds per year (e.g., 2 million individuals per year in France in Bro 2016; see also Buner et al. 2011; Bro and Crosnier 2012). In most cases, these programs have failed to help population recovery (Bro and Mayot 2006; Buner 2009; Jenny 2015; Harmange et al. 2019). Increased predation and shooting pressure have been identified as two of the main proximal causes for the decline of partridges over the last decades (Kuijper et al. 2009; Aebischer and Ewald 2012). However, these act in contrasting ways: predation mainly occurs at night on birds located closer to roads or tracks, while birds that are killed by hunters during the day are located in areas farther from hedgerows (i.e., in more open areas) during daytime (Harmange et al. 2021). Such contrasting pressures should result in a partitioning in the use of space between day and night (Moreno et al. 1996; Monterroso et al. 2013, 2014; Lone et al. 2014, 2017), but whether and how individual traits may affect behavioral adjustments remains unknown in the context of management (see Merrick and Koprowski 2017).

In this study, we investigated the relationship between individual traits (morphometry, personality, and health status) and individual response to risk across the diel cycle. We did this by monitoring released partridges equipped with GPS devices, allowing to correlate individual traits to use of space. Although naïve at release, we already showed that captive-reared partridges are able to adjust to some extent their use of space in ways consistent with a reduction of risk from nocturnal carnivores at night and of human-induced disturbance and/or raptor predation risk during daytime (Harmange et al. 2021). In particular, landscape features such as woodlands and built-up areas, which are predator reservoirs, and hedgerows and roads, which are predator corridors (Pereira and Rodríguez 2010; Krauze-Gryz et al. 2012; Bischof et al. 2019; Pita et al. 2020), present a high risk to partridges. We therefore assume that distance to risky landscape features may be a reasonable proxy of risk-taking behavior and used these distances to estimate to what extent individual partridges adjust their use of space in response to the spatial variation in risks between day and night. We thus contrasted the average distance to risk-related features between the night and day by calculating difference in the mean nocturnal less the mean diurnal distances (following Harmange et al. 2021). A positive difference would indicate high levels of behavioral adjustment, that is avoidance of features with high risk at night and greater proximity to shelter during daytime, in response to human disturbance and diurnal birds of prey (Moreno et al. 1996; Lone et al. 2017), or food-rich habitats (e.g., roadside habitats: Hopwood 2008; von der Lippe et al. 2013). We predicted that bolder individuals would adjust better to such contrasting environmental pressures because of their capacity for rapid exploration (Verbeek et al. 1994; Van Oers et al. 2004a; Fucikova et al. 2009), their fast decision-making ability in a risky situation (Burns and Rodd 2008; Sih and Del Giudice 2012), their ability to return faster to a place after a disturbance (Van Oers et al. 2004a, b; Quinn and Cresswell 2005), and their ability to adopt routine behaviors (Groothuis and Carere 2005). Boldness was measured through behaviors indicative of birds' fearfulness when handled (Edelaar et al. 2012; Garcia-Longoria et al. 2014). Because high investment in the immune function is often associated with reduction in the locomotion abilities, birds with low health conditions were expected to be less mobile and thus to adjust their use of space less than healthy birds. Finally, individuals with low wing loading were expected to adjust better because of their better flying ability. As the gray partridge is a gregarious species in winter (Beani and Dessì-Fulgheri 1986), we did not expect a strong difference in spatial adjustment between sexes.

Material and methods

Study area

The study was conducted on the long-term socio-ecological research (LTSER) platform "Zone Atelier Plaine & Val de Sèvre", *Département des* Deux-Sèvres, in Western France. Study area covers 435 km^2, which is characterized by intensive cereal production. Land-cover use has been surveyed annually since 1994 and is represented by winter cereals (41.5%, mean value calculated over the years 2009–2016), sunflower (10.4%), corn (9.6%), rape (8.3%), meadows (13.5%), woodlands (2.9%), and built-up areas (9.8%) (Bretagnolle et al. 2018). The densities of hedgerows and roads/tracks are respectively 34 and 50 m/ha. In the study area, the main predators of partridges are mammalian carnivores including the red fox *Vulpes vulpes*, mustelids, and the domestic cat *Felis catus*, and to a lesser extent, raptors mainly represented by the hen harrier *Circus cyaneus*.

The population density of gray partridge was very low during the years in which the study was conducted (Harmange et al. 2019). Important annual releases of captive-reared birds are carried out by hunter associations (around 250 birds per commune, see Harmange et al. 2019). Hunting activity occurs twice a week on Thursdays and Sundays in the LTSER area (Casas et al. 2009) during daylight hours (from 1 h before sunrise to 1 h after sunset). While the hunting season for partridges starts in mid-September and ends in mid-November, disturbance from hunting extends for longer because of shooting of other game species such as the brown hare (*Lepus europaeus*) and the common pheasant (*Phasianus colchicus*). Although shooting of the gray partridge had been suspended for 3 years at the release site, shooting of the red-legged partridge and other game species was still allowed.

GPS monitoring

Five-month old captive-reared gray partridges were released into the area of the Communal Hunting Society of Marigny. Released birds were raised in a commercial game farm following a standard game-rearing method (Sokos et al. 2008): the rearing farm receives 1-day-old chicks from an egg production farm (around 30 generations bred in captivity). Chicks are then artificially reared using brooders without parents. Three sessions of releases were carried out (mid-December 2016, mid-September 2017, and late October 2017; see Table 1), following the same protocol: partridges were transported by car from the rearing farm to the release sites (transportation time of ca. 40 min), in cardboard boxes of 8 individuals, separating the males and females. Flocks of 12–16 individuals were then released (with the same proportion of each sex), 6–8 of whom were equipped with a GPS device. The birds were left in acclimation pens of approximately 5 m^2 for 5 days. Prior to placement in acclimation pens, birds were weighed using a spring scale (Pesola 500 g, accuracy: ± 5 g), measured (wing length, using a ruler, accuracy: ± 1 mm), sexed, ringed (with colored and numbered metal gamebird rings), and fitted using GPS loggers (CatLog-S2, Catnip Technologies Ltd, Hong Kong). These loggers were placed on the breast of the bird using a necklace. Other birds were fitted using better performing but more expensive GPS devices allowing for remote data transmission (5 units of UvA-BiTS GPS-transmitters, www.uva-bits.nl, Bouten et al. 2013, in 2016; and 2 units of Milsar's GsmRadioTag-S9, www.milsar.com, in 2017). These GPS transmitters were fitted onto the back using a Teflon harness (Table 1). The average handling time was 3–4 min per bird. The GPS loggers (CatLog-S2) were turned on at release and locations recorded as one fix every 15 min during daytime and one fix per hour at night. GPS transmitters were initially

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 is given first, with the 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)

programmed to record one fix per 10 min during daytime and one fix every 30 min at night and then remotely reprogrammed to a finer temporal resolution (up to one fix every 5 min during daytime and one fix every 15 min at night), when the battery charge allowed. Permission to handle the study birds was given by the authority Préfecture Départementale des Deux-Sèvres (Number 2017/1). All applicable French guidelines for the ethical use of animals in the research were followed.

Data collection

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

Individual traits

Morphometric traits were measured again on individuals recaptured in the cages ($n = 16$). The ratio of body mass to wing length was determined as a proxy for *wing loading*. Then, we used the handling of the birds as an experimental procedure allowing to measure their reaction to a stressful or risky situation, by assessing the following seven personality traits indicative of birds' fearfulness (Møller et al. 2011; Edelaar et al. 2012; Garcia-Longoria et al. 2014): *flight initiation distance (FID), wriggle score*, *feather loss*, *distress call*, *tonic immobility*, *alarm call*, and *escape flight distance* (see Online Resource 1, Table S1 for details). All traits were assessed by the same operator to standardize the recapture protocol and limit any bias in measurements.

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

Statistical analyses

Computation of personality and health status variables

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

Adjustment in the use of space

As GPS data often contains erroneous or inaccurate fixes (see Lewis et al. 2007; Bjørneraas et al. 2010), a filter was applied to the data before analysis, that resulted in a reduction of approximately 4% of the dataset and a mean GPS location error of 15 m after filtering (see Harmange et al. 2021). We calculated the distances between each GPS fix (mean number of fixes per bird = 3322; min = 339; max = 11,346) and the nearest hedgerow, road/track, woodland, and building for the sixteen individuals. Then, for each individual, each monitoring day (mean duration = 55 days ± 32 SD), the mean distance between the bird and the four risky features were calculated during the day- and night-time periods. Day- and night-time periods used to compute these distances were defined as follows: from 75 min after dawn to 45 min before dusk and from 75 min after dusk to 45 min before dawn, respectively (see Harmange et al. 2021). The time deviations from dawn and dusk were computed using the *suncalc* package (Agafonkin and Thieurmel 2018). To study the influence of individual traits on the adjustments in the use of space in response to risk variation, synthetic dependent variables capturing the magnitude and the sense of the adjustment were needed. Diel adjustments in the use of space were thus computed for each individual as the difference in the mean night- less the mean day-time ($\Delta_{\text{night–day}}$) distances to each risky feature, averaged over the days monitored in the study and thus resulting in one synthetic value per bird.

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

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

Results

Correlation in individual traits

The PCA synthetizing personality traits accounted for 55.6% of the behavioral variability of individuals in the first two dimensions (Fig. 1a; see Table S2 in Online Resource 1 for contributions). The first dimension of the PCA (PC1-personality, accounting for 33.9% of total variance; Table S2) was positively correlated with alarm calls displayed at release (PCA correlation coefficient between axis and variable $r=0.83$) and the wriggle score ($r=0.60$), and was negatively correlated with escape

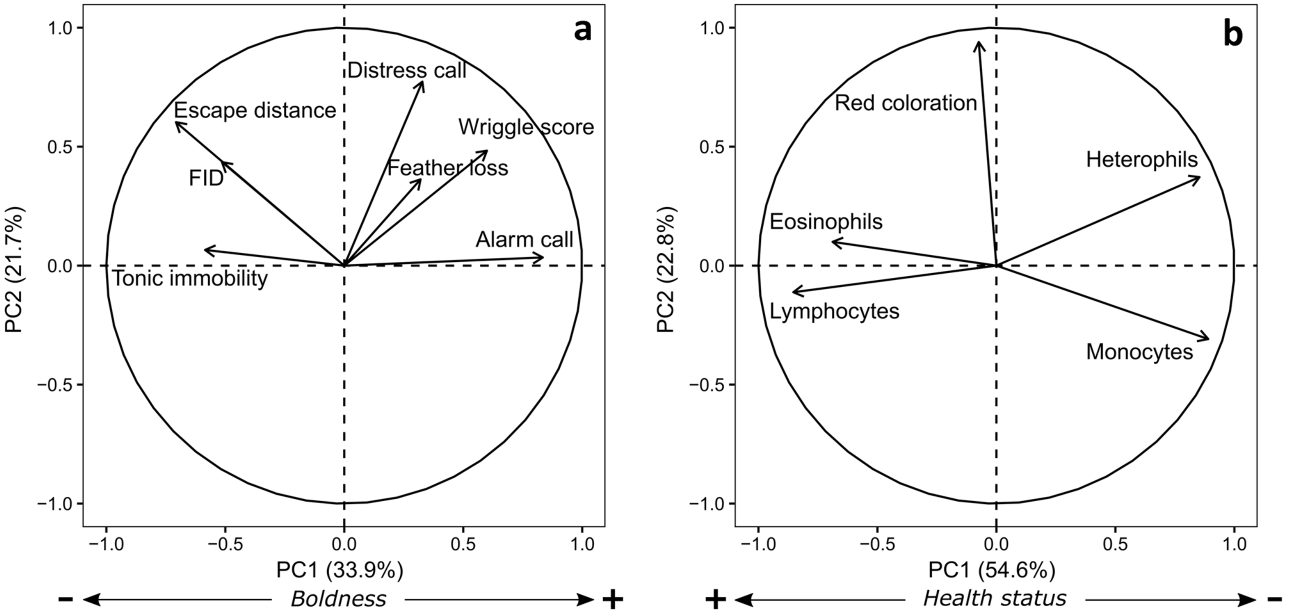

Fig. 1 Correlation circles of principal component analyses synthetizing the measures of the partridge personality **a** and health status from immune parameters **b**. The inertia of each dimension is reported on the axes. Apparent gradients of boldness **a** and intensity of the immune response **b**,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

distance ($r = -0.71$), tonic immobility ($r = -0.59$) and flight initiation distance ($r = -0.51$). These results suggest a gradient in boldness in individuals: the higher the PC1-personality score, the bolder the behavior of the individual (Fig. 1a). PC2-personality (21.7% of total variance; Table S2) was positively correlated with distress calls displayed when handled ($r = 0.77$) and escape distance ($r = 0.60$).

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

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

Individual traits and adjustments in the use of space

Model selection showed that individual traits affected the adjustments in the use of space relative to risky features (Table 2). Analyses showed that $\Delta_{\text{night–day}}$ distances to hedgerows were positively related to PC1-personality (Table 3): bolder individuals (high PC1-personality score) showed significant greater $\Delta_{\text{night–day}}$ distances to risky hedgerows (Fig. 2a), suggesting that the birds stayed farther from risky features at night than in the day. Based on model estimates (Fig. 2a), bolder individuals moved 127 m (± 7 SE) farther from hedgerows at night than in the day, while shyer individuals moved only 69 m (± 12) farther

Table 2 Statistical support for models testing the effects of individual traits (morphometry, personality (PC1), health status (PC1) and sex) on the adjustments in the 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 (ΔAICc) 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) $\Delta_{\text{night–day}}$ 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) $\Delta_{\text{night–day}}$ 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) $\Delta_{\text{night–day}}$ 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) $\Delta_{\text{night–day}}$ 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 the 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 (± SE)	*P* value	Adj. R^2
$\Delta_{night–day}$ distances to hedges				0.60
	(Intercept)	109.03 (4.79)	< 0.01	
	Health status	− 7.43 (2.94)	0.03	
	Personality	11.77 (3.15)	< 0.01	
$\Delta_{night–day}$ distances to roads				0.64
	(Intercept)	14.13 (11.30)	0.23	
	Health status	− 35.73 (6.84)	< 0.01	
$\Delta_{night–day}$ distances to woodlands				0.36
	(Intercept)	98.25 (20.15)	< 0.01	
	Health status	− 37.22 (12.19)	< 0.01	

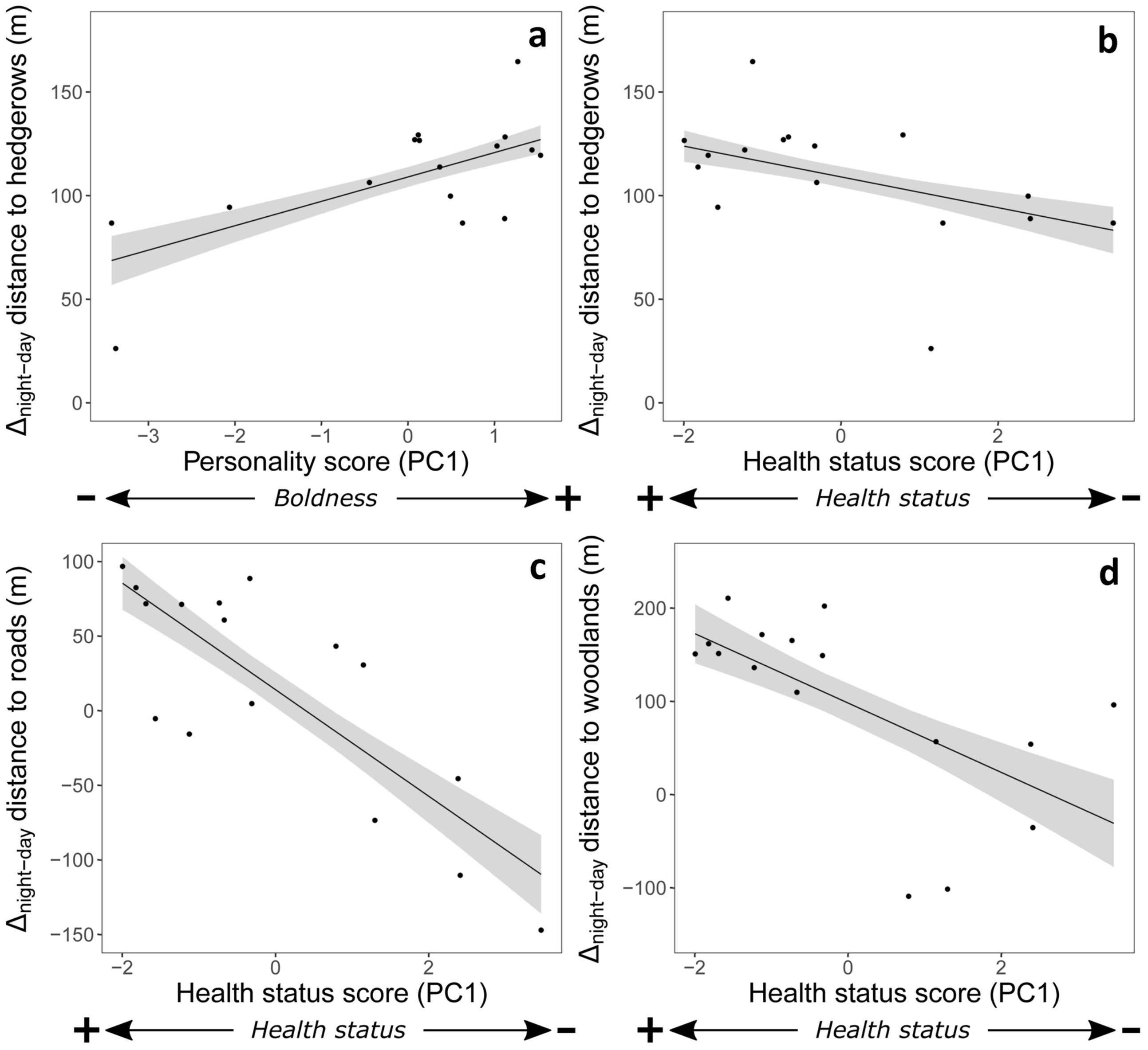

Fig. 2 Effect of personality traits **a** and health status **b**–**d** on the diel adjustments in the use of space by the gray partridge, measured as the difference in distance to risky features (i.e., hedgerows, roads/tracks, and woodlands), between night and day ($\Delta_{night–day}$). Predicted values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

away. $\Delta_{\text{night–day}}$ distances to hedgerows, roads/tracks, and woodlands were significantly related to PC1-health status (Table 3). Individuals in good health moved at a distance of 124 m (± 8) farther from hedgerows, 173 m (± 32) farther from woodlands, and 85 m (± 18) farther from roads at night than during the day (Fig. 2b–d). In contrast, individuals with poorer health moved at only 83 m (± 11) farther from hedgerows at night than during the day, did not change their distance from woodlands day or night, and were closer to roads (by 50 to 110 m) at night than during the day (Fig. 2b–d).

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

Discussion

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

Inter-individual variability in personality and health status

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

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

Influence on adjustments in the use of space

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

2012; Madden and Whiteside 2014), as a result of their escape strategy. Bold individuals are more likely to attempt to escape by flying over hunters and are thus more likely to be shot than shy birds adopting more discrete behaviors such as freezing, running, or flying low to the ground (Robertson et al. 1993; Quinn and Cresswell 2005; Madden and Whiteside 2014).

Birds that appeared to be in good health conditions (with low levels of heterophils and monocytes) were located farther from three of the four tested risky features (hedgerows, roads/tracks, and woodlands) at night than during the day. This suggests that healthy individuals might be more inclined to avoid carnivore predation risk at night and human activity in open areas during the day. The gray partridge achieves diel adjustments in the use of space by commuting flights between diurnal and nocturnal sites and habitats (Harmange et al. 2021). The energetic cost of short flights is high (see Tatner and Bryant 1986; Nudds and Bryant 2000), and birds in poor health may thus invest more energy in fighting infection, rather than in costly adjustments in the use of space (Lindström et al. 2003; Dunn et al. 2011; van Dijk et al. 2015). For example, Kollias et al. (2004) showed that, within 4 days of an infection administered experimentally, the house finch (*Haemorhous mexicanus*) demonstrated a 50% reduction in motor activity. The interplay between parasitism and personality or cognition (Kortet et al. 2010; Ducatez et al. 2020) could also explain such behavior, since individuals with higher exploratory behavior and boldness would be more exposed to parasites and subjected to infection (Wilson et al. 1993; Boyer et al. 2010). Despite the absence of a correlation between personality and health in the present study, we cannot exclude the possibility that such interplay may operate over time (see Kortet et al. 2010; Barber and Dingemanse 2010).

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

Management implications

Particular attention should be paid to management and conservation programs that rely on the translocation of captive-bred animals (McDougall et al. 2006; Smith and Blumstein 2008). Captive-bred animals often represent the only opportunity to restore self-sustainable populations, e.g., in conservation reintroductions or restocking game populations (Fischer and Lindenmayer 2000; Sokos et al. 2008; Jule et al. 2008), but the quality of such individuals is in the same time the greatest challenge of translocation success (Griffith et al. 1989; Sokos et al. 2008; Champagnon et al. 2012a). Several generations of captivity and inbreeding may contribute to the impoverishment of the variability of immunogenetics (Ewen et al. 2012; Keller et al. 2012) and heritable personality traits, such as risk-taking and exploratory behaviors (Dingemanse et al. 2002; Van Oers et al. 2004b). This jeopardizes the ability of individuals to adapt to novel environmental conditions and risks the recovery of these vulnerable populations (Ewen et al. 2012; Merrick and Koprowski 2017).

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

Supplementary information The online version contains supplementary material available at https://doi.org/10.1007/s10344-021-01526-x.

Acknowledgements We owe special thanks for the valuable assistance received from T. Rinaud, A. Villers, M. Souchet, C. Palma, and N. Chabaud in the release, monitoring, and recapture of the partridges, and to T. Rinaud, M. Crépin, and F. Derouin Tochon for the preparation and analyses of blood smears and partridge coloration. We thank all the fieldworkers who contributed to data collection, especially R. Bonnet, P. Lagrange, J-B. Perrotin, G. Lemonnier, J. Léauté, P. Harmange, T. Joubin, and M. Saillard. We also thank N. Aebischer, E. Bro, D. Fortin, R. Julliard and two anonymous reviewers for their valuable comments on the manuscript. Finally, we thank the Fédération Départementale 79 and the Communal Hunting Society of Marigny for their support.

Funding This work was supported by the Fédération Nationale des Chasseurs (grant number FNC-PSN-PR15-2014) and the French National Center for Scientific Research (CNRS).

Availability of data and material The datasets analyzed during the current study are available in the Open Science Framework repository, https://dx.doi.org/10.17605/OSF.IO/G6PQV.

Code availability The code associated with this manuscript is available in the same repository as the data.

Declarations

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

Conflict of interest The authors declare no competing interests.

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