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Diet diversity, individual heterozygosity and habitat heterogeneity influence health parameters in Eurasian Kestrels (*Falco tinnunculus*)

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The loss of habitat heterogeneity due to agricultural intensification has led to a global decline in farmland birds. Among them is the Eurasian Kestrel *Falco tinnunculus*, which occupies high trophic levels and may be adversely affected by reduced food quantity or quality and consequent health impacts. In this study, we investigate the effects of habitat heterogeneity, individual heterozygosity and diet diversity on five different health indices (integument coloration, dietary antioxidants, haematocrit, body condition and parasite infection). The study was conducted in farmland areas of western Finland during a year of exceptionally low vole abundance. We found no obvious relationship between diet diversity and habitat heterogeneity. An interaction between diet diversity and individual heterozygosity in females suggested that diet specialists were able to maintain more intensely coloured integuments only if they had higher genetic diversity. In addition, more heterozygous females were less likely to be infected with *Haemoproteus* than females with lower individual genetic diversity. Finally, specialist males with lower diet diversity had higher body condition than males with a more generalist diet. Our results suggest that variation in individual quality and foraging ecology should be considered in conjunction with spatial variation in habitat heterogeneity to understand sex-specific variation in kestrel health. These findings add to a better understanding of the mechanisms linking land-use change to health indices in a common avian predator, which can be used as a health sentinel in European agroecosystems.

Keywords: agricultural intensification, dietary antioxidants, farmland birds, individual quality, multiple health indices.

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Globally, large parts of the land surface have been converted from natural landscapes to intensive silvicultural and agricultural areas (Foley *et al.* 2005) with an ongoing intensification of land use in recent decades (Rudel *et al.* 2009). This intensification is aimed at increasing harvests, by applying

fertilizers and pesticides and creating large monocultural fields (Stoate *et al.* 2001, Tscharntke *et al.* 2005). These practices are accompanied by an overall decline in habitat quality characterized by increasing homogenization in agricultural habitats (Lindenmayer *et al.* 2012).

Habitat homogenization may lower resource availability for birds, for example with respect to nesting habitat and food availability, such as through loss of non-cultivated elements like hedges and fallows, leading to population declines in farmland birds (Hart *et al.* 2006, Guerrero *et al.* 2012, Traba & Morales 2019, Rigal *et al.* 2023). Limited nesting habitat and food supply can result in increased inter- and intraspecific competition (Korpimäki 1987, Gustafsson 1988, Rosvall 2008). Lowered and unpredictable food availability can decrease foraging efficiency – for example through increased foraging time, longer foraging distance and less time allocated for self-maintenance (Monaghan *et al.* 1994, Cunningham *et al.* 2021). These constraints may lower body condition (Kitaysky *et al.* 1999, Santangeli *et al.* 2012, Almasi *et al.* 2015) and weaken the immune system of birds (Hegemann *et al.* 2013) which, in turn, can have population-level consequences (Paquette *et al.* 2014).

The Eurasian Kestrel *Falco tinnunculus* (hereafter 'kestrels') is a declining farmland bird species in Europe (24% population decline between 1980 and 2016; Pan-European Common Bird Monitoring Scheme PECBMS: https://pecbms.info/). The causes of this decline remain poorly understood and are probably multi-factorial, but land-use changes seem to be an important driver of population declines in Western Europe (Butet *et al.* 2022). Overall, habitat heterogeneity is linked to an increase of biodiversity in agricultural landscapes (Benton *et al.* 2003) and is potentially a good indicator of prey abundance and diversity for kestrels in such habitats.

Here, we studied kestrels in western Finland, where the species occupies a gradient of agricultural intensification, ranging from more heterogeneous habitats, which consist of a mixture of arable land, young to old forests and clear cuts, to more homogeneous open habitats, which consist mainly of intensely managed, large agricultural fields (Sumasgutner *et al.* 2019). The kestrel is a generalist predator, but breeding density and diversity of its diet are tightly linked to the 3-year vole cycle in northern Europe (Korpimäki & Norrdahl 1991). Voles of the genera *Microtus* and *Myodes* are the main prey group during peak years, whereas alternative prey (birds, insectivores such as shrews and lizards, or arthropods) is more abundant in the kestrel diet in years of low vole abundance (Korpimäki 1985a, 1985b). In addition, the diversity of hunting habitats increases in low vole years when kestrels partly shift their hunting from agricultural fields to forest edges and clear-cut areas (Korpimäki 1986). As alternative prey abundance is expected to be higher in heterogeneous habitats, we predict that diet diversity and health parameters will be positively associated with habitat heterogeneity (but see Navarro-López & Fargallo 2015) particularly during periods of low main-prey abundance.

Multiple health indices are increasingly used to better understand the response of animal populations to global environmental changes (Booth & Elliott 2002, Fair *et al.* 2007, Olimpi *et al.* 2022). These indices can provide a relevant faster alternative to long-term population surveys to assess the ability of these populations to cope with variations in environmental conditions during short sampling events (Duval *et al.* 2022). The degree of individual health can be inferred from various indices but, most commonly, body condition, haematocrit or parasitic burden is used for this purpose. Healthier individuals are expected to be in better body condition (Almasi *et al.* 2015), with higher proportions of red blood cells to plasma (Fair *et al.* 2007) and fewer parasites (Krone *et al.* 2008). In this study, we expanded the range of indices from body condition, haematocrit levels and parasitic infection status to also include carotenoids (circulating blood volumes and integument coloration intensity), which are directly linked to diet, and multiple physiological pathways (Hill & McGraw 2006), to obtain a better picture of the overall health of breeding individuals across the intensification gradient (conceptual framework is shown in Fig. 1). These indices allowed us to assess how breeding kestrels respond to spatial variation in habitat heterogeneity in terms of health. We also aimed to understand how this response was influenced by individual variations in trophic specialization and in individual quality, through heterozygosity levels, as individual heterozygosity has been associated with several fitness-related parameters including breeding success (Charpentier *et al.* 2005), disease resistance (Hoffman *et al.* 2014) and survival (Hansson *et al.* 2001).

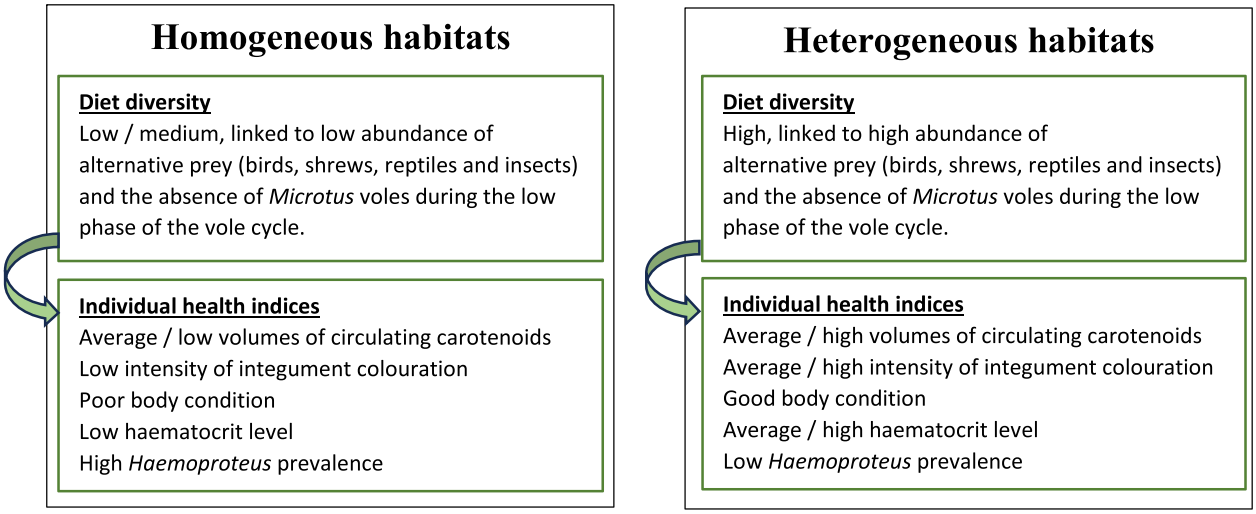

Figure 1. Theoretical framework on how diet diversity might impact individual quality and health of breeding Eurasian Kestrels in homogeneous versus heterogeneous habitats.

We chose a low vole abundance year in western Finland to capture a situation in which kestrels use a wide range of prey species and habitat types. First, we tested the core hypothesis, that (1) diet composition differs along a gradient of habitat heterogeneity. Kestrels in more heterogeneous habitats might profit from a mosaic landscape with many edge habitats and a high abundance of alternative prey species (Benton *et al.* 2003) allowing a better health status to be maintained in such habitats during a low vole year. We predicted higher proportions of birds and insectivores (shrews and lizards) in the diet, as reflected by the isotope profiles of kestrels, with increasing degree of habitat heterogeneity. Secondly, (2) we predicted that the five health indices would be positively associated with habitat heterogeneity, diet diversity and individual heterozygosity, and that there might be variation between sexes due to the different role taken by males and females during the energy-demanding breeding season.

METHODS

Study system

The study site (coordinates: 62°59′N–63°10′N, 22°5′E–23°20′E) is located in the Kauhava and Lapua region in western Finland (Fig. 2). Breeding kestrels are mostly found in a more homogeneous open habitat (dominated by large agricultural fields) in the west, and in a more heterogeneous habitat (a mixture of smaller agricultural fields and forest patches) in the east. In 2013, a total of 358 nestboxes were monitored. For each occupied nestbox (n = 82) the degree of habitat heterogeneity, expressed as Territory Land-Cover Heterogeneity (TLCH), was calculated. We expect land-cover heterogeneity to be a better proxy of habitat quality than the proportion of farmland per se, because this latter category does not discriminate between intensive and extensive agricultural areas. Furthermore, habitat diversity at the landscape scale is related to the abundance and availability of important prey species for kestrels. For example, young Fieldfares *Turdus pilaris* are an important alternative prey during the breeding season; however, Fieldfares are dependent on the occurrence of forest patches within the agricultural matrix and are captured by kestrels at the edges between forests and fields. Therefore, we believe that TLCH allows us to integrate the 'enhancing' effect of habitats that are not directly used by kestrels but that affect prey abundance and diversity across kestrel territories.

From Landsat images, a land-cover map was produced (following the procedure of Morosinotto *et al.* 2017) for the land-cover types: built-up, roads and mines as sealed land, as opposed to clear cuts, young forests, mature forests, old forests, peatland bogs, farmland and water (Fig. 2). TLCH was calculated with Simpson's Index

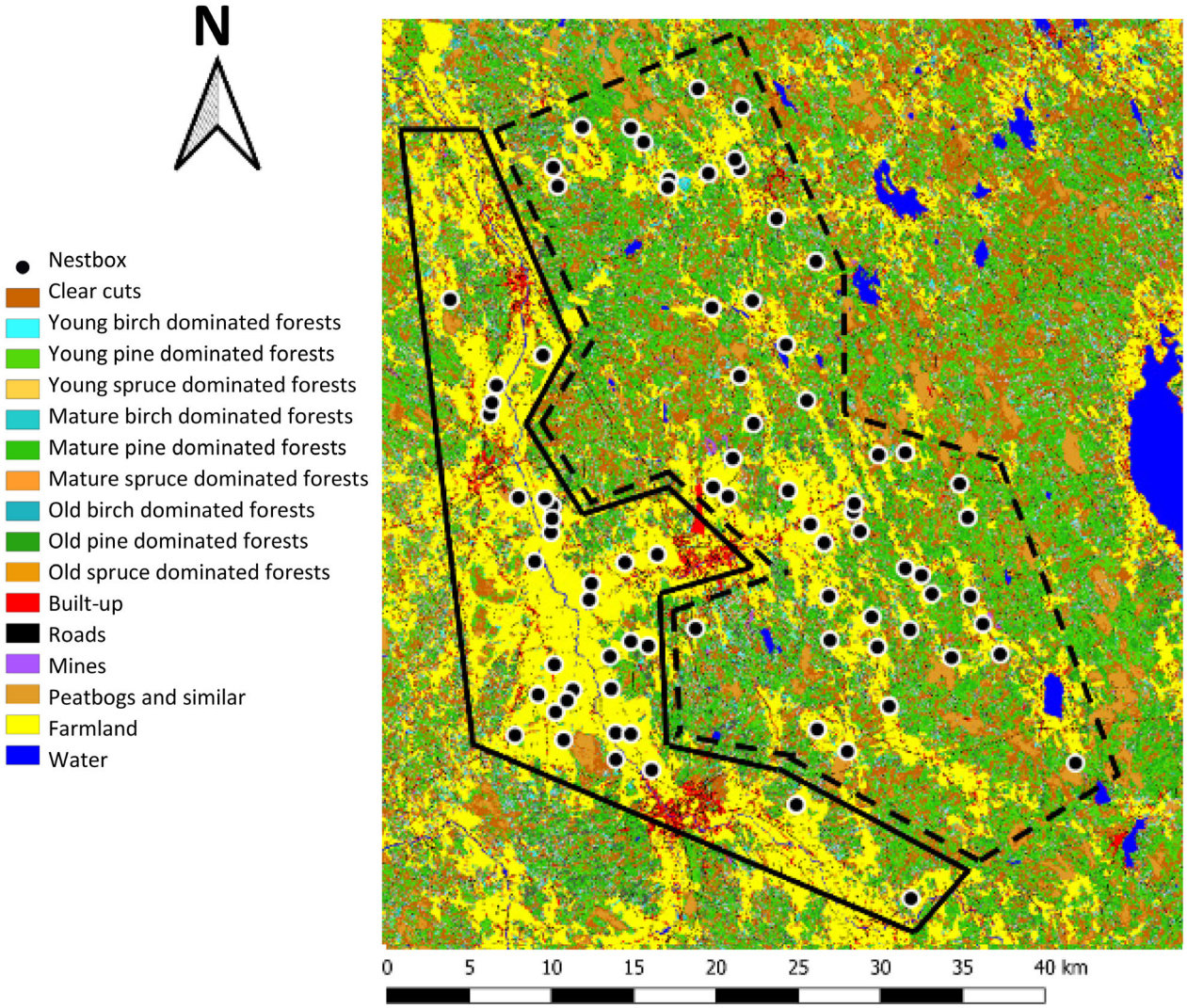

Figure 2. Study site (coordinates: 62°59′N–63°10′N, 22°5′E–23°20′E) located in the Kauhava and Lapua region in western Finland with different land-cover types. Black dots represent occupied nestboxes in the breeding season of 2013 (n = 82). In the area within the black continuous line polygon, small mammal trapping and bird counting of large fields (homogeneous habitat) were performed. In the area within the black dotted line polygon, small mammal trapping and bird counting of small fields (heterogeneous habitat) were performed.

(Magurran 2004), by using the 'diversity' function of the 'vegan' package (Oksanen *et al.* 2019). A radius of 843 m around each nestbox was considered as kestrel territory, corresponding to the average inter-nest distance between occupied nestboxes (Sumasgutner *et al.* 2019).

Prey abundance estimates

Abundance estimates of voles (vole index V*i*) were calculated by pooling the numbers of trapped individuals of *Microtus* voles (*Microtus agrestis* and *Microtus levis*), Bank Voles *Myodes glareolus* and Water Voles *Arvicola amphibius* per 100 trap-nights in areas with small and large fields, respectively, in spring 2013 (Fig. S1). For more details of small mammal trapping see Korpimäki and Norrdahl (1991) and Korpimäki *et al.* (2002). Abundance estimates of birds (bird index B*i*) were calculated by averaging the numbers of counted birds per kilometre road transect (driven at walking pace with two observers: one driver and one

passenger) per bird-counting event. Nine transects were done in the large agricultural fields (homogeneous habitat; average transect length 1.96 km ± 0.82 standard deviation (sd)) and 18 in the small agricultural fields and clear cuts (heterogeneous habitat; average transect length 1.50 km ± 1.64 sd). Bird-counting events were carried out in July 2013 (Fig. S2). Only bird species known to be preyed upon by kestrels were considered (Korpimäki 1985a, 1985b, 1986, Sumasgutner *et al.* 2013), and are summarized in Table S1.

Adult captures and individual quality indices

Nestboxes in the study area were checked three or four times during the early stage of breeding (end of April to early May) to get information about occupancy of nestboxes and egg-laying date. Two to three weeks after hatching, parent kestrels were captured directly at nestboxes by using a swing-door trap affixed to the entrance (Vasko *et al.* 2011). In total, 157 kestrel parents were captured.

Body condition index

Kestrels were weighed (Pesola spring scale, accuracy 1.0 g), and wing length was measured (zero-stop ruler, accuracy 1.0 mm). Residuals of the regression of body weight on wing length (both log-transformed) and sex (adjusted $R^2 = 0.5795$, $P < 0.05$; females are heavier than males: Kruskal–Wallis test: $P < 0.05$; Massemin *et al.* 2000) were extracted and used as a body condition index in statistical analyses (Schulte-Hostedde *et al.* 2005). Low values represent low individual body condition and vice versa.

Haematocrit level

A blood sample of up to 65 µL per kestrel was taken by brachial venepuncture with sterilized 27-gauge needles and capillary action. Within 12–24 h after brachial venepuncture, blood samples were centrifuged in 75-µL capillary tubes for 15 min. Haematocrit levels were expressed as the ratio of red blood cells to total blood volume, and measured with a calliper. Afterwards, red blood cells were separated from blood plasma by breaking the capillary tube at the separation line, and were stored at −60°C until DNA extraction (see below).

Parasite infection status

Haemosporidian parasites are receiving increasing attention, and are related to the causative agents of avian malaria (*Plasmodium* sp.) and its sister groups *Haemoproteus* sp. and *Leucocytozoon* sp. In our study population, *Haemoproteus* parasites especially reach high levels in kestrels (53% in females, 34% in males; Korpimäki *et al.* 1995). To measure *Haemoproteus* infection status, we extracted DNA from 151 blood samples of adult kestrels at the Center of Evolutionary Applications, University of Turku, Finland. DNA samples were genetically screened thereafter by following an adapted method of Aljanabi and Martinez (1997) at the Molecular Ecology and Evolution Laboratory, Lund University, Sweden. A nested polymerase chain reaction with the primers HaemNFI/HAEMNR3 was used, followed by an amplification with the primers HAEMF/HAEMR2 or HAEMFL/HAEMR2L (Hellgren *et al.* 2004, Bensch *et al.* 2009). Sixty-four out of the 151 blood samples of kestrels were infected with *Haemoproteus* (prevalence of 42%).

Genetic diversity

Standardized heterozygosity was estimated on the basis of 17 microsatellites with the 'genhet' function in R (Coulon 2010) for 151 individuals in the Central Laboratories of the Natural History Museum, Vienna, Austria. For detailed description of laboratory procedures, see additional file 1 of Sumasgutner *et al.* (2019). Standardized heterozygosity, hereafter 'individual genetic heterozygosity', represents genetic diversity and can be defined as the proportion of heterozygous loci of one individual divided by the average heterozygosity of the same loci of all individuals of the population (Selonen & Hanski 2010). Higher values of individual genetic heterozygosity represent higher individual genetic diversity and vice versa.

Carotenoids

Carotenoids are micro-nutrients, which are strictly dietary in vertebrates and can serve several functions (Hill & McGraw 2006) whereby every prey type has characteristic micro-nutritional components and caloric content (Fargallo *et al.* 2020). Both are crucial to maintain body condition, and are specifically important during the energy-demanding breeding season (Wiehn & Korpimäki 1997) and for survival (Aihie Sayer

et al. 2001, Mayntz & Toft 2001). The higher the carotenoid content of a prey species, the more carotenoids can be allocated either as antioxidants to health-related functions or as yellow–red pigments to integument coloration (Casagrande *et al.* 2009). Both components of the carotenoid pathway can be measured, as circulating carotenoids in the bloodstream on the one hand, and as carotenoid-based coloration of integumentary tissues on the other (Hill & McGraw 2006). As a result of their limited availability, carotenoid-dependent integument coloration has been considered as an 'honest' signal, potentially reflecting individual quality (Blas *et al.* 2013, Hernández *et al.* 2021).

Circulating carotenoids

Blood plasma samples of 88 kestrels were analysed to identify the levels of lutein and zeaxanthin (main xanthophylls in kestrel and other birds of prey (Casagrande *et al.* 2006, Sternalski *et al.* 2012)) and vitamin E. Carotenoid measures were carried out following the method of McGraw *et al.* (2002), whereby 20 µL of blood plasma was mixed with 200 µL acetone, vortexed (10 s), mixed with 100 µL tert-butyl methyl ether, and again vortexed (10 s) before centrifugation (at 10°C for 5 min). The supernatant was transferred and evaporated to dryness under nitrogen. Afterwards, the residue was dissolved with 100 µL methanol–acetonitrile (30 µL methanol and 70 µL acetonitrile mixed) and vortexed (10 s). High-performance liquid chromatography was performed with an isocratic system (HP 1050 Series Isocratic Pump) with constant flow rate of 1.2 mL/min for 25 min. Carotenoids were detected at 450 nm using a Hitachi L-4250 UV/VIA detector. Pearson's correlation analysis showed a significant relationship between lutein and zeaxanthin concentrations ($P < 0.001$, cor = 0.95). As vitamin E was not as strongly correlated, a principal component analysis (PCA) was performed. The PCA resulted in two principal components, together explaining 98.52% of the variation in the data (Table S2). PC1 mainly comprised lutein and zeaxanthin concentrations (Fig. S3a,b) and was used as 'main circulating carotenoids' in the following statistical analysis. PC2 mainly explained vitamin E concentrations (Fig. S3c).

Carotenoid-based integument coloration

To determine the coloration of tarsus, orbital-ring and cere of 105 kestrels, spectral reflectance was measured using a portable JAZ photo-spectrometer (Ocean Optics, Inc.; optical range between 300 and 750 nm), and data were analysed with the 'pavo' package (Maia *et al.* 2013). The function 'spec2rgb' was used to identify the average red–green–blue (RGB) components as hexadecimal colour codes. These codes were converted into individual average red, green and blue colour components, each with a brightness value between zero and 255. Using the relative differences among these three colour component values, the hue of actual colour can be determined (Mougeot *et al.* 2007). Following the calculations of Sumasgutner *et al.* (2018, 2023), a yellowness score was determined for tarsus, orbital-ring and cere measurements and used as a continuous variable in the following statistical analyses. A PCA on yellowness of tarsus, orbital-ring and cere resulted in one principal component explaining 46.08% of the variation in the data (Table S3). As there was a positive relationship among all three variables, PC1 was used as 'intensity of yellowness' in the following statistical analysis (Fig. S4).

Diet composition based on stable isotope analysis

We measured stable carbon and nitrogen isotope ratios in 87 blood samples of adult kestrels at the Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany. Prey categories show different isotopic signatures because they are at different trophic positions (Layman *et al.* 2007). These isotopic signatures were derived from 60 additional tissue samples (i.e. small pieces of muscle from prey carcasses found at nestboxes in the study area) of the four main categories (voles, birds, shrews and lizards). We loaded tissue samples (approximately 0.5 mg of kestrel blood or prey tissue) into tin capsules (IVA Analysentechnik). The samples were transferred to an autosampler, and stable isotope ratios were measured with an elemental analyser (Flash EA 1112 Series; Thermo Fisher) connected in continuous mode via a Conflo III device (Thermo Fisher) to an isotope ratio mass spectrometer (IRMS, Delta V Advantage; Thermo Fisher). Stable isotope ratios are expressed in the delta notation ($\delta^{13}C$ and $\delta^{15}N$) as parts per thousand deviations from the international standards Vienna Pee Dee Belemnite (V-PDB) and atmospheric nitrogen (Air N2), respectively, using the

equation $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$. Samples were measured together with in-house protein standards of tyrosine ($\delta^{13}C = -24.0‰$, calibrated with NBS22; $\delta^{15}N = 4.4‰$ calibrated with IAEA-N1) and leucine ($\delta^{13}C = -30.3‰$ calibrated with NBS 22, $\delta^{15}N = 11.0‰$ calibrated with IAEA-N1) for drift correction and standardization. Analytical precision based on the repeated analyses of stable isotope ratios in laboratory standards was always better than 0.5‰ (1 sd). We used the Bayesian Model package 'siar' (Parnell & Jackson 2013) to estimate the relative contribution of main prey categories to the diet of individual kestrels. The proportion of each main prey category was used for diet breadth expressed as the Shannon–Weaver Index (SWI) (Petraitis 1979). A high proportion of voles in the kestrel's diet was expressed as a low SWI value (Fig. S5). The higher the SWI value, the more generalist the diet, and so the more alternative prey items were consumed by kestrels. The lower the SWI value, the more specialist the diet (towards largely voles).

Statistical analysis

All statistical analyses were performed in R (Version 3.6.1; R Core Team 2020); the significance level was set to $P \leq 0.05$ and confidence intervals (CIs) were set to 95%. To ensure that effect sizes were on a comparable scale, all quantitative explanatory variables were centred and scaled and correlations between fixed effects were examined to avoid collinearity in our models. First, to test the link between habitat heterogeneity and SWI, a linear mixed model (LMM) with Gaussian error distribution and identity link function was fitted. The LMM was built with the 'lmer' function in the 'lme4' package (Bates *et al.* 2015). Nestbox ID (individual ID number of nestbox) was used as a random factor to account for pseudo-replication arising from the lack of independence of data collected from both adults at the same nestbox. Although we initially considered sex as an additional co-variate in this model, we found neither an interactive effect with TLCH nor an additive effect and so dropped the sex term from the final model.

The five health indices, integument coloration, circulating carotenoids, body condition, haematocrit level and *Haemoproteus* parasite infection status, were not very inter-correlated and we failed to combine them into one principal component (see PCA in Table S4). For this reason, we tested whether each one of the five health indices separately was influenced by TLCH, SWI, individual genetic heterozygosity and/or interactive effects between these variables. Sexes were separately tested from each other as health index associations might vary between sexes. Full linear models (LMs; for integument coloration, circulating carotenoids, body condition and haematocrit level) and generalized linear model (GLMs, for *Haemoproteus* infection status with binomial distribution) with all these parameters were built. Binomial models were checked for overdispersion. For LMs, the assumption of normality of residuals was checked by visually inspecting residual plots. For the response variables integument coloration and haematocrit level, respectively, in males and for body condition in both sexes a box-cox-transformation (with the 'boxcox' function in the 'EnvStats' package (Millard 2013)) was used to reach a normal distribution. For model selection, we used an information theoretic approach with the packages 'MuMIn' (Bartón 2020) and 'AICcmodavg' (Mazerolle 2020). For each of the five health indices, a candidate model set was built with the same response variable and changing predictor variables. All candidate model sets contained the global model with TLCH, SWI, genetic heterozygosity, the interaction terms TLCH with SWI, TLCH with genetic heterozygosity, and SWI with genetic heterozygosity, respectively, the null model (intercept only) and a set of candidate models with all possible combinations of the predictor variables (the structure of the 14 models built for each health index is shown in Table S5). Each dataset contained no missing values to ensure accurate model comparisons throughout the whole selection process. Based on correct Akaike information criterion (AIC_c) scores, model set ranking was performed (see AIC_c of all candidate models and each dataset in Table S5; see also parameter estimates of the best model of each health index in Table S6). The model with the lowest AIC_c score was considered as the final, most parsimonious model and is presented in the Results section.

Residual distributions of the models were inspected visually to assess model fit by evaluating the model criticism plots produced by the 'plot' function in the base package and the 'mcp_fnc' function in the 'LMERConvenienceFunctions' package (Tremblay & Ransijn 2020). Additionally, all models were tested for potential spatial

autocorrelation in all response variables by using Moran's I ('ape' package; Paradis *et al.* 2004). We found no spatial autocorrelation for any of the five health indices (see Fig. S6). The significance of fixed effects was calculated with the 'Anova' type III function in the 'car' package (Fox *et al.* 2020b). The R-packages 'effects' (Fox *et al.* 2020a), 'ggplot2' (Wickham *et al.* 2020) and 'gridExtra' (Auguie 2017) were used to create and arrange model visualization plots.

RESULTS

A total of 157 adult kestrels (78 females, 79 males) were captured in the breeding season of 2013. From these adult kestrels, 151 were identified as breeding birds originating from 82 different nestboxes. We were not able to trap both breeding adults at all nestboxes. Complete datasets were available for the variables TLCH and individual genetic heterozygosity, whereas other measurements were incomplete because of logistical constraints or insufficient sample material to process all physiological assays. Varying sample sizes are indicated accordingly.

Prey abundance and diet composition

Microtus voles were absent from both habitat types, and overall abundance estimates of voles (vole index V*i*) were similar between homogeneous (V*i* = 1.78) and heterogeneous (V*i* = 0.21; $t_{(df = 5)} = 1.12$, standard error (se) = ± 0.25, $P = 0.072$) habitats. Water Voles were only captured in more homogeneous habitat, where also more Bank Voles were captured (Fig. S1). Abundance estimate of birds (bird index B*i*) were also similar between more homogeneous habitat (B*i* = 14.75) and more heterogeneous habitat (B*i* = 12.64; $t_{(df = 26)} = 1.649$, se = ±7.672, $P = 0.111$). Open-land-dwelling and shrub-dwelling bird species were more often observed in more homogeneous habitat. Forest-dwelling species and generalist species were more often observed in more heterogeneous habitat (Fig. S2; Table S1).

The SWI of both sexes together ranged from −0.977 (48% voles, 20% birds and 32% insectivores) to 1.158 (33% voles, 34% birds and 33% insectivores; $mean_{SWI} = 0.65 \pm 0.44$ sd; mean proportion of each prey group: 0.40 voles, 0.28 birds and 0.32 insectivores). In females, SWI ranged from −0.881 (49% voles, 22% birds and 29% insectivores) to 1.158 (33% voles, 34% birds and 33% insectivores; $mean_{SWI} = 0.65 \pm 0.44$ sd; mean proportion of each prey group: 0.40 voles, 0.28 birds and 0.32 insectivores). In males, SWI ranged from −0.977 (48% voles, 20% birds and 32% insectivores) to 1.116 (35% voles, 32% birds and 33% insectivores; $mean_{SWI} = 0.65 \pm 0.44$ sd; mean proportion of each prey group: 0.40 voles, 0.27 birds and 0.32 insectivores). When comparing SWI with the single explanatory variable TLCH to understand the relationship between diet composition and habitat heterogeneity, no obvious association was found (estimate −0.18 ± 0.11 se, $P = 0.093$, Fig. 3).

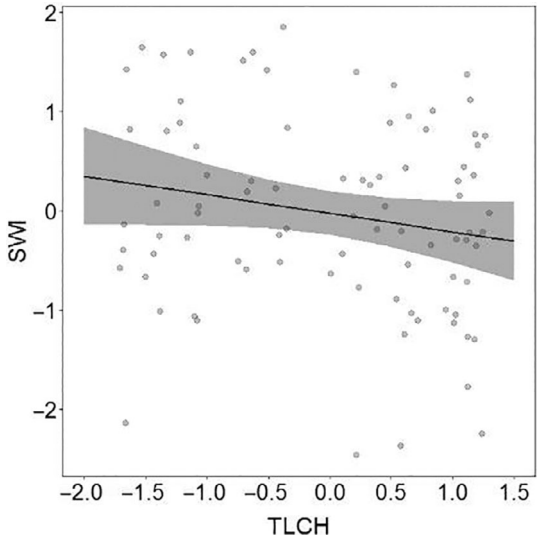

Figure 3. Shannon–Weaver Index of diet breadth (SWI) against Territory Land-Cover Heterogeneity (TLCH) in Eurasian Kestrels (*Falco tinnunculus*) in western Finland (estimate, −0.18 ± 0.11 se, $P = 0.093$). Low SWI values indicate a high proportion of voles in the kestrel's diet, and high SWI values indicate more alternative prey items in the kestrel's diet. Low TLCH values indicate large homogeneous agricultural fields, and high TLCH values indicate a mosaic of diverse heterogeneous habitats including small fields, clear-cuts and forest patches. All quantitative variables were scaled and centred. Plot shows raw data in background scatter, effect size of the linear mixed model and 95% confidence intervals.

Health indices

The best model for female integument coloration included individual heterozygosity, SWI, TLCH, and the interaction between SWI and TLCH (Table S5). Integument coloration in females was

Table 1. Parameter estimates with standard error (se) for the best model assessing the effect of individual heterozygosity, Shannon–Weaver Index (SWI) and Territory Land-Cover Heterogeneity (TLCH) on the intensity of integument coloration in female kestrels (n = 44 individuals); factors highlighted in bold have confidence intervals that do not contain zero.

Effect size of explanatory variables	Estimate	se	*P*	2.5%	97.5%
Intercept	**−0.43**	**0.16**	**0.012**	**−0.76**	**−0.10**
Heterozygosity	−0.27	0.17	0.115	−0.60	0.07
SWI	0.07	0.17	0.653	−0.26	0.42
TLCH	0.32	0.17	0.060	−0.01	0.66
Heterozygosity: SWI	**−0.60**	**0.21**	**0.007**	**−1.03**	**−0.17**

Table 2. Parameter estimates with standard error (se) for the best model assessing the effect of individual heterozygosity, Shannon–Weaver Index (SWI) and Territory Land-Cover Heterogeneity (TLCH) on *Haemoproteus* infection status in female kestrels (n = 46 individuals); factors highlighted in bold have confidence intervals that do not contain zero.

Effect size of explanatory variables	Estimate	se	*P*	2.5%	97.5%
Intercept	**−1.06**	**0.37**	**0.004**	**−1.84**	**−0.38**
Heterozygosity	**−0.94**	**0.39**	**0.007**	**−1.79**	**−0.25**

influenced by SWI in interaction with individual heterozygosity (estimate −0.60 ± 0.21 se, P = 0.007, Table 1, Fig. 4). Among females with low individual heterozygosity, increased SWI was associated with higher integument coloration intensity, whereas those females with high individual heterozygosity showed a slight decrease in integument coloration with increased SWI. Integument coloration in females did not vary with habitat heterogeneity (estimate 0.32 ± 0.17 se, P = 0.060; Table 1).

The best model for parasite infection status included only individual heterozygosity, whereby females with low individual heterozygosity were more often infected with *Haemoproteus* parasites compared with females with higher individual

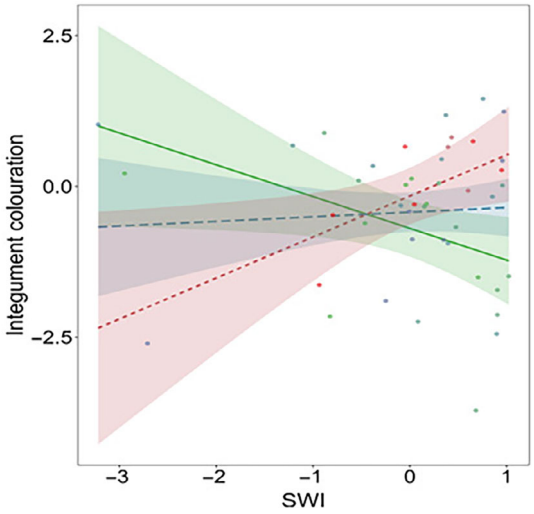

Figure 4. Intensity of carotenoid-based integument coloration in female kestrels in relation to Shannon–Weaver Index (SWI) (ranging from dietary 'specialists' with low SWI values to dietary 'generalists' with high SWI values) with genetic heterozygosity in an interaction term (lower individual genetic heterozygosity, red dots and red dashed line; mean genetic diversity, blue dots and blue dashed line; upper individual genetic heterozygosity, green dots and green solid line; estimate = −0.60 ± 0.21 se, P = 0.007). All quantitative variables were scaled and centred. Plot shows raw data in background scatter, effect size of the linear model and 95% confidence intervals. Parameter estimates can be found in Table 1.

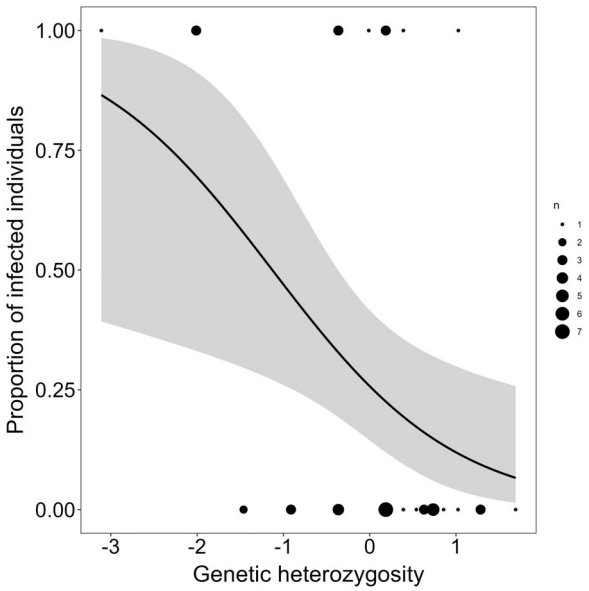

Figure 5. *Haemoproteus* infection status in female kestrels in relation to genetic heterozygosity (low values indicate low genetic diversity, high values indicate high genetic diversity; estimate = −0.94 ± 0.39 se, P = 0.007). All quantitative variables were scaled and centred. Plot shows raw data in background scatter, effect size of the generalized linear model and 95% confidence intervals. Parameter estimates can be found in Table 2.

heterozygosity (estimate −0.94 ± 0.39 se, $P = 0.007$; Table 2, Fig. 5). In males, the best model for body condition included only SWI, whereby body condition decreased with increasing diet diversity (estimate −0.01 ± 0.01 se, $P = 0.043$, Table 3, Fig. 6).

Body condition in females, integument coloration and parasite infection status in males, and amount of circulating carotenoids and haematocrit level in both sexes were not influenced by any of the explanatory variables (TLCH, SWI and genetic heterozygosity; Table S5 showing models ranked by AIC_c).

Table 3. Parameter estimates with standard error (se) for the best model assessing the effect of individual heterozygosity, Shannon–Weaver Index (SWI) and Territory Land-Cover Heterogeneity (TLCH) on body condition in male kestrels ($n = 40$ individuals); factors highlighted in bold have confidence intervals that do not contain zero.

Effect size of explanatory variables	Estimate	se	*P*	2.5%	97.5%
Intercept	**0.10**	**0.01**	**< 0.001**	**0.09**	**0.11**
SWI	**−0.01**	**0.01**	**0.043**	**−0.03**	**−0.00**

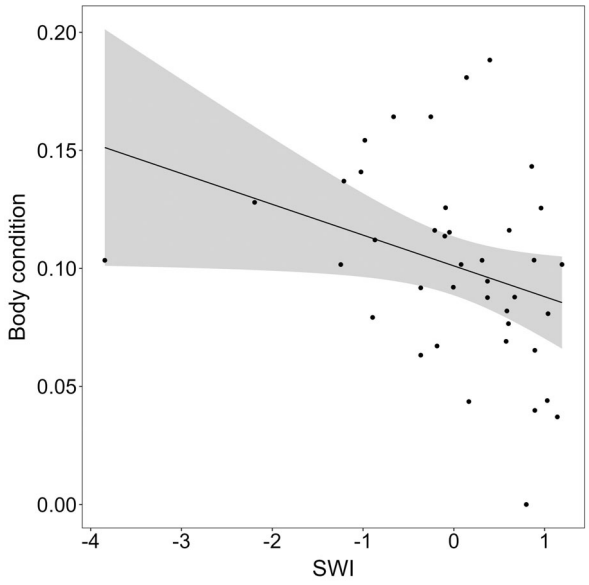

Figure 6. Body condition in male kestrels in relation to Shannon–Weaver Index (SWI) (low SWI values indicate a high proportion of voles in the kestrel's diet, and high SWI values indicate more alternative prey items in the kestrel's diet; estimate = −0.01 ± 0.01 se, $P = 0.043$). All quantitative variables were scaled and centred. Plot shows raw data in background scatter, effect size of the linear model and 95% confidence intervals. Parameter estimates can be found in Table 3.

DISCUSSION

Our results revealed that spatial variation in habitat heterogeneity had a limited effect on diet diversity, which could be related to higher-than-expected abundance of alternative prey (e.g. insectivores) or prey capturability in homogeneous habitats. Diet diversity and individual heterozygosity had an effect on several health indices. However, contrary to our predictions (see framework in Fig. 1), our results did not reveal a directional relationship between habitat heterogeneity and individual health. We did, however, find a remarkable direct effect of individual heterozygosity on parasite infection status in female kestrels and of diet diversity on body condition in males. These findings are discussed in more detail in the following sections.

Prey abundance and diet composition

We found limited variation in SWI between individuals. However, it is not surprising that most individual kestrels have a more generalist diet in a low vole year. *Microtus* voles were indeed very low in abundance throughout the study area, regardless of habitat type, but, contrary to our predictions, vole abundance was higher in homogeneous habitats. This was mainly driven by Water Voles. In our study area, Water Voles are known to reach high densities in large agricultural fields, where the presence of large drainage ditches provides high-quality habitat where nest tunnels are less accessible to terrestrial predators. In addition, the three times higher body mass of juvenile Water Voles compared with other vole species (Korpimäki 1985b) makes juvenile Water Voles energy-rich prey for kestrels, and they are particularly preyed upon during the chick-rearing period.

Although we found no spatial variation in bird abundance in different habitat types, the abundance and capturability of important alternative prey species may be higher in homogeneous habitats. Although voles are the most profitable prey for kestrels, hunting success of alternative prey is also generally higher in open areas (Korpimäki 1986, Village 1990). Therefore, higher diet diversity in homogeneous habitats may be related to the fact that alternative prey (i.e. farmland

birds, reptiles) are easier to catch where shelter is scarce (Valkama *et al.* 1995). However, the way in which avian prey abundance was measured is a clear limitation of our study, where we could only assess a broad index per habitat type and could not capture potential fine-scale variation along the agricultural intensification gradient (as done, for instance, in Orrock *et al.* 2000 and Suri *et al.* 2017).

Parameters affecting health indices

We found an important difference in integument coloration intensity for specialist females, i.e. those with low diet diversity, depending on their level of individual heterozygosity. This difference in coloration between females with low genetic diversity and females with high genetic diversity decreases when they adopt a broader diet and have high SWI values. Interestingly, this result highlights that specialist females are only able to maintain high levels of integument coloration intensity if they have high genetic diversity.

Individuals with lower heterozygosity levels are more likely to be in poor condition (Brambilla *et al.* 2015), and our study suggests that these individuals also suffer more in terms of individual health when affected by a lack of carotenoid-rich prey than individuals with higher heterozygosity levels. This is related to the observation that higher diet diversity is associated with a higher proportion of birds in the diet (Table S5), and that birds have higher overall carotenoid content (García-Heras *et al.* 2017, based on Goodwin 1984). Therefore, these low-quality individuals may be more dependent on this additional intake of dietary carotenoids to enhance the intensity of integument coloration than more heterozygous individuals. The observation that heterozygous individuals had higher coloration intensity even at low SWI values suggests that high-quality individuals are more likely to maintain quality signals even when dietary input carotenoid is low.

Previous research has demonstrated that only healthy individuals can allocate more carotenoids to integument coloration rather than health-related functions (Pérez-Rodríguez *et al.* 2013). Therefore, specialist females with low genetic diversity may need more carotenoids as antioxidants to combat higher parasite loads (Martínez-Padilla *et al.* 2007), to cope with exposure to pollutants (Almasi *et al.* 2015, Lopez-Antia *et al.* 2015, Costantini *et al.* 2022) or to limit the destructive effects of oxidative stress associated with overall poorer habitat quality (von Schantz *et al.* 1999) – which explains their paler coloration – while specialist females with high genetic diversity can cope and are more intensely coloured. However, regarding the use of carotenoids as antioxidants for health-related functions, some studies doubt their importance in a direct pathway (Costantini & Møller 2008, Koch *et al.* 2018, Costantini *et al.* 2022) and rather emphasize indirect effects of carotenoids that contribute to health, such as through higher efficiency in vitamin E uptake and so better antioxidant protection. Furthermore, it is currently unknown whether circulating carotenoids are completely used up for such health-related functions or whether they could still be recycled to some extent for integument coloration (Koch & Hill 2018). These uncertainties may explain why we did not find any direct relationships between circulating carotenoids and the predictor variables habitat heterogeneity and diet diversity.

Females with low genetic heterozygosity were more frequently infected with *Haemoproteus* parasites than females with higher genetic heterozygosity. Genetic heterozygosity in hosts can influence susceptibility to parasitic infections through several mechanisms (Keller & Waller 2002, Szulkin *et al.* 2010). A key factor is the host immune system, which can vary in effectiveness depending on the genetic background of the individual (e.g. Bonneaud *et al.* 2005, Osborne *et al.* 2015). Studies in passerine birds have shown that individuals with higher genetic heterozygosity in major histocompatibility complex genes are more resistant to *Haemoproteus* and other avian blood parasites (Westerdahl *et al.* 2005, Loiseau *et al.* 2011). However, our study was limited to the infection status with *Haemoproteus* parasites. Infection status (once positive) does not change throughout life, whereas infection intensity can vary (Valkiūnas, 2004) and so could respond to stress exposure (Remple 2004). This means that an effect of habitat heterogeneity or diet diversity may only become apparent when *Haemoproteus* infection intensity is quantified (e.g. Frixione & Rodríguez-Estrella. 2023).

Finally, we found a negative effect of diet diversity on the body condition of males. This result is explained by the fact that higher diet diversity was

associated with a lower proportion of voles in the diet. As mentioned above, *Microtus* voles were absent from the study area in 2013 and *Myodes* voles were quite rare, so most of the voles captured by kestrels were young Water Voles, which are highly profitable prey in terms of biomass and capturability. Therefore, the high proportion of Water Voles in the diet of male kestrels seems to be associated with a higher individual diet specialization index and higher body condition.

We did not find any effect of our explanatory variables on other health indices in male kestrels. Years of very low vole abundance, such as our study year, are challenging for kestrels in terms of breeding investment, especially for males that have provided food for the female and brood for most of the breeding season. Therefore, only high-quality males may choose to breed in such unfavourable years. This relative homogeneity in the quality of the breeding pool of male kestrels across the breeding area may explain why we found no effect of habitat heterogeneity, individual heterozygosity or diet diversity on their health.

CONCLUSION

We aimed to understand how habitat quality, individual quality and individual levels of trophic specialization might interact to influence health in Eurasian kestrels during the breeding season, when energy demands are highest. Our results showed that individual variation in quality and foraging ecology had an effect on three of the five health indices considered, which means that they should be considered in conjunction with spatial variation in habitat heterogeneity. Further research is needed to understand the sex-specific effects of agricultural intensification on kestrel health and vital rates. Overall, our results contribute to a better understanding of the mechanisms linking land-use change to health indices in a common avian predator that can be used as a health sentinel in European agroecosystems.

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AUTHOR CONTRIBUTIONS

Lukas Hochleitner: Investigation; methodology; visualization; writing – original draft; formal analysis. **Erkki Korpimäki:** Conceptualization; funding acquisition; investigation; writing – review and editing; project administration; resources. **Nayden Chakarov:** Data curation; writing – review and editing; resources; methodology. **Caroline Isaksson:** Methodology; resources; writing – review and editing. **Carina Nebel:** Writing – review and editing; data curation. **Swen C. Renner:** Writing – review and editing. **Ville Vasko:** Data curation. **Christian C. Voigt:** Methodology; data curation; writing – review and editing. **Julien Terraube:** Conceptualization; investigation; writing – original draft; formal analysis; supervision; writing – review and editing; methodology; data curation. **Petra Sumasgutner:** Writing – original draft; writing – review and editing; supervision; funding acquisition; conceptualization; investigation; methodology; formal analysis; data curation.

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CONFLICT OF INTEREST

The authors declare that they have no competing interests.

CONSENT FOR PUBLICATION

The manuscript has been approved by all co-authors.

ETHICS STATEMENT

Data of this study were acquired strictly following Finnish and EU law, as well as the Weatherall Report and guidelines for the treatment of animals in behavioural research and teaching (ASAB 2012). The study was performed under licence from the animal experiment committee at Turku University (permit number ESAVI-2010-05480/Ym-23).

Data Availability Statement

The underlying dataset is available as electronic material on PHAIDRA: https://doi.org/10.25365/phaidra.500.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Number of trapped individuals of small mammals.

Figure S2. Number of counted individuals of bird species per kilometre of bird counting events in more homogeneous habitat (green bars) and in more heterogeneous habitat (orange bars) in July 2013.

Figure S3. Simple correlation plots as visualization of results of PCA of Table S1.

Figure S4. Simple correlation plots as visualization of results of PCA of Table S2.

Figure S5. Shannon–Weaver Index (SWI) of diet breadth based on the proportions of voles, birds, and insectivores such as shrews and lizards.

Figure S6. Spatial distribution of (a) intensity of integument coloration in males and (b) in females, (c) circulating carotenoids in males and (d) in females, (e) body condition in males and (f) in females, (g) haematocrit level in males and (h) in females, and (i) parasite infection status in males and (j) in females in the study area.

Table S1. List of bird species per habitat type.

Table S2. Results of a principal component analysis on the measurement in the blood of circulating lutein, zeaxanthin and vitamin E.

Table S3. Results of a principal component analysis on the measurement of the integument coloration of skin of tarsus, orbital-ring and cere.

Table S4. Results of a principal component analysis on the five health indices integument coloration, circulating carotenoids, body condition, haematocrit level and *Haemoproteus* parasite infection status.

Table S5. Candidate models ranked by AIC_c of health indices.

Table S6. Parameter estimates for the best model of each health index.