

Forest management is associated with physiological stress in an old-growth forest passerine

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We investigated how physiological stress in an area-sensitive old-growth forest passerine, the Eurasian treecreeper (*Certhia familiaris*), is associated with forest fragmentation and forest structure. We found evidence that the concentrations of plasma corticosterone in chicks were higher under poor food supply in dense, young forests than in sparse, old forests. In addition, nestlings in large forest patches had lower corticosterone levels and a better body condition than in small forest patches. In general, corticosterone levels were negatively related to body condition and survival. We also found a decrease in corticosterone levels within the breeding season, which may have been a result of an increase in food supply from the first to the second broods. Our results suggest that forest fragmentation may decrease the fitness of free-living individual treecreepers.

Keywords: forest fragmentation; physiological stress; offspring quality; corticosterone; treecreeper

1. INTRODUCTION

Loss of forest area and large-scale fragmentation are considered to be major threats to world biodiversity (Barbault & Sastrapradja 1995). Previously continuous forests have turned into managed forests, where small forest patches are usually separated by agricultural matrix, clear-cuts and young successional forests (Forman & Godron 1986; Gustafsson & Parker 1992). In small forest fragments, individuals may experience food shortage (Zanette *et al.* 2000). Lack of food may cause chronic physiological stress in individuals (Romero & Wikelski 2001). Chronic stress causes deleterious effects such as suppression of growth and of the immune system, severe protein loss and neuronal cell death, all of which may decrease the survival of individuals (Wasser *et al.* 1997; Wingfield *et al.* 1997; Romero & Wikelski 2001). Chronically high corticosterone concentrations can be especially deleterious to growing young (Martin 1985; Sapolsky 1987).

Physiological stress occurs in response to environmental factors such as food shortage and temperature and may depress resistance to diseases, survival and reproduction in a variety of species (see Harvey *et al.* 1984; Munck *et al.* 1984; Wingfield & Farner 1993; Wingfield *et al.* 1997; Romero & Wikelski 2001). However, direct measurements of physiological stress in relation to territory and habitat characteristics are scarce. We assessed chronic environmental stress at the individual level by assay of plasma corticosterone. It is the major glucocorticoid in birds (Norris 1996), and glucocorticoids are the primary hormones investigated in the study of responses to stress.

Our model species, the Eurasian treecreeper (*Certhia familiaris*) prefers forests of over 100 years old (Haila *et*

al. 1989; Virkkala *et al.* 1994; Väisänen *et al.* 1998). The occupancy of nest-boxes is low in young and fragmented managed forests (own unpublished data). The species specializes in searching for invertebrates, especially spiders (65% of nestling food mass) on large tree trunks (Suhonen & Kuitunen 1991a). The treecreeper starts breeding in early April when snow cover and night frosts still prevail in central Finland. Both males and females rear the first broods. In our nest-box population ca. 30% of the first breeders raise a second brood in June and July that is usually reared by the female only (Aho *et al.* 1999).

We studied how habitat structure affects the stress level of treecreeper chicks at three spatial scales:

- (i) territory core scale (at a radius of 30 m from the nest),
- (ii) territory scale (at a radius of 200 m from the nest), and
- (iii) large scale (at a radius of 500 m from the nest).

Our goals were to establish:

- (i) whether circulating corticosterone levels differ as a function of habitat structure at the three spatial scales,
- (ii) whether food supply changes with habitat structure at the territory cores, and
- (iii) whether food supply influences plasma corticosterone levels.

2. MATERIAL AND METHODS

(a) Study area and design

Corticosterone data were collected from the study area covering 115 000 ha in central Finland (62°37' N, 26°20' E) in the

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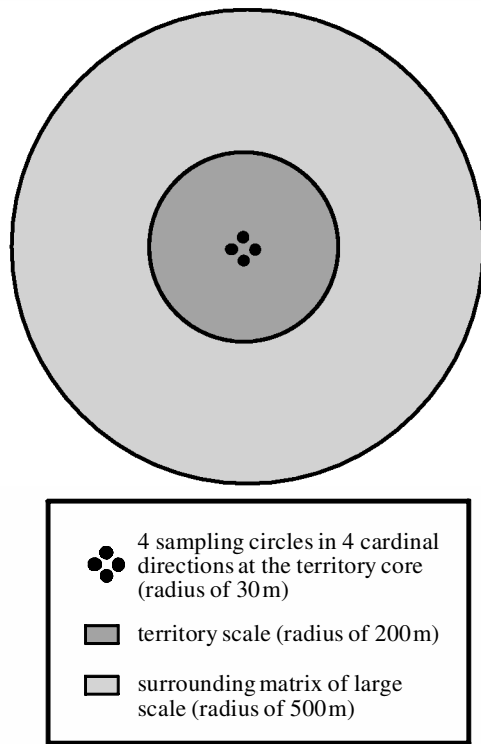


Figure 1. The three spatial scales around a territory centre.

summer of 2000. Forested land covered 71% of the study area, whereas the remainder consisted of man-made open habitats, such as cultivated fields (16%), clear cuts (3%), roads, etc. (5%) and natural open habitats, such as lakes (5%) and treeless bogs (0.1%).

Two nest-boxes were placed 30 m apart in the interior of a forest patch in the autumn of 1998. Each forest patch contained two nest-boxes for the possibility of a second breeding attempt by the territorial pair. We used 229 nest-box pairs in 229 forest patches differing in area, forest structure and age. Only one treecreeper pair occupied a nest-box pair at a time. Thus, we regarded the midpoint of nest-box pair as a territory centre and used territory as a sampling unit. Of the 229 nest-box pairs, 160 were occupied and considered territories. Of the 160 territories we were able to sample for corticosterone in 90 territories during the first broods and in 34 territories during the second broods. A forest patch with an occupied nest-box pair is hereafter referred to as a nesting forest patch. Habitat structure varied within these 124 territories as follows: nesting forest patch area (ha) range 0.1–71.1, mean 37.5 ± 17.9 (s.d.) at the large scale, and tree density (trunks per 50 m^2) range 1.5–11.8, mean 4.4 ± 1.6 and forest age (years) range 32–81, mean 52.3 ± 10.7 at the territory core scale.

(b) *Habitat structure of territories and surrounding landscape matrix*

Habitat structure around territory centres was established at three spatial scales (figure 1). We measured *territory core structure* (radius of 30 m) in the field as a result of the inaccuracy of satellite image-based land use and forest data on a small scale. Vegetation cover was measured within four sampling circles, each having a radius of 4 m. The non-overlapping sampling circles (50 m^2) were placed in four cardinal directions *ca.* 30 m from the territory centre (figure 1). The distance of 30 m was chosen explicitly, because most of the foraging trips of parent birds are in the vicinity of the territory centre during the nestling period:

range of trips from the nest 0–200 m, mean 23 m (Aho 1997). Measurements from the four sampling circles were averaged to a territory core level.

The structural variables of forest at the territory core area included mean density of tree trunks, mean circumference of tree trunks (cm), mean volume of trunks ($\text{m}^3 \text{ ha}^{-1}$) and mean trunk surface area (m^2) within a sampling circle (50 m^2). The floristic variables measured were the total numbers of pines, spruces, birches and other deciduous trees of more than or equal to 30 cm circumference at chest height. Thinner trunks were not included, because only 6% of observations of foraging parent birds involve trees of less than 30 cm circumference, suggesting that they are of minor importance at the nestling phase (own unpublished data). Forest age was estimated as follows. We first regressed the accurate age of stumps ($n = 145$, based on stump-derived annual rings) versus their circumference from 9 clear-cut territories in the summer of 2002 (linear regression, $\text{adjusted } r^2 = 0.42$, $t_{1,144} = 10.29$, $p < 0.0001$). We then interpolated the age of all territory core areas from the regression line, using mean circumferences measured at the territory core (mean trunk circumference = $[1.252 \times \text{age}] + 17.641$).

Forest structure and forest fragmentation variables at the *territory scale* (radius of 200 m) and at the *large scale* (radius of 500 m) were established from the classified Landsat TM 5 satellite images (from 1995 to 1997) produced by the National Land Survey of Finland (NLS) (Vuorela 1997). The satellite image-based land-use and forest data was imported to a Geographic Information System (GIS). The treecreeper territory is about 10 ha (Kuitunen & Törmälä 1983). During the nestling period the foraging trips of parents extend to a distance of 200 m from the nest (unpublished data). Hence, use of a scale of 200 m (12.6 ha) as a territory base was justified in this study. The large scale of 500 m (78.5 ha) is considered landscape level in this study, because in addition to territory it includes 65.9 ha of surrounding landscape matrix. Configuration of the landscape varied considerably at the larger scale, from continuous forests to fragmented areas including open habitats and saplings.

Forest structure variables included percentages of old forest, open habitat, spruce mire, pine mire, pine forest, spruce forest, deciduous forest, mixed forest, and saplings at both the territory and large spatial scales. The forest fragmentation variables were calculated using FRAGSTATS, a spatial analysis program (McGarigal & Marks 1995) and included forest patch density (number per 100 ha), mean forest patch size (ha), forest-open land edge density (m ha^{-1}), total edge (m), mean shape index, mean nearest-neighbour forest patch distance (m), and nesting forest patch (ha), at both the territory and large scales. A forest patch was defined in hectares as a separate forested area containing more than $50 \text{ m}^3 \text{ ha}^{-1}$. By using this criterion a forest patch was clearly separable from the neighbouring open habitats and saplings in the field.

The mean age of forests at the territory cores was used to classify old forests (more than 52 years) at the territory core scale. At the territory and large scales the proportion of old forest was classified according to the total volume of timber of greater than or equal to $102 \text{ m}^3 \text{ ha}^{-1}$, a figure that indicates a forest age of 50 years in central Finland (Tomppo *et al.* 1999). This corresponded well with the classification of old forest at the territory cores.

(c) *Food abundance*

The treecreeper specializes in searching for invertebrates, especially spiders on tree trunks. We measured food abundance

at the territory cores using vacuum cleaners on the tree trunks during the period immediately after fledging of young treecreepers (Aho *et al.* 1999). The trunk surface between the heights of 0.5 and 1.5 m was vacuumed in dry weather between 0900 and 1800. Time of day (to the nearest hour) had no effect on invertebrate densities (linear regression, $t_{1,119} = 1.17$, $p = 0.245$). Invertebrate samples were collected from six randomly selected tree trunks greater than or equal to 30 cm in circumference at a distance of 30 m from the nest. The distance of 30 m was chosen to fit the food supply measurements with vegetation descriptions at the territory core and because parents may deplete food resources less than 30 m from the nest (Jäntti *et al.* 2001). We did not try to standardize the area of tree trunk vacuumed for two reasons: first, because foraging treecreepers use all trunks greater than or equal to 30 cm and second, because we wanted to measure the variation in food supply on different sized trunks. The prey length of treecreepers ranges from 1 to 15 mm (Suhonen & Kuitunen 1991b); therefore, only invertebrates greater than or equal to 1 mm in size were included in the analyses. The mean invertebrate density (number of invertebrates per m² of trunk) and the mean volume index of invertebrates (mm³ per m² of trunk), except for ants, on six trunks were used as estimates of food supply at each territory core. Volume indices of invertebrate specimens ($n = 7347$) were calculated from the function $\pi(4Lw^2)$ for cylinder-like bodies, e.g. caterpillars, and from the function $\pi(6Lw^2)$ for ellipsoid-like bodies, e.g. spiders, where L is the length and w is the width of the body (Blondel *et al.* 1991).

(d) Blood samples and corticosterone assay

Nest-boxes were checked daily when necessary, to determine the accurate hatching date and the age of nestlings. Wing length was measured to 0.1 mm by the maximum method (Svensson 1992) and mass weighed to 0.1 g. Subcutaneous fat in the abdomen and tracheal pit was recorded on a five-point index (0–4) (Kaiser 1993). Nestlings were placed in a bag, moved to a vehicle, measured and blood sampled at the age of 9 days between 0800 and 1800. Time of day had no influence on stress hormone levels (linear regression, $t_{1,123} = 0.01$, $p = 0.995$). The age of 9 days was selected because it enabled us to measure post-hormone sampling nestling mortality and because the tarsometatarsal veins of the chicks were large enough to enable us to obtain an adequate blood sample. Blood samples of 50–80 μ l were taken in heparinized microhaematocrit capillary tubes after puncture of a tarsometatarsal vein. The tubes were centrifuged at $(3000 \text{ rpm}/1000)^2 \times 83 \text{ mm} \times 1.118 = 835.146 \times g$ for 10 minutes in the field. Plasma was extracted and stored immediately in liquid nitrogen.

Plasma concentrations of corticosterone were measured using Amersham radioimmunoassay (RIA) kits (Biotrak rat corticosterone [¹²⁵I]; Amersham, UK). The assay is based on competition between unlabelled corticosterone and a fixed quantity of ¹²⁵I-labelled corticosterone for a limited number of binding sites on corticosterone-specific antibodies. The antibody-bound fraction of corticosterone was separated and radioactivity was measured to quantify the amount of labelled corticosterone in the bound fraction. The concentration of unlabelled corticosterone in the sample was then determined by interpolation from a standard curve.

The baseline levels of corticosterone in a plasma sample may be confounded by at least two factors. First, handling stress is known to elevate corticosterone levels, especially in adult birds (Wingfield & Farner 1993). Second, autolysis of corticosterone

after bleeding may decrease the levels and may even overcome the effects of handling stress, a possibility that surprisingly has not been taken into account in earlier studies. We examined the effects of handling stress on corticosterone levels by measuring handling time I , defined as the length of time (s) from capture to bleeding. In our data, handling time I (14 ± 6 min; mean \pm s.d.) was not related to corticosterone ($t_{1,241} = -1.32$, $p = 0.189$), probably as a result of the early developmental state of 9-day-old nestlings, which did not appear distressed while handling, compared with 14-day-old fledglings, for example. The chicks may also have not been ready to show an acute stress response (see Sims & Holberton 2000). We examined the autolysis of corticosterone by measuring the length of handling time II (s) from bleeding to storing of plasma in liquid nitrogen. Given the known effects of handling time I on corticosterone concentrations (Wingfield & Farner 1993), we sampled blood from the nestlings as soon as possible. This increased handling time II in regard to the heaviest chicks, especially in those broods where all nestlings were sampled, because the first collected blood samples from the heaviest chick awaited centrifugation while the lighter chicks were having blood taken. Corticosterone levels were negatively associated with handling time II (20 ± 8 min; mean \pm s.d.), suggesting autolysis (*adj.* $r^2 = 0.04$, $t_{1,239} = -3.21$, $p = 0.001$). The total handling time, i.e. handling time I + handling time II (34 ± 10 min) was also negatively associated with corticosterone concentrations (*adj.* $r^2 = 0.04$, $t_{1,239} = -3.38$, $p = 0.001$) and was thus used as a covariate in the analyses.

(e) Statistical analyses

A total of 124 nests contained nestlings from which we sampled blood (90 first broods and 34 second broods). Of these nests all chicks were sampled for blood in 25 cases (13 first broods and 12 second broods). In the remaining 99 nests only the heaviest chicks were sampled for blood, in order to obtain a sufficiently large sample size from various landscapes. The sampling of all chicks within a brood would have been too time consuming owing to laborious fieldwork procedures, long distances between territories and synchrony of broods in the study area. The heaviest nestlings were chosen because high body mass is known to be related to high chick quality (Martin 1987). By selecting the heaviest chicks we chose the most conservative method to analyse the relationship between corticosterone levels and habitat structure, because the largest chicks are least likely to show variation in corticosterone levels among territories.

We modelled the relationship between corticosterone concentrations and habitat characteristics by using linear stepwise forward regression analysis. The plasma corticosterone level of the heaviest chick was treated as a dependent variable in the analysis. The habitat variables with timing of breeding and total handling time were used simultaneously as independent variables in the analysis (table 1). The timing of breeding was ranked according to the Julian date of hormone sampling as follows: first of May = 1 and first of June = 32, etc. The mean distance (\pm s.e.m.) between the nearest territory centres was (1446.6 \pm 110.3 m) in the first broods and (2586.0 \pm 320.9 m) in the second broods. Thus, spatial autocorrelation did not confound the analyses of corticosterone concentrations and forest structure. The collinearity of explanatory variables may lead to multicollinear results in multiple regression analyses. Multicollinearity was assessed by using a variance inflation factor (VIF), assuming that high VIF values for any of the explanatory

Table 1. Results of stepwise forward regression analysis of the relationship between corticosterone levels (ng ml^{-1}) and habitat characteristics ($F_{4,119} = 23.39$, adjusted $r^2 = 0.429$, $p < 0.001$). Abbreviations used: *, territory core scale (radius 30 m); †, territory scale (radius 200 m); ‡, larger scale (radius 500 m); DoT, density of trunks; NFP, nesting forest patch. Adjusted r^2 values, variance inflation factors (VIF) and regression coefficients with standard errors are presented.^a

dependent variable	independent variable	r^2 adj.	VIF	regression coefficient	s.e.m.	t	p
corticosterone level of the heaviest chick	DoT*	0.098	1.028	0.182	0.046	4.002	< 0.001
	NFP‡	0.015	1.036	-0.009	0.004	-2.037	0.044
	timing of breeding	0.284	1.148	-0.026	0.004	-6.619	< 0.001
	total handling time	0.032	1.142	-0.028	0.010	-2.809	0.006

^a Probability of F to enter a variable, less than or equal to 0.05 and to remove, greater than or equal to 0.1. Variables excluded from the model by stepwise forward analysis: number of nestlings within a brood, coefficient of variation of trunk density (%)*, mean trunk circumference*, mean height of trees*, mean trunk surface area*, mean wood volume ha^{-1} *, spruce %*, pine %*, birch %*, deciduous trees %*, greater than or equal to $102 \text{ m}^3 \text{ ha}^{-1}$ of forested land %†‡, open habitats %†‡, spruce mire %†‡, pine mire %†‡, pine forest %†‡, spruce forest %†‡, deciduous forest %†‡, mixed forest %†‡, saplings %†‡, old forests as per cent of total area †‡, patch density†‡, mean patch size (ha)†‡, edge density (m ha^{-1})†‡, total edge (m)†‡, mean shape index†‡, mean nearest-neighbour forest patch distance (m)†‡ and nest patch size†.

variables indicate that the fit of the model is affected by multicollinearity.

The data from 25 broods blood sampled as a whole were used in two within-brood comparisons: (i) the corticosterone level in the heaviest chick compared with the corresponding brood mean; and (ii) the corticosterone level in the heaviest chick compared with that in the corresponding lightest chick. The same data were also used in analysis of the relationship between food supply and brood means of corticosterone. In comparisons involving the three handling times (I, II, total) and corticosterone, an individual was used as a sampling unit and all chicks sampled for blood ($n = 243$) were used. These data were also used in survival analysis.

Between-habitat comparisons of the density and volume indices of invertebrates at the territory core areas were carried out separately for the first and second broods. We divided the territories according to quartiles of tree density at the territory core areas. The lower quartile, containing less than 3.25 trees per 50 m^2 , was considered sparse forest, whereas the upper quartile, containing more than 5.35 trees per 50 m^2 , was defined as dense forest. In this way we categorized 20 and 8 sparsely forested cores versus 22 and 8 densely forested territory cores for the first and second broods, respectively. As a measure of body condition of chicks, we used deleted residuals from the regression association between wing length and body mass. In general, all degrees of freedom are given as subscripts to test abbreviations. In the methods and results sections mean \pm s.d. are given unless otherwise indicated. All analyses were performed with SPSS version 10.0.

3. RESULTS

(a) Corticosterone, body condition and habitat structure

Corticosterone levels among the heaviest chicks were negatively associated with the area of nesting forest patch at the large scale (radius of 500 m) (table 1). In our study area young forests were characterized by a high tree density (linear regression $\text{adj. } r^2 = 0.45$, $t_{1,122} = -10.02$, $p < 0.001$). Consequently, the corticosterone levels in the

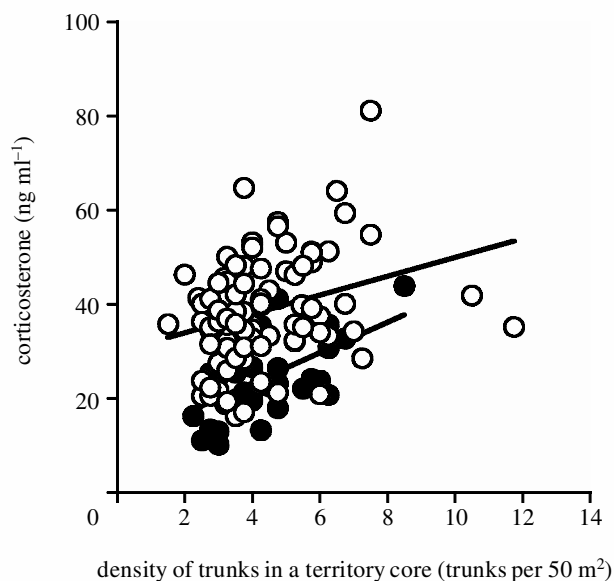


Figure 2. Relationship between density of tree trunks (trunks per 50 m^2) at the territory core area and the corticosterone level in the heaviest chick of each brood. First broods (open circles) (linear regression, $\text{adj. } r^2 = 0.08$, $t_{1,88} = 2.94$, $p = 0.004$), second broods (filled circles) ($\text{adj. } r^2 = 0.35$, $t_{1,33} = 4.34$, $p < 0.001$, interaction term, brood \times trunk density, $p = 0.860$).

heaviest chicks were higher in young and dense than in sparse and old forests at the territory core scale (table 1; figures 2 and 3). The results were parallel between the first and the second broods (figures 2 and 3). The total handling time was not associated with the density of trunks nor with the nesting forest patch area (multiple regression $t_{2,119} = -1.0$, $p = 0.320$, $t_{2,119} = -0.68$, $p = 0.495$, respectively). The residual body mass of the heaviest chicks was higher in large than in small nesting forest patches at the large scale, but it was not related to the density of trunks at the territory core scale when the ranked Julian date of hormone sampling was used as a

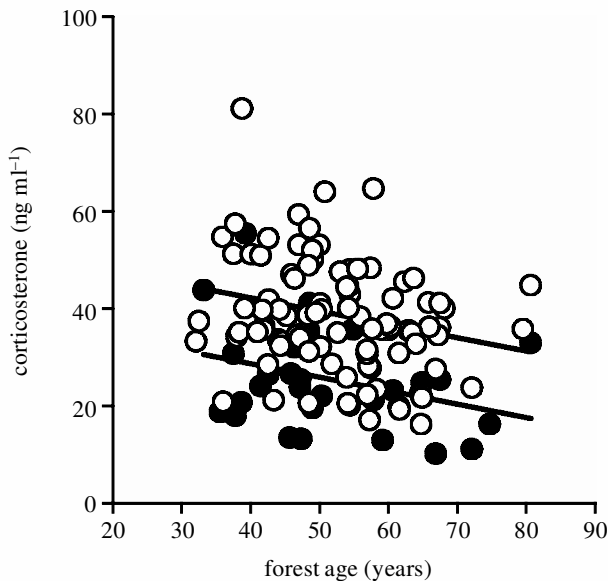


Figure 3. Relationship between forest age at the territory core area and corticosterone level in the heaviest chick of each brood. First broods (open circles) (multiple regression, $adj. r^2 = 0.05$, $t_{1,88} = -2.37$, $p = 0.020$), second broods (filled circles) ($adj. r^2 = 0.09$, $t_{1,33} = -2.03$, $p = 0.051$, interaction term, brood \times forest age, $p = 0.99$).

covariate (multiple regression, $adj. r^2 = 0.07$, $t_{3,113} = 3.19$, $p = 0.002$, $t_{3,113} = -0.35$, $p = 0.731$, respectively).

(b) Food supply at territory cores

In a between-habitat comparison of the first broods the density of potential prey items was 33.8% higher at the territory core areas within sparse forests (9.2 ± 3.7 individuals per m^2 , $n = 20$) than at the territory core areas within dense forests (6.8 ± 3.7 individuals per m^2 , $n = 22$, $F_{1,41} = 3.95$, $p = 0.054$). In addition, the mean volume index of spiders was 64% larger in sparse (1.6 ± 1.0 $mm^3 m^{-2}$, $n = 20$) than in dense forests (1.0 ± 1.0 $mm^3 m^{-2}$, $n = 22$, $F_{1,41} = 4.43$, $p = 0.042$). Forest age *per se* was positively correlated with invertebrate density (linear regression, $adj. r^2 = 0.04$, $t_{1,87} = 2.22$, $p = 0.029$). During the second broods, prey densities no longer differed between forest types, but the mean prey volume index was 98% greater in sparse (3.6 ± 1.3 $mm^3 m^{-2}$, $n = 8$) than in dense forests (1.6 ± 1.3 $mm^3 m^{-2}$, $n = 8$, $F_{1,15} = 9.81$, $p = 0.007$).

(c) Food supply and corticosterone levels

The mean corticosterone levels in the first broods (all nestlings sampled) were negatively associated with the amount of invertebrate prey within a territory (figure 4). The role of food was also supported indirectly. In within-brood comparisons of 25 broods sampled as a whole, the heaviest nestlings had 30.0% lower corticosterone levels (22.9 ± 7.6 $ng ml^{-1}$, $n = 25$) than the lightest nestlings (32.7 ± 16.0 $ng ml^{-1}$, $n = 25$, Wilcoxon $Z_{24} = -3.23$, $p = 0.001$) and 19.4% lower corticosterone levels than the corresponding brood means (28.4 ± 8.6 $ng ml^{-1}$, $n = 25$, $Z_{24} = -3.70$, $p < 0.001$). Among all the heaviest chicks sampled ($n = 124$), residual body mass was negatively associated with corticosterone levels (multiple regression, $adj. r^2 = 0.33$, mass $t_{2,114} = -2.06$, $p = 0.042$, covariate:

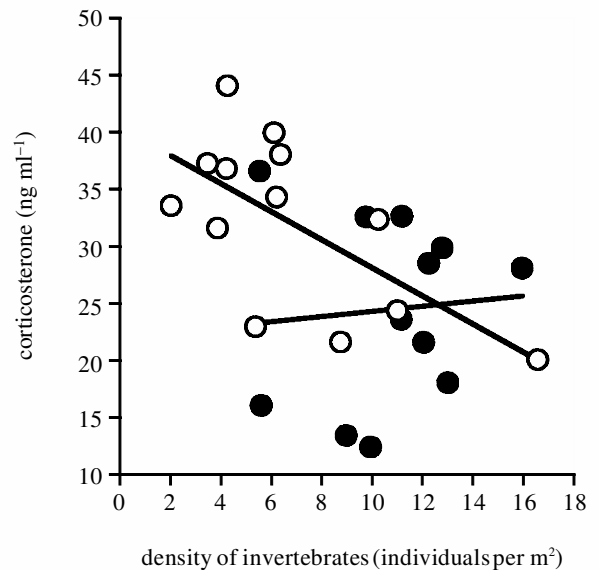


Figure 4. Relationship between mean density of invertebrates on tree trunks and the mean corticosterone level in the brood (all nestlings sampled). First broods (open circles) (linear regression, $adj. r^2 = 0.37$, $t_{1,12} = -2.76$, $p = 0.018$), second broods (filled circles) ($t_{1,11} = 0.27$, $p = 0.796$, pooled data: $adj. r^2 = 0.19$, $t_{1,24} = -2.61$, $p = 0.016$).

ranked Julian date of hormone sampling $t_{2,114} = -7.23$, $p < 0.001$).

The amount of food supply increased by 33% at the territory cores and corticosterone levels decreased by 43% among the heaviest chicks from the first (May) to the second broods (June, July) (table 2). Further, chicks in the second broods had 7.5% higher body masses, 15.5% longer wings, 12.9% more subcutaneous fat and a 14.7% better survival rate than chicks in the first broods (table 2).

Among all the nestlings sampled for blood ($n = 243$) elevated corticosterone levels were associated with increased individual chick mortality (logistic regression, Wald $\chi^2 = 5.02$, $p = 0.025$) and the effect of corticosterone on chick mortality did not vary among territories (interaction term: corticosterone \times territory, $p = 0.270$). Twenty-five chicks found deceased in the nests 5 days after sampling for blood had had 13.4% higher corticosterone levels (37.04 ± 10.0 $ng ml^{-1}$, $n = 25$) than the survivors (32.7 ± 13.1 $ng ml^{-1}$, $n = 218$, *t*-test: $t_{241} = -2.45$, $p = 0.019$). Deceased nestlings also had weighed 7.3% less (7.8 ± 0.9 g, $n = 25$) than the survivors (8.4 ± 0.7 g, $n = 208$, $t_{231} = 3.83$, $p < 0.001$), when still alive at the age of 9 days.

4. DISCUSSION

Our research is among the very few studies showing an association between physiological stress in a free-living animal and forest habitat characteristics (see Wasser *et al.* 1997). Restriction of food may lead to an increase in the baseline corticosterone levels in chicks and a poor body condition may be associated with elevated physiological stress (Nunez-de la Mora *et al.* 1996; Kitaysky *et al.* 1999). In this study we found evidence that plasma corticosterone concentrations are associated with habitat structure, body condition and food supply. We suggest that low density and quality (small size) of prey were mainly responsible

Table 2. Variation in food abundance, plasma corticosterone levels, mass, subcutaneous fat and wing length of the heaviest nestlings, and nestling survival between the first and second broods. (*F*, repeated measures ANOVA; *t*, *t*-test; *Z*, Mann–Whitney *U*-test.)

	first broods mean \pm s.d.	<i>n</i>	second broods mean \pm s.d.	<i>n</i>	test	<i>P</i>
invertebrate density on trunks (individuals per m ²)	7.5 \pm 3.1	19	9.9 \pm 4.2	19	(<i>F</i>) 6.571	0.020
corticosterone in plasma (ng ml ⁻¹)	43.8 \pm 12.7	19	25.0 \pm 8.0	19	(<i>F</i>) 44.377	< 0.001
mass (g)	8.4 \pm 0.7	90	9.0 \pm 0.6	25	(<i>t</i>) -4.114	< 0.001
subcutaneous fat index (range 0–3)	1.8 \pm 2.1	90	2.1 \pm 0.3	25	(<i>Z</i>) -2.117	0.034
wing length (mm)	29.0 \pm 3.6	90	33.5 \pm 3.9	25	(<i>t</i>) -5.357	< 0.001
nestling survival (fledglings/clutch size)	77.5 \pm 0.3	90	92.2 \pm 0.1	34	(<i>Z</i>) -2.601	0.009

for the high corticosterone levels in nestlings growing up in dense young forests and in small forest patches.

Food supply, physiological condition, body mass and wing growth rate improved, whereas stress-hormone levels decreased from the first to the second broods. These observations further support the suggestion that the origin of the environmental stress was mainly nutritional. Furthermore, our earlier results showed that tree creeper parents may deplete their food resources by almost a half in the vicinity of their nest during the breeding season (Jääntti *et al.* 2001). This suggests that their food resources within a territory are limited, which can lead to elevated stress-hormone levels if food resources are diminished and scattered as a result of forest management. These costs may be associated with small-scale territory characteristics, such as tree density, in the vicinity of a nest site. Accordingly, the tree creepers in our study area do not prefer thin tree trunks when foraging (Suhonen & Kuitunen 1991a), probably because repeated sampling of trunks is energetically more costly (Tatner & Bryant 1986).

At the large scale the costs of forest fragmentation in terms of elevated stress-hormone levels and a poorer body condition appeared particularly in small forest patches. Nutritional factors might be behind these observations too, because there is evidence that food abundance decreases with decreasing forest fragment size (Burke & Nol 1998; Zanette *et al.* 2000). We conclude that reduction in food quantity and quality as a result of forest management may lead to elevated physiological stress and a poorer body condition in nestlings, with a potential to decrease the quality and survival of offspring.

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