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# Agricultural land use and human presence around breeding sites increase stress-hormone levels and decrease body mass in barn owl nestlings

Bettina Almasi[1] · Paul Béziers[2] · Alexandre Roulin[2] · Lukas Jenni[1]

**Abstract** Human activities can have a suite of positive and negative effects on animals and thus can affect various life history parameters. Human presence and agricultural practice can be perceived as stressors to which animals react with the secretion of glucocorticoids. The acute short-term secretion of glucocorticoids is considered beneficial and helps an animal to redirect energy and behaviour to cope with a critical situation. However, a long-term increase of glucocorticoids can impair e.g. growth and immune functions. We investigated how nestling barn owls (*Tyto alba*) are affected by the surrounding landscape and by human activities around their nest sites. We studied these effects on two response levels: (a) the physiological level of the hypothalamus–pituitary–adrenal axis, represented by baseline concentrations of corticosterone and the concentration attained by a standardized stressor; (b) fitness parameters: growth of the nestlings and breeding performance. Nestlings growing up in intensively cultivated areas showed increased baseline corticosterone levels late in the season and had an increased corticosterone release after a stressful event, while their body mass was decreased. Nestlings experiencing frequent anthropogenic disturbance had elevated baseline corticosterone levels, an increased corticosterone stress response and a lower body mass. Finally, breeding performance was better in structurally more diverse landscapes. In conclusion, anthropogenic disturbance affects offspring quality rather than quantity, whereas agricultural practices affect both life history traits.

**Keywords** Anthropogenic disturbance · Breeding success · Corticosterone · Disturbance · Fitness

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## Introduction

Human presence and land use modify environmental conditions constantly and unpredictably for most free-ranging organisms. In particular the modification of habitats by humans or the creation of new types of habitats (e.g. agricultural land, human settlements) determines the occurrence of many organisms (Konstantinov 1996; Marzluff 2001). Broadly we can divide species into three groups: those which are restricted to pristine habitats; those which tolerate or depend on human-influenced or human-made habitats, but do not live or breed in human settlements; and the synanthropic species which live close to humans or even depend largely on human settlements and buildings for reproduction.

Human activities can have a suite of positive and negative effects on animals (Johnston 2001; Müllner et al. 2004). Understanding the extent to which animals can tolerate or

benefit from diverse human activities is an important issue in conservation biology. Effects of humans on animals may be indirect through alterations of habitats (including food availability, parasites, etc.) or direct through disturbance and destruction of individuals (e.g. hunting) or nest sites. For example, profound changes in habitat through agriculture has allowed the expansion of many species living in open land, but the recent intensification of agriculture has led to dramatic declines in many species (e.g. Donald et al. 2001). Synanthropic species directly depend on human settlements, but may suffer from continuous disturbance. Humans often affect animals unpredictably (e.g. during the harvest). Since animals rely on specific evolved cues to choose their breeding habitats, human interventions can lead to maladaptive settlement decisions with reduced reproductive performance (Hollander et al. 2011).

Human activities, whether direct or indirect, can affect one or several response levels: (a) physiological or behavioural responses (mostly short term); (b) fitness parameters (e.g. survival, productivity) and habitat use (mostly medium term); and (c) long-term consequences for populations and species. Because an effect on one response level does not necessarily result in an effect on another response level, and because many different parameters may be affected, the effects of human activities are often difficult to ascertain.

In cases in which animals do not disappear (emigration or death), the diverse direct and indirect human activities manifest themselves often in a common physiological response (Wingfield et al. 1998; Partecke et al. 2006). Hence, physiological measures could be an appropriate tool to monitor the well-being of individuals (Wikelski and Cooke 2006). The level of glucocorticoids (stress hormones) is such a physiological measure (Madliger and Love 2014), which integrates the effects of e.g. human-induced habitat deteriorations (Zhang et al. 2011; Bauer et al. 2013; Chavez-Zichinelli et al. 2013) and direct anthropogenic disturbance (Romero and Wikelski 2002; Müllner et al. 2004; Thiel et al. 2008; Strasser and Heath 2013). Commonly, two different measures of corticosterone are used: (a) baseline glucocorticoid levels, which have an important role in energy regulation and maintain homeostatic energy balance; and (b) the release of glucocorticoids to an acute standardized stressor such as handling (acute glucocorticoid response), which mediates physiological and behavioural changes in order to cope with an acute stress situation (reviewed in Sapolsky et al. 2000); this can be regarded as a measure of how animals respond to an acute stressor. Human-derived environmental alterations or direct disturbances can last for days and lead to chronic stress which can negatively affect health and fitness (Sapolsky et al. 2000). It is commonly assumed that chronic stress leads to an increase in baseline corticosterone levels (Bonier et al. 2009b). While the majority of studies support a positive relationship between baseline glucocorticoid levels and chronic stress, especially those of food stress, there is a substantial number of studies showing no change in baseline corticosterone due to chronic stress (Dickens and Romero 2013). For the effect of chronic stress on the acute glucocorticoid stress response, there is no general prediction from the literature (Dickens and Romero 2013). The lack of a uniform pattern may be due to large between-individual variation (Cockrem and Silverin 2002; Almasi et al. 2010; Lynn et al. 2010) and the additional interference of life history stage, age, sex and context. Hence there is a need for studies investigating which direct or indirect human activities are reflected in elevated baseline corticosterone, indicative of a disturbance of homeostasis, or an altered glucocorticoid stress response, and whether such changes translate into a reduction of fitness parameters.

Indirect effects of human activities (habitat alterations) are well known to affect habitat use, occurrence and fitness parameters (e.g. survival, productivity). Less well known are direct effects of human presence, especially in synanthropic species which are seemingly well adapted to humans. The aim of this study is to simultaneously study the effects of both direct and indirect effects of human activities on two response levels (physiology and fitness parameters) in a synanthropic bird species, the barn owl. On the European continent the barn owl is almost entirely dependent on buildings for nesting, and hunts for voles and mice in open landscapes, mostly human-made agricultural areas where availability and accessibility of small rodents depend mainly on crop types, vegetation height, and agricultural intensity (Arlettaz et al. 2010). Hence, barn owl nestlings are potentially affected by both direct (human-made noise and disturbance at the breeding site) and indirect (the type of agriculture determining the availability of food) human activities.

We therefore investigated how nestling barn owls are affected by the surrounding landscape and agricultural intensity (agricultural area around breeding sites, crop type, rural settlements, hedges, etc.) as well as by human activities around the nest site located in buildings (human presence and noise around breeding sites). We studied these effects on two response levels: (a) the physiological level of the hypothalamus–pituitary–adrenal (HPA) axis, represented by baseline concentrations of corticosterone and the concentration attained by a standardized stressor (hereafter referred to as the 'acute corticosterone response'); (b) fitness parameters: growth of the nestlings, which in many species is a good predictor of survival in the nest and after fledging (Roulin 2002), and breeding performance, i.e. number of eggs and fledglings.

## Materials and methods

### Study species and study area

Barn owls breed between February and August. Females lay between two and 11 eggs per clutch and start incubation for 32 days after the first egg is laid. Females lay eggs at intervals of 2–3 days, which leads to a pronounced within-brood age hierarchy. Nestlings fledge at the age of 50–60 days (Mebs and Scherzinger 2000). The study was carried out in 2004–2006, 2009, and 2010 in an open rural landscape dominated by intensive agriculture in western Switzerland (46°49′N, 06°56′E). All breeding males ($n = 89$) and females ($n = 99$) were captured during the nestling period and classified as 'yearling' or 'adult'. If adults had not been ringed as nestlings, we classified them as yearling if all primary and secondary feathers belonged to the same generation, and as adult otherwise (Taylor 1993). Females were distinguished from males by the presence of a brood patch.

In 4 of the 5 years we carried out cross-fostering experiments by swapping eggs or hatchlings between pairs of randomly chosen nests (no cross-fostering was carried out in 2005). This design was useful to partition phenotypic variation into genetic and environmental components. These experiments have already been the topic of several publications where we explain the method in detail (e.g. Roulin et al. 2010). Two hundred and sixteen nestlings for which we measured body mass were raised in a different nest (nest of rearing; $n = 77$ nests) to the one where they hatched (nest of origin; $n = 80$ nests), whereas 370 nestlings were raised in the same nest in which they hatched.

### Potential disturbance parameters and landscape characteristics

Data on potential disturbance parameters were collected for 190 nest boxes mounted on farms in an area of 560 km$^2$ during the breeding season in 2009. For each nest box we measured the following two disturbance parameters, which we consider as potential sources of stress for barn owls: distance (m) to the next inhabited house, and whether there were livestock present during the breeding season within a radius of 20 m around the barn where the nest box was located. Both potential disturbance parameters (livestock present around barns with nest boxes and distance to the next inhabited house) stand for a more frequent and longer presence of farmers at the breeding site. We verified with the farmers whether the use of the barns had changed considerably during the last 6 years and, if necessary, adjusted the measurements.

The environment surrounding the 190 nest boxes was described with the help of geographic information system software and aerial orthophotographs (0.5-m resolution; Geodata Swisstopo—DV084371, 2004). The landscape within a radius of 1 km around the nest box [which corresponds to the mean home range used by breeding barn owls (Arlettaz et al. 2010)] was described with nine habitat variables: areas of wood, village, hedgerow and trees, river, orchard, vineyard, open water, swamp and agricultural land. In summer 2009, the agriculture land of the region was further subdivided into cereals (wheat, barley, rye, triticale, oats), sugar beet, meadow, maize, tobacco, sunflower, potato, colza, pea, wildflower fields and market gardening by field surveys. In the study area, meadows include fertilised grasslands that are part of the crop rotation or pastures. To estimate the degree of parcelling of the landscape, the total perimeter of the fields in a radius of 1 km around each nest box was calculated, so that the higher the total perimeter of the fields was, the smaller the fields were. For further details on the assessments of the landscape characteristics see Frey et al. (2011).

For the statistical analyses we considered the area of the four main landscape variables (wood, agricultural land, urban area, hedgerow and trees), of the four main crop types (cereals, sugar beet, maize, meadow) and the total perimeter of all categories, but omitted the habitat variables with areas below 5 % of the total area. These variables together give a set of nine landscape characteristics. To obtain a reduced set of landscape characteristics out of the nine variables, we performed a principal components (PC) analysis and selected the components with eigenvalues larger than one (Table 1). The PCs were calculated with the library psych (Revelle 2012)

**Table 1** Principal components (*PC*s) analysis of eight habitat variables and the parcelling of the landscape (sum of the perimeters of all the fields measured in a radius of 1 km around each barn owl nest box)

| Habitat variables | PC1 | PC2 | PC3 |
|---|---|---|---|
| Parcelling of the landscape | | *0.46* | *0.76* |
| Hedgerow area | | *0.61* | 0.23 |
| Village area | | *0.86* | −0.15 |
| Wood area | *−0.75* | *−0.56* | |
| Agriculture land area | *0.93* | | 0.31 |
| Sugar beet area | *0.81* | | −0.29 |
| Maize area | *0.65* | | |
| Meadow area | −0.13 | −0.13 | *0.89* |
| Cereal area | *0.84* | −0.15 | −0.15 |
| Eigenvalue | 3.3 | 1.7 | 1.6 |
| Cumulative variance | 0.36 | 0.55 | 0.73 |

The correlations between the original variables and the first three PCs (eigenvalues >1) are given. The factor scores of the first three PCs (PC1–3) were used in the mixed-effect model analyses. Values in *italic* represent parameters with a high factor score

and we rotated the axis with the varimax function from the library GPArotation (Bernaards and Jennrich 2012). To link the landscape characteristics in 2009 to measurements of nestling corticosterone levels, body mass and breeding performance over the last 6 years, we assumed that the habitat did not change considerably during this period. Farms are usually small in the study area (26.6 ha) and they follow a crop rotation which lasts usually for 6 years. This means that locally there can be differences between years but on the level of the farm the agricultural land use should be quite stable (Bundesamt für Landwirtschaft 2014). This assumption is supported by the observation that the proportion of a given prey species in a given nest site was significantly repeatable over the years in the study area (Roulin 2004a). Over a longer period of time there is a small trend that crop area decreased and intensive meadows increased (Bundesamt für Landwirtschaft 2014).

## Assessment of baseline and stress-induced corticosterone levels

We collected several blood samples of barn owl nestlings of various ages [range 4–60 days, mean 32 ± 0.4 (SE) days] to measure baseline corticosterone and the acute corticosterone response to handling for other studies. Baseline samples were taken within 3 min after opening the nest box as the increase in corticosterone during the first 3 min of the onset of the stress situation is marginal (Romero and Reed 2005; Roulin et al. 2010). After taking the baseline sample birds were weighed (range 30–460 g, mean 304 ± 3 g) and then kept in cloth bags until a second blood sample was taken 25 min after capture to measure the acute corticosterone response to handling. In the barn owl the 25-min blood sample captures the peak of the corticosterone response to an acute stress situation (mean baseline corticosterone, 8 ± 1.1 ng/ml; 10 min after capture, 24 ± 1.8 ng/ml; 25 min after capture, 37 ± 1.7 ng/ml; 40 min after capture, 33 ± 3.6 ng7 ml; own unpublished data).

## Total corticosterone assay

Plasma total corticosterone concentration was determined by using an enzyme immunoassay (Munro and Stabenfeldt 1984; Munro and Lasley 1988) following Müller et al. (2006). Ten microlitres of plasma was added to 190 µl water, and from this solution we extracted corticosterone with 4 ml dichloromethane, which was re-dissolved in phosphate buffer and measured in triplicate in the enzyme immunoassay. The dilution of the corticosterone antibody (Chemicon; cross-reactivity—11-dehydrocorticosterone 0.35 %, progesterone 0.004 %, 18-hydroxy-11-deoxycorticosterone 0.01 %, cortisol 0.12 %, and aldosterone

0.06 %) was 1:8000. We used horseradish peroxidase (1:400 000) linked to corticosterone as the enzyme label and 2,2′-azino-bis(3-ethylbenzthiazoline-6-sulphonic acid as substrate. The concentration of corticosterone in plasma samples was calculated by using a standard curve run in duplicate on each plate. If the corticosterone concentration was below the detection threshold of 1 ng/ml the analysis was repeated with 15 or 20 µl plasma. Plasma pools from chicken with a low and high corticosterone concentration were included as internal controls on each plate. Intra-assay variation ranges from 5 to 17 % and inter-assay variation from 12 to 25 %, depending on the concentration of the internal control.

## Statistical analyses

We modelled the effects of different landscape characteristics and two potential disturbance parameters on baseline corticosterone, the acute corticosterone response, and body mass of nestling barn owls, and on breeding performance of adult barn owls, with linear mixed-effect models. We used model selection and model averaging based on Akaike's information criterion corrected for small sample size (AICc) (Burnham and Anderson 2002). For all analyses we used the statistical software R version 2.15.1 (R Development Core Team 2012) and the package lme4 (Bates et al. 2012). To directly compare effect sizes of fixed effects on different measurement scales and to allow comparison of main effects when interactions were present, we standardized numeric input variables to means of zero and SDs of one.

To model the effects of landscape characteristics and potential disturbance parameters on the two corticosterone measurements and nestling body mass we created three different sets of mixed-effects models. To account for different origins of the nestlings we always included the nest of origin and nest of rearing as two random intercepts. Nestling identity was introduced as an additional random intercept to account for repeated measurements of individuals. Our full models for the model sets with baseline corticosterone and the acute corticosterone response as dependent variables contained nestling age in days, relative body mass [residuals of mass (g) in relation to age and age$^2$], Julian date (hereafter 'date'), and brood size (number of nestlings in the nest box on the day of sampling), the three PCs of landscape characteristics (PC1, PC2, PC3; Table 1) and the two potential disturbance variables (distance of the nest box to the next inhabited house, and whether livestock were present within 20 m of the nest box). The first PC represents the total agricultural area as well as the different crop type areas. Since vegetation height of these areas varies strongly over the course of the season we also included the interaction date × PC1. The full model with nestling body

mass as dependent variable contained the above-mentioned variables except relative body mass and additionally age$^2$ and age$^3$ and time (time of day when we collected the blood sample). For the three dependent variables we constructed three sets of models with all possible combinations of the landscape (PC1, PC2, PC3) and disturbance (distance to inhabited house, and livestock present) variables and calculated AICc for all models. To account for model selection uncertainty and to assess the importance of the PCs and the potential disturbance variables we used model averaging (Burnham and Anderson 2002) of all models with a difference in AICc < 4 from the model with the lowest AICc (hereafter called 'top models'). The functions available in the R package MuMln were used. We calculated Akaike model weights (Anderson et al. 2000) of the top models, which indicate the probability that a given model is the best among the whole set of candidate models. Weights of models sum up to 1 by definition. Parameter estimates are multiplied by the weight of the particular model and summed over all top models to give the weighted average of the estimated parameters. We always present averaged standardised effect sizes, averaged SEs and averaged 95 % confidence intervals (CI) using the function model.avg and confint from the package MuMln. Averaged effect sizes are significantly different from zero if their 95 % CI do not include zero.

Note that the predictor variables of interest (distance to inhabited house, PC1, PC2, PC3, and livestock present around breeding sites) were not correlated among each other. There was a weak correlation between PC1 and date ($r = 0.21$), and between brood size and distance to inhabited house ($r = -0.25$), which did not cause any numeric problems in the models. All other predictor variables of interest were not correlated with the other covariables.

To visualize the effect sizes we used Bayesian methods. For the top models we simulated a random sample ($n$ total = 2000, $n$ for each model = $n \times$ model weight) from the joint posterior distribution of the model parameters using the function sim of the package arm. For each of the 2000 sets of simulated model parameters, we obtained predicted values for all new values of the predictor variables. The new values of the predictor variables always span the whole range of the variable (or each factor level) of interest; all other variables were held constant at their mean. In this way, we obtained for each new value of the variable of interest a sample of 2000 random draws from the posterior distribution of the model predictions. From this sample, we used the mean as predicted value and the 2.5 and 97.5 % quantiles as lower and upper limits of the 95 % credible interval (CrI).

To model the effects of landscape characteristics and potential disturbance parameters on breeding performance of the adult barn owls we used clutch size and number of fledglings as proxies for breeding performance and created two sets of mixed-effects models which always contained mother identity, father identity and brood identity as random effects. Our full models for the model sets with clutch size and number of fledglings as dependent variables contained mother and father age category (yearling or adult), relative nestling body mass [residuals of mass (g) in relation to age and age$^2$], date, the three PCs of landscape characteristics (PC1, PC2, PC3; Table 1) and the two potential disturbance variables (distance to the next inhabited house, and whether livestock were present). We then built the model sets, model averaging and predictions as described above.

Assumptions of normality for linear mixed-effect models were verified for each of the full models per set by visual inspection of the residuals.

## Results

### Baseline corticosterone

The model selection procedure for baseline corticosterone yielded eight models with similar AICc values ($\delta$AICc < 4; ESM Table S1A). Among the three landscape parameters (PC1–3), PC3 was the variable with the largest averaged effect size whose 95 % CI did not contain zero (Tables 2, S1) and was present in all eight top models. A high factor score of PC3 represents a landscape with many small field parcels and many meadows and was weakly positively correlated with baseline corticosterone (Fig. 1c). The second most important landscape variable based on averaged effect size obtained from the model selection procedure was the interaction of PC1 with date and was present in six out of the eight top models (Tables 2, S1). A high factor score of PC1 represents intensive agricultural land use [PC1 was positively related with agricultural area and the area of the three main crop types (cereal, sugar beet and maize) and negatively with wood area; Table 1]. Early during the breeding season baseline corticosterone was weakly negatively correlated with the intensity of agricultural land use, while late in the season baseline corticosterone concentration was higher in more intensively cultivated areas (Fig. 1a). The potential disturbance variable livestock present had the largest averaged effect size and was present in six of the eight top models (Tables 2, S1). Nestlings had lower baseline corticosterone levels when growing up at sites where livestock were present (Table 2; Fig. 2). The large and overlapping 95 % CrI in the effect size plot (Fig. 2a) shows that there is a significant difference between nestlings in sites with or without livestock but the mean corticosterone concentration can only be estimated with a large uncertainty. The second PC and the distance to

**Table 2** Model-averaged standardised estimates, unconditional SE, and 95 % confidence intervals (*CI*) for three models with the dependent variables baseline corticosterone, the acute corticosterone response, and nestling body mass of nestling barn owls

| Explanatory variables | Log (baseline corticosterone)[a, b] | | | Acute corticosterone response[c] | | | Nestling body mass[d] | | |
|---|---|---|---|---|---|---|---|---|---|
| | Estimate | SE | 95 % CI | Estimate | SE | 95 % CI | Estimate | SE | 95 % CI |
| *i* | *203.3* | *0.2* | *(169.7, 237.1)* | *44.1* | *7.4* | *(29.6, 58.5)* | *356.8* | *61.8* | *(345.4, 368.1)* |
| *a* | 0.1 | 2.0 | (−4.03, 4.3) | *10.0* | *1.2* | *(7.5, 12.6)* | *48.9* | *1.9* | *(45.1, 52.7)* |
| $a^2$ | – | | | – | | | *−29.2* | *0.8* | *(−30.8, −27.6)* |
| $a^3$ | – | | | – | | | *1.9* | *0.6* | *(0.7, 3.1)* |
| *m* | *−2.0* | *0.1* | *(−0.33, −0.1)* | −0.1 | 0.02 | *(−0.16, −0.07)* | – | | |
| *b* | 2.0 | 2.0 | (−2.80, 6.9) | −2.0 | 1.4 | (−4.7, 0.8) | −0.1 | 1.6 | (−3.3, 3.1) |
| *t* | | | | | | | *−3.8* | *1.1* | *(−5.8, −1.7)* |
| *d* | −1.0 | 2.0 | (−6.3, 3.2) | 1.2 | 1.3 | (−1.3, 3.7) | *−5.4* | *1.6* | *(−8.5, −2.3)* |
| dh | 4.2 | 2.6 | (−0.8, 9.2) | *−2.1* | *1.2* | *(−4.5, −0.3)* | 2.01 | 2.0 | (−1.0, 5.1) |
| ah | *−11.08* | *5.1* | *(−21.0, −1.2)* | 1.1 | 2.7 | (−4.5, 5.9) | *−10.4* | *3.3* | *(−16.9, −3.9)* |
| PC1 | 2.20 | 2.5 | (−2.7, 7.2) | *2.8* | *1.3* | *(0.5, 5.5)* | *−3.8* | *1.6* | *(−7.0, −0.6)* |
| PC2 | −1.52 | 2.4 | (−6.2, 3.1) | 1.8 | 1.3 | (−0.7, 4.3) | 0.2 | 0.6 | (−2.9, 3.2) |
| PC3 | *6.6* | *2.1* | *(1.5, 11.7)* | 0.7 | 1.4 | (−2.1, 3.5) | −1.3 | 1.7 | (−4.7, 2.0) |
| PC1 × *d* | *5.7* | *2.2* | *(1.3, 10.0)* | 0.3 | 1.2 | (−2.1, 2.8) | 1.5 | 1.4 | (−1.2, 4.3) |

Year, brood identity and nestling identity nested in brood identity were introduced as random factors. The full models contained: intercept (*i*); age of the nestling (*a*; $a^2$, and $a^3$ for the model with nestling body mass); Julian date (*d*); brood size (*b*); time of day for the model with nestling body mass as dependent (*t*); relative body mass (*m*; for the corticosterone analysis only); livestock present within a radius of 20 m around the nest box (yes/no) (*ah*); distance to the nearest inhabited house (*dh*); PCs of Table 1 (*PC1–3*); and the interaction of PC1 × *d*

Values in *italic* represent significant parameters

[a] Log (baseline corticosterone) × 100

[b] The analyses are based on 1018 measurements of 519 individuals from 141 broods

[c] The analyses are based on 647 measurements of 405 individuals from 111 broods

[d] The analyses are based on 1116 measurements of 533 individuals from 141 broods

the next inhabited house were not good predictors for baseline corticosterone (all 95 % CI of the averaged effect sizes included zero; Table 1; Figs. 2b, 3a).

**Acute corticosterone response**

The model selection procedure for the acute corticosterone response yielded 22 models with similar AICc values (δAICc < 4; ESM Table S1B). The most important variable of the habitat characteristics and potential disturbance parameters was the first PC which was present in 19 of the 22 top models and had the largest averaged effect size whose 95 % CI did not contain zero. The models showed that stress-induced corticosterone was higher in more intensively cultivated areas throughout the season compared to less intensively cultivated areas (Fig. 1d). The variable with the second largest effect size was distance to the nearest inhabited house, which was present in 14 of the 22 top models and its 95 % CI did not include zero. The model predictions showed that stress-induced corticosterone concentrations were higher when the nest was closer to an inhabited house (Fig. 2b). The second and third PCs

of landscape characteristics, the interaction of the first PC with date and the potential disturbance parameter livestock present were not good predictors for stress-induced corticosterone (all 95 % CI of the averaged effect sizes included zero; Table 2).

**Nestling body mass**

The model selection procedure for nestling body mass yielded 15 models with similar AICc values (δAICc < 4; ESM Table S1C). The potential disturbance parameter livestock present was present in all top models and had the largest averaged effect size whose 95 % CI did not include zero (Table 1). Body mass was lower when nestlings grew up in sites where livestock were present compared to sites without livestock (Fig. 2c). The second important variable was the first PC of landscape characteristics, which was present in 14 of the 15 best models and whose 95 % CI did not include zero. Nestling body mass was lower in more intensively cultivated areas compared to less intensively cultivated areas (Fig. 1g). The second and third PCs, the interaction of date with the first PC and the distance to
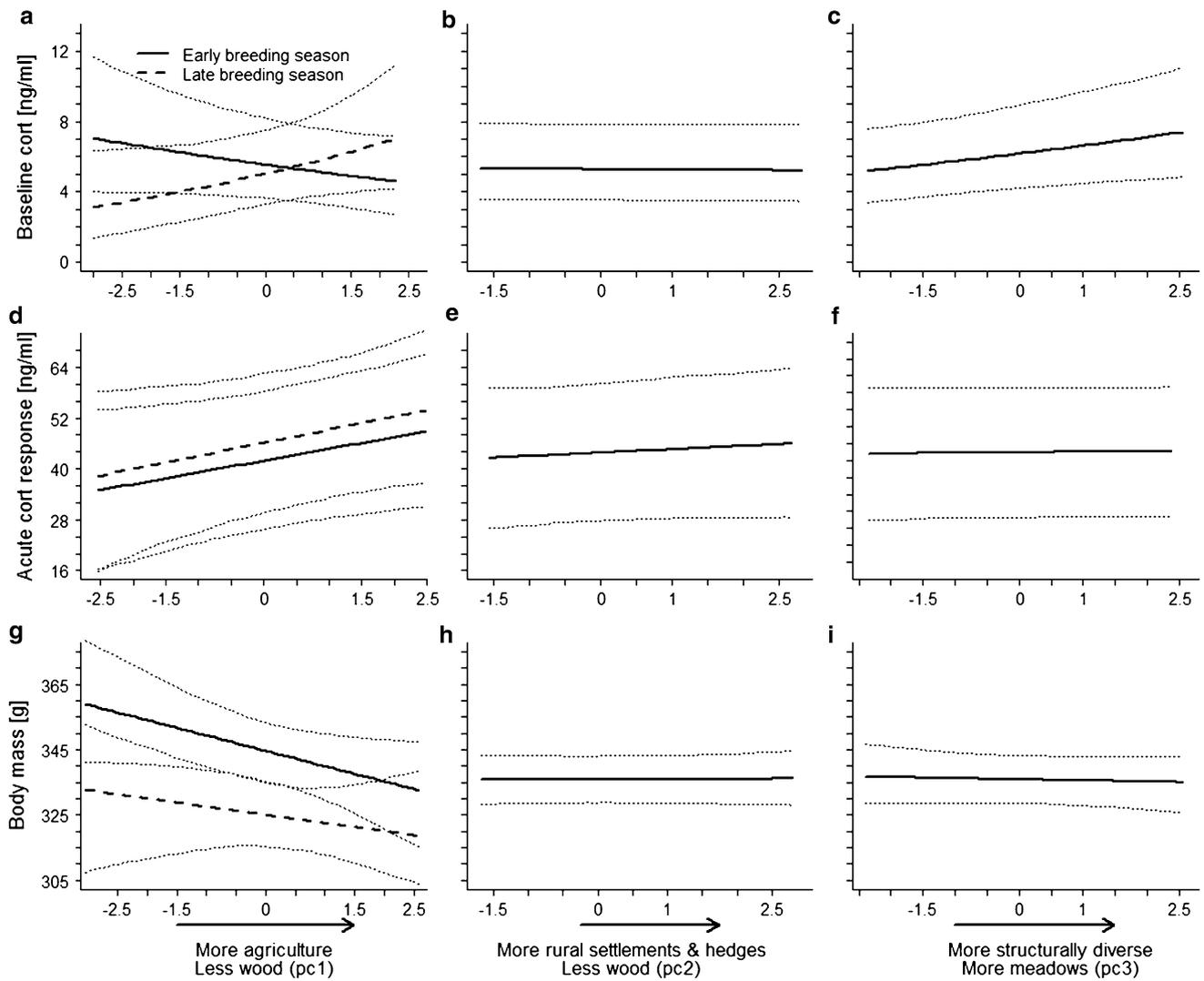
**Fig. 1** **a–c** Predicted baseline corticosterone levels [with 95 % credible intervals (CrI); *dotted lines*] of barn owl nestlings in relation to landscape characteristics in a radius of 1 km around the nest box, based on model averaging of Table S1 with **a** the first, and **b** the second, and **c** the third principle component (*PC*) (see Table 1). **d–f** Similar graphs of the predicted acute corticosterone response (with 95 % CrI) in relation to the three PCs. **g–i** Similar graphs of predicted nestling body mass (with 95 % CrI) in relation to the three PCs based on model averaging of the models given in Table S1. To illustrate the interaction of PC1 with date in graphs **a** and **g** (see Table 2), we arbitrarily selected an early date (*solid line* 25 % quantile of the date, 5 May) and a late date (*broken line* 75 % quantile of the date, 8 September)

the nearest inhabited house were not good predictors for nestling weight (all 95 % CI of the averaged effect sizes included zero; Table 2).

### Clutch size and number of fledglings

The model selection procedure for clutch size yielded 16 models with similar AICc values (δAICc < 4; ESM Table S2A). The 95 % CI of the interaction of PC1 with date, which was present in five of the 16 best models, did not include zero. Clutch size increased along the season and was larger in more intensively cultivated areas late in the

season than in less intensively cultivated areas (Fig. 3). The second and third PCs of landscape characteristics, whether livestock were present, and the distance to the nearest inhabited house were not good predictors for clutch size (its 95 % CI of the averaged effect sizes included zero; Table 3).

The model selection procedure for number of fledglings yielded 13 models with similar AICc values (δAICc < 4; ESM Table S2B). Eleven of the 13 best models contained the second PC of landscape characteristics which was also the only parameter of interest whose 95 % CI did not include zero. Number of fledglings was higher in areas
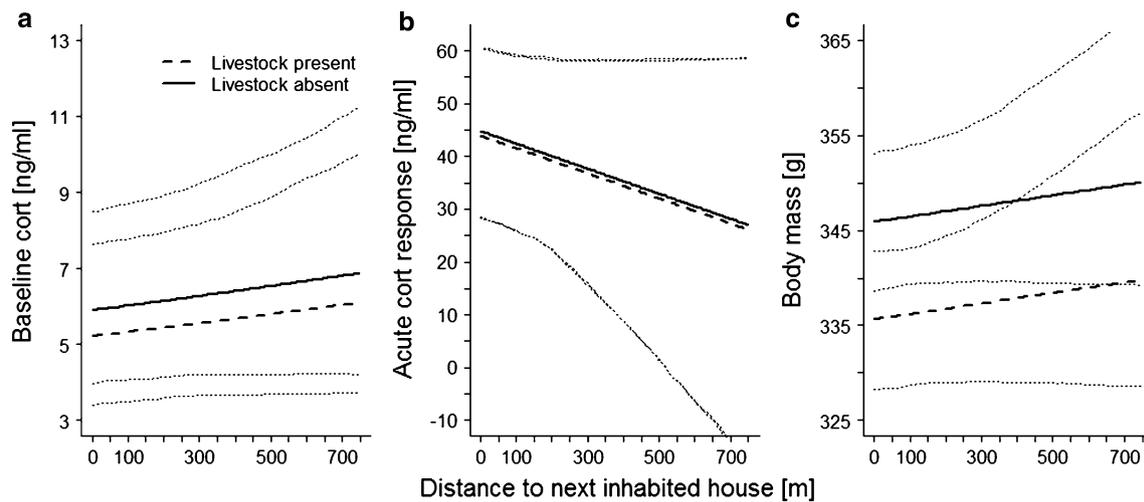
**Fig. 2** **a** Predicted baseline corticosterone level (with 95 % CrI), **b** predicted acute corticosterone response (with 95 % CrI), and **c** predicted body mass (with 95 % CrI) of barn owl nestlings in relation to the distance of the nest box to the next inhabited house and whether livestock were present in a radius of 20 m around the nest box, based on model averaging of the models given in Table S1
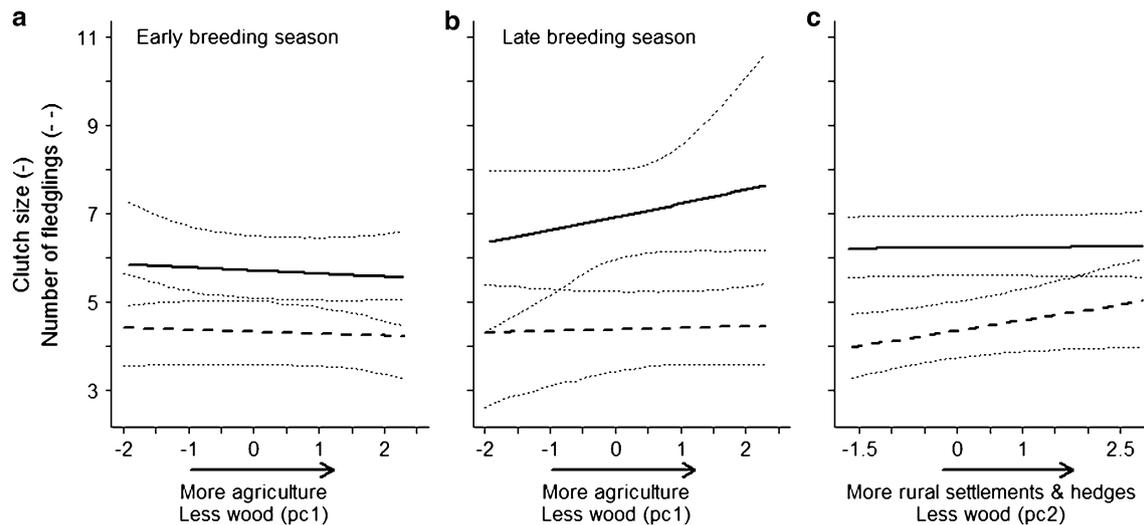


**Fig. 3** Predicted clutch size (*solid line*) and number of fledglings (*dotted line*) (with 95 % CrI) in the barn owl **a** early in the season (25 % quantile of the date, 5 May) in relation to PC1; **b** late in the season (75 % quantile of the date, 8 September) in relation to PC1; and **c** in relation to PC2, based on model averaging of the models given in Table S2. For abbreviations, see Fig. 1

with more small rural settlements and hedges and less wooded areas (Fig. 3c). The difference between clutch size and number of fledglings was smaller in areas with more small rural settlements and hedges and less wooded areas, indicating that the rearing success in these areas was higher (Fig. 3c).

## Discussion

We investigated how man-made habitat characteristics and anthropogenic disturbance are related to glucocorticoid levels and body mass of nestling barn owls and parental breeding performance. We found that both the intensity of agriculture and indices of anthropogenic disturbance had an effect on baseline corticosterone and the acute corticosterone response and resulted in a lower nestling body mass (Table 4), which suggest that overall agricultural intensity negatively affects nestling fitness. Further, in areas with more small rural settlements and hedges more nestlings survived until fledging. This finding probably reflects that food abundance is generally higher and more stable in areas with more small rural settlements and hedges than in agricultural areas (Table 4).

**Table 3** Model-averaged standardised estimates, unconditional SE, and 95 % CIs for two mixed-model analyses with the dependent variables clutch size, and number of fledglings in the barn owl

| Explanatory variables | Clutch size | | | Number of fledglings | | |
|---|---|---|---|---|---|---|
| | Estimate | SE | 95 % CI | Estimate | SE | 95 % CI |
| *i* | *1.73* | *0.07* | *(1.63, 1.84)* | *3.68* | *0.44* | *(2.83, 4.54)* |
| fa | −0.02 | 0.07 | (−0.11, 0.08) | 0.60 | 0.36 | (−0.11, 1.32) |
| ma | *0.10* | *0.05* | *(0.03, 0.18)* | 0.01 | 0.29 | (−0.57, 0.61) |
| *d* | *0.05* | *0.02* | *(0.01, 0.09)* | 0.03 | 0.13 | (−0.23, 0.29) |
| dh | 0.02 | 0.02 | (−0.02, 0.05) | −0.13 | 0.12 | (−0.38, 0.11) |
| ah | 0.01 | 0.05 | (−0.06, 0.07) | 0.17 | 0.25 | (−0.33, 0.66) |
| PC1 | 0.02 | 0.02 | (−0.01, 0.06) | −0.03 | 0.13 | (−0.28, 0.21) |
| PC2 | 0.01 | 0.02 | (−0.02, 0.04) | *0.27* | *0.12* | *(0.03, 0.51)* |
| PC3 | −0.01 | 0.02 | (−0.04, 0.03) | −0.03 | 0.13 | (−0.28, 0.21) |
| PC1 × d | *0.04* | *0.02* | *(0.01, 0.07)* | 0.18 | 0.12 | (−0.05, 0.42) |

Year, and female identity were introduced as random factors. The analyses are based on 126 broods of 89 breeding females. The full model contained: *i*, age of the biological mother (*ma*), age of the biological father (*fa*), *ah* (yes/no), *d*, *dh*, *PC1–3* PCs of Table 1, and the interaction of PC1 × *d*. For other abbreviations, see Table 2

**Table 4** Summary of the effects of landscape characteristics and anthropogenic disturbance around the nest box on physiological and fitness parameters of barn owls

| | Baseline corticosterone | Acute corticosterone response | Nestling body mass | Clutch size | Number of fledglings |
|---|---|---|---|---|---|
| **Landscape characteristics** | | | | | |
| Intense agriculture, early season | *Lower* | *Higher* | *Lower* | No association | No association |
| Intense agriculture, late season | *Higher* | *Higher* | *Lower* | *Larger* | No association |
| More small rural settlements and hedges | No association | No association | No association | No association | *Higher* |
| Smaller field parcels | *Higher* | No association | No association | No association | No association |
| **Disturbance factors around nest boxes** | | | | | |
| Short distance to house | No association | *Higher* | No association | No association | No association |
| Livestock present | *Lower* | No association | *Lower* | No association | No association |

## Effects of landscape characteristics on glucocorticoids, growth, and breeding performance

Baseline corticosterone concentrations in barn owl nestlings varied along the season and with landscape characteristics around the breeding site. Early in the breeding season, when prey abundance is low (Aschwanden et al. 2007) but prey accessibility high, baseline corticosterone levels of nestlings were weakly negatively correlated with the intensity of the agricultural land use surrounding the breeding site. Late in the breeding season, when prey abundance is generally high but prey less accessible due to a dense and high vegetation cover (Aschwanden et al. 2005, 2007), we found a positive correlation between baseline corticosterone levels and the intensity of agricultural land use. This pattern most likely represents food availability for the

nestlings and corroborates patterns found in other species, with baseline corticosterone levels increasing when food availability becomes scarce (Kitaysky et al. 2007, 2010) or the habitat becomes suboptimal (Bonier et al. 2007). Further, the negative correlation of relative body mass with baseline corticosterone (Table 2) also indicates that baseline corticosterone increases when the energy requirements of the nestlings are no longer satisfied. One function of corticosterone is to slow down growth (Hull et al. 2007; Müller et al. 2009) and to mobilise stored energy via gluconeogenesis (Wingfield et al. 1998) and baseline corticosterone often negatively correlates with body mass (Wingfield et al. 1994; Schoech et al. 1997). An explanation of the weak negative correlation of agricultural intensity and baseline levels early in the breeding season might be that a large proportion of the agriculture area is used for winter wheat

which already accommodates a fair number of voles early in the breeding season (Arlettaz et al. 2010). With the available data we cannot distinguish between the direct effect of habitat quality (baseline levels increase when habitat quality decreases) and the indirect effect via the quality of the parents (low-quality territories might be occupied by low-quality parents).

Nestling body mass was generally lower late in the season than early and was lower in more intensively cultivated areas, which is an indication that food availability for nestlings in these areas may have been lower. The difference in body mass between habitat types might even affect post-fledging survival, as has been shown in other species (e.g. Perrins and McCleery 2001). The seasonal effect on nestling body mass helps to explain why some barn owls start breeding as early as spring conditions allow, even if this means that the birds lay smaller clutches [in contrast to most other bird species, clutch size increases along the season in barn owls (Frey et al. 2011)]. Vole and mice populations also increase along the season, but their accessibility or detectability decreases with vegetation cover (Arlettaz et al. 2010). For owls and other birds of prey it has been shown that vegetation structure is more important than small mammal abundance for the selection of hunting areas (Bechard 1982; Aschwanden et al. 2005; Arlettaz et al. 2010). Overall, our findings suggest that characteristics of man-made habitats influence both baseline corticosterone and growth.

We also found a strong correlation between the corticosterone response to an acute stressor and habitat characteristics. Nestlings reared in more intensively cultivated areas were more reactive to a new stressor, i.e. responded with a stronger release of corticosterone. Our results support findings of several studies showing that habitat condition and low food availability increase the reactivity of the HPA axis (Kitaysky et al. 2007; Romero and Wikelski 2010; Kitaysky et al. 2010). The increased reactivity of the HPA axis in more intensively cultivated areas did not depend on the season, while the effect on baseline corticosterone did. This suggests that baseline corticosterone and the acute glucocorticoid response to a stressor respond to different environmental cues or to different time scales. Baseline corticosterone seems to be more sensitive to the amount of food brought to the nest and hence to short-term conditions, while the acute corticosterone response appears to be correlated with the overall intensification of the area (including anthropogenic disturbance which occurs more frequently in intensively cultivated areas) and hence to longer-term conditions.

Clutch size, but not number of fledglings, increased along the season and this effect was more pronounced in more intensively cultivated areas. Also number of fledglings was strongly related to landscape characteristics. In areas with more anthropogenic landscape structures more nestlings survived until fledging than in areas with less structural diversity. In areas with more anthropogenic structures, and hence more different habitat types, overall food availability is probably more stable over the season and fledgling success is increased. A recent analysis of a larger data set (23 years) from the same population could not detect a significant correlation between landscape characteristics and clutch size or number of fledglings (Frey et al. 2011). This contradictory result may be explained by the fact that the change in landscape characteristics over the 23 years may not have been captured by this latter study and, therefore, might have caused substantial noise preventing the detection of correlations between current habitat characteristics and previous breeding performance. The present study only considered 5 years around the time point when the data on landscape characteristics were collected and might therefore have a better accuracy in describing them.

## Effects of human activities around breeding sites on glucocorticoids, growth, and breeding performance

Our two disturbance parameters (livestock present around barns with nest boxes and distance to the next inhabited house) stand for increased frequency and duration of presence of farmers at the breeding site. We found that nestlings growing up at sites where livestock were present had lower baseline corticosterone levels than nestlings at sites without livestock. Further, the acute corticosterone response to handling stress of nestlings was negatively related to the distance of the nest box to the next inhabited house. Frequent anthropogenic disturbance can cause chronic stress (e.g. Fowler 1999; Müllner et al. 2004; Walker et al. 2005) and that chronic stress can decrease baseline corticosterone as shown in previous studies in the wild and in captivity (Rich and Romero 2005; Cyr et al. 2007; Cyr and Romero 2007) and might be a sign of desensitisation of the HPA axis to a certain chronic stressor (Cyr and Romero 2009). The increased acute corticosterone response of nestlings living close to humans shows, on the other hand, that these nestlings are not habituated to anthropogenic disturbance (Cyr and Romero 2009). The latter finding is in line with results by Müllner et al. (2004) in the hoatzin (*Opisthocomus hoazin*). Even when parents choose to breed in a site with increased anthropogenic disturbance, and probably are habituated to it, nestlings may nevertheless be susceptible to anthropogenic disturbance which negatively affects their body mass and eventually survival. Whether an anthropogenic disturbance increases or decreases the HPA responsiveness depends strongly on the strength of the disturbance and on the life cycle stage of the animal [e.g. adults, nestlings, or older offspring may differ in how they

perceive anthropogenic disturbance; (Romero and Wikelski 2002; Walker et al. 2005; Dickens and Romero 2013)]. Frequent anthropogenic disturbance around the breeding sites can also change female brooding behaviour. Personal observations suggest that if we visit nest boxes frequently during early brooding, females start to sleep outside the nest boxes sooner and hence can no longer thermoregulate and feed prey remains to the young nestlings during the day. It is also known from mammalian studies that maternal separation at early age can increase the acute corticosterone response later in life (reviewed in Romero 2004). Unfortunately, we do not have any information regarding when females started sleeping outside the nest boxes.

Whether livestock were present around the breeding site had also a strong effect on nestling body mass. Nestlings located in sites with livestock had significantly lower body mass than in sites without livestock (Table 4). That we could not detect any effect of the variable livestock present on the acute corticosterone response may be due to the more predictable occurrence of the farmers on a regular feeding scheme for their animals. Nestlings may get used to the presence of the farmers in the buildings and no longer respond with corticosterone secretion. However, because nestling barn owls eat the prey remains from the night during daylight hours (Roulin 2004b), they nevertheless might have been disturbed in their feeding behaviour. Also we cannot exclude the possibility that sites with livestock may be of poorer quality (fewer voles) than sites without livestock.

Variation in breeding performance, on the other hand, could not be explained by the anthropogenic disturbance measurements. For adult barn owls the landscape characteristics seem to be more relevant for breeding success than anthropogenic disturbance. The changes in the HPA reactivity and the effects on nestling body mass could, in the end, lead to reduced survival of nestlings and hence reduced reproductive success for the parents. However, it still has to be shown whether a more reactive HPA axis and/or lower body mass during development have fitness consequences for the barn owls beyond fledging.

## Conclusion

Understanding the mechanism by which human activities affect reproduction and other fitness-related traits is crucial to mitigating the conflicts between human activities and wild animal populations. In the present study we showed that in nestlings of a synanthropic species the HPA axis (represented by baseline concentrations of glucocorticoids and the concentration attained by a standardized stressor), growth of the nestlings, and breeding performance are affected by landscape characteristics and anthropogenic activity around the breeding site. Small-scale anthropogenic

activity and large-scale landscape characteristics affected baseline corticosterone concentration, HPA axis reactivity and nestling body mass. Whether baseline corticosterone concentration and HPA reactivity correlate with fitness measures is still under debate and results are contradictory (e.g. Breuner et al. 2008; Bonier et al. 2009a; Angelier et al. 2010). However, our study indicates that landscape characteristics could also explain one measure of breeding performance, namely the number of fledglings a breeding couple could raise. Overall, anthropogenic disturbance seems to affect offspring quality rather than quantity; whereas agricultural practice affects both offspring number and quality.

Our study clearly showed that even in a synanthropic species, which largely depends on human buildings for breeding, anthropogenic activity affects nestlings. We therefore recommend ornithologists to install nest boxes at sites with the least possible human activity.

**Author contribution statement**  B. A., A. R. and L. J. conceived and designed the experiments. B. A. and P. B. performed the experiments. B. A. and P. B. analysed the data. B. A., A. R. and L. J. wrote the manuscript.

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