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Forest fragmentation is associated with primary brood sex ratio in the treecreeper (Certhia familiaris)

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We studied the primary brood sex ratio of an old-growth forest passerine, the Eurasian treecreeper (*Certhia familiaris*), along a gradient of forest fragmentation. We found evidence that male nestlings were more costly to produce, since they suffered twofold higher nestling mortality and were larger in body size than females. Furthermore, the proportion of males in the brood was positively associated with the provisioning rate and the amount of food delivered to the nestlings. During the first broods, a high edge density and a high proportion of pine forests around the nests were related to a decreased production of males. The densities of spiders, the main food of the treecreeper, were 38% higher on spruce trunks than on pine trunks. This suggests that pine-dominated territories with female-biased broods may have contained less food during the first broods. The observation was further supported by the fact that the feeding frequencies were lower in territories with high proportions of pines. In the second broods, territories with a high forest patch density produced female-biased broods, whereas high-quality territories with a large amount of deciduous trees and mixed forests produced male-biased broods. Our results suggest that habitat quality as measured by habitat characteristics is associated with sex allocation in free-living birds.

Keywords: forest fragmentation; habitat quality; sex ratio; treecreeper; feeding effort; provisioning

1. INTRODUCTION

Birds have chromosomal sex determination in which heterogametic females set the offspring sex (Fridolfsson & Ellegren 1999). It has been suggested that sex ratios in birds do not differ from unity as a result of random Mendelian determination of sex (Williams 1979). Accordingly, evidence for primary sex-ratio differences from unity at hatching was scarce (reviews by Clutton-Brock 1986; Breitwisch 1989). However, there are studies reporting non-random sex allocation in laying sequence (see Clotfelter 1996 and references therein). Recent experimental studies suggest that female birds can control for the sex of their offspring (Komdeur *et al.* 1997; Kilner 1998; Nager *et al.* 1999). Two novel works have found evidence of surprisingly large pre-ovulation control of the sex (Sheldon *et al.* 1999; Komdeur *et al.* 2002) although the actual mechanism behind female control is unknown.

In species where males and females differ in size, the larger sex may require more energy for growth and maintenance (Fiala & Congdon 1983; Slagsvold *et al.* 1986; Anderson *et al.* 1993). This size differential most often begins while the offspring are still under parental care (Myers 1978). So, the larger sex should be more costly to raise to independence (Teather & Weatherhead 1989). Myers (1978) proposed that poor environmental conditions will lead to the production of the cheaper sex, allowing maximization of the number of young produced. In support of this there are studies showing that parents may adjust their reproductive effort according to resource availability by manipulating offspring sex ratios. For example, poor food availability and parent condition were associated with male- (cheaper sex) biased sex ratios in American kestrels *Falco sparverius* (Wiebe & Bortolotti 1992). Additionally, an excess of female chicks (the more expensive sex) was produced on territories with a high amount of food in tawny owls (*Strix aluco*; Appleby *et al.* 1997).

One cause of poor environmental conditions is the destruction of natural habitats as a result of habitat loss and fragmentation (Gates & Gysel 1978). The strict definition of fragmentation refers to the separation of continuous habitat into several pieces representing the same overall amount of habitat (Fahrig 1997). In small forest fragments, individuals may experience food shortage (Zanette *et al.* 2000). One result of habitat fragmentation is an increasing amount of habitat edges (Hanski 1999). Thus, many studies have investigated the biotic consequences of edge effects (Harris 1988; Temple & Cary 1988; Yahner 1988; Mills 1995). Forest birds dependent on resources within woodlands tend to avoid forest edges, as a result of the lowered proximity of food resources and enhanced competition, predation and brood parasitism (reviewed in McCollin 1998).

We studied the relationship between habitat characteristics and the primary brood sex ratio in the Eurasian treecreeper (*Certhia familiaris*) by providing nest-boxes on a gradient from fragmented low-quality forest landscapes to more continuous high-quality forest landscapes. We addressed the following questions.

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(i) Do the sexes differ in body size and nestling mortality?
(ii) Is there a relationship between habitat structure and primary brood sex ratio?

We examined the habitat structure around a nest at three spatial scales as follows:

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

2. MATERIAL AND METHODS

(a) *Study species and breeding data*

The Eurasian treecreeper is an old-growth forest passerine preferring forests of over 100 years old (Haila *et al.* 1989; Virkkala *et al.* 1994; Väisänen *et al.* 1998). The species is altricial and the chicks fledge at an age of 14–16 days. Clutch size varies from 3 to 8 (5.5 ± 0.9 eggs (mean ± s.d.); P. Suorsa and H. Hakkarainen, unpublished data). The treecreeper specializes in searching for invertebrates on tree trunks (Cramp & Perrins 1993). Nests are placed behind the flaps of loose bark or in the crevices of tree trunks (Cramp & Perrins 1993), but females also accept specially designed nest-boxes (Kuitunen 1985). In our nest-box population, the first eggs are laid in early April, when snow cover and night frosts still prevail in central Finland. Approximately 30% of the first breeders raise a second brood in June and July, which is usually reared by only the female (Aho *et al.* 1999). Almost all juveniles migrate from the study area as a result of natal dispersal, whereas breeding birds are suggested to be sedentary (P. Suorsa and H. Hakkarainen, unpublished data).

We used 229 nest-box pairs in 229 forest patches differing in habitat structure. Each forest patch contained two nest-boxes to allow for the possibility of a second breeding attempt by the territorial pair. Only one treecreeper pair occupied a nest-box pair at a time. Thus, we regarded the midpoint of the nest-box pair as the territory centre and used territory as a sampling unit. Nests were checked frequently to determine laying date, clutch size, brood size, fledging success and the fate of breeding attempts. Parents were trapped at the nest when the nestlings were 9 days old. The parents were aged according to the extent of postjuvenile or postnuptial moult and sexed according to the presence of an incubation patch and a form of cloacal protuberance (Svensson 1992). We also measured the maximum wing, beak and tarsus lengths of individuals (Svensson 1992). Subcutaneous fat in the abdomen and tracheal pit (Kaiser 1993) and a condition of the pectoral muscle modified after Gosler (1991) were recorded. Individuals were weighed to the nearest 0.1 g. In addition to the parents' measurements, the corresponding measurements were carried out on all nestlings at the ages of both 9 and 14 days. Nestling mortality rate was determined by subtracting the number of chicks that fledged from the number of nestlings.

(b) *Study area and habitat structure around nests*

Breeding data were collected from the study area covering 115 000 ha in central Finland (centred on 62°37′ N, 26°20′ E) in the summers of 1999 and 2000. Forested land covers 71% of the study area, and the remaining 29% consists of open habitats, such as cultivated fields, clear-cuts, lakes, treeless bogs and other open habitats. The most common forest types are coniferous forests dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), which cover 42% and 21% of the forested land, respectively. Deciduous forests and mixed forests of conifers, birches (*Betula* spp.) and other deciduous trees cover 30% of the forested area. The remaining 7% consists of saplings and spruce and pine mires. Intensive forest management with clear-cuttings as the main renewing method has been carried out since the 1950s. After the trees are removed the clear-cut areas are planted (depending on the soil characteristics) with spruces, pines and birches to enhance forest succession.

The habitat structure around the territory centres was established at three spatial scales. We measured territory core structure a (radius of 30 m) in the field because of inaccurate satellite-image-based land-use and forest data on a small spatial scale. Vegetation cover was measured within four sampling circles, each having a radius of 4 m. The non-overlapping sampling circles (50 m^2 each) were placed in the four cardinal directions *ca.* 30 m from the territory centre. We used mean measurements from the four sampling circles in the analyses (Suorsa *et al.* 2003). The structural variables of the forest in the territory core area included the mean density of tree trunks (number per 50 m^2), the mean circumference of tree trunks (cm), the mean volume of trunks ($m^3\,ha^{-1}$) and the mean trunk surface area (m^2) within a sampling circle. The floristic variables measured were the total numbers of pines, spruces, birches and other deciduous trees of at least 30 cm circumference at chest height. Thinner trunks were not included, because they are of minor importance at the nestling phase (P. Suorsa and H. Hakkarainen, unpublished data).

The forest-structure and forest-fragmentation variables at territory scale b (radius of 200 m covering 12.6 ha) and large scale c (radius of 500 m covering 78.5 ha) were established from the classified Landsat TM 5 satellite images (1995–1997) produced by the National Land Survey of Finland (Vuorela 1997). The satellite-image-based land-use and forest data were imported to a geographical information system.

The forest-structure variables included the percentages of the old forest, open habitat, spruce mire, pine mire, pine forest, spruce forest, deciduous forest, mixed forest and saplings for both b and c spatial scales. The forest-fragmentation variables were calculated using FRAGSTAT, a spatial-analysis program (McGarigal & Marks 1995), and included forest patch density (number per 100 ha), mean forest patch size (ha), edge density between the forest and open land ($m\,ha^{-1}$), total edge (m), mean nearest-neighbour distance (m) and nesting forest patch size (ha), for both b and c spatial scales. The edge density between the forest and open land is hereafter referred to as such. A forest patch was defined as a separate forested area containing more than 50 $m^3\,ha^{-1}$ of timber. By using this criterion a forest patch was clearly separable from the neighbouring open habitats and saplings in the field. The amount of old forest was defined as forested area where the total volume of timber was at least 102 $m^3\,ha^{-1}$, a figure that indicates a forest age of 50 years in central Finland (Tomppo *et al.* 1999).

(c) *Sexing of chicks*

The determination of the offspring sex was based on blood samples collected at the age of 9 days.

A few drops of blood were stored in Eppendorf tubes after puncturing the tarsometatarsal vein. The blood samples were diluted with field buffer and kept at –20 °C prior to molecular analysis. The DNA was isolated from the blood cells using a Qiagen QIAamp kit following the manufacturer's instructions. The primers 2550F and 2718R were used in PCR amplification (Fridolfsson & Ellegren 1999). Sex was determined according to a constant size difference between the introns of two genes (CHD1W and CHD1Z). The PCR products were visualized by ethidium bromide staining after agarose electrophoresis. Females showed fragments of genes CHD1Z (600–650 bp) and CHD1W (400–450 bp), whereas males showed only one fragment, CHD1Z (600–650 bp) (Fridolfsson & Ellegren 1999). Samples taken from adult males ($n = 8$) and females ($n = 8$) were all sexed correctly using this method without revealing the origin of the samples to the tester.

(d) *Monitoring of the provisioning rates*

Parental feeding was filmed 1 day after capture of the adults, when the nestlings were 10 days old. The nests were recorded for 1.5 h on 8 mm video tape (Hitachi, VM-E340E), using a camera that was placed on a tripod 3–5 m from the nest. The feeding-rate calculations were started from the first feed using 1 h of recordings after this initial feed (Nour *et al.* 1998). Complete broods with 60 min of undisturbed recordings ($n = 66$) were included in the analyses. The total feeding rate was calculated as the total number of loads delivered into the nest-box per hour. Load size, ranging from 1 to 17, was indexed by comparing the two-dimensional area of a load in the beak with the nearest area of the parent's eye. The amount of food delivered to the nestlings per hour was estimated by multiplying the load size by the feeding rate.

(e) *Food abundance*

The treecreeper specializes in searching for invertebrates, especially spiders (65% of the nestling food mass), on tree trunks (Suhonen & Kuitunen 1991). We measured food abundance using vacuum cleaners on spruce and pine trunks during the period immediately after the fledging of the 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 09.00 and 18.00. Invertebrate samples were collected from six randomly selected tree trunks that were at least 30 cm in circumference and located at a distance of 30 m from the nest. The prey length of treecreepers ranges from 1 to 15 mm (Suhonen & Kuitunen 1991); therefore, only invertebrates of at least 1 mm in size were included in the analyses. The mean invertebrate density (number of invertebrates per m^2 of trunk) and the mean volume index of invertebrates (mm^3 per m^2 of trunk), with the exception of ants, were used as estimates of the food supply on the main tree species, i.e. spruces and pines. The volume indices of invertebrates were calculated from the functions using the length and width of the specimens (see details in Blondel *et al.* 1991).

(f) *Statistical analyses*

The sex-ratio data included nests defined as complete broods (i.e. the number of sexed young equals the clutch size) and as incomplete broods (primary sex ratio not recorded because of unhatched eggs and nestling mortality before sexing; table 1). We used the dataset of complete broods as a base for the analyses, because of our main interest in the variation of the primary brood sex ratio. However, the analyses of the habitat characteristics in relation to the sex ratio were carried out separately for the complete broods and the pooled dataset of complete and incomplete broods. There was a considerable change in breeding conditions from the first to the second broods in terms of elevated ambient temperature and food abundance (Suorsa *et al.* 2003) and altered parental effort (only females rear the second broods). Thus, the first and second broods were analysed separately.

Forest percentage classes that summed to 1 were transformed to $n - 1$ log-ratios using the proportion of spruce forests as a denominator to render the compositional variables independent. The proportion of a missing habitat type was set to 0.001 (Aitchison 1986; Aebischer & Robertson 1992; Aebischer *et al.* 1993). From the five Fragstat metrics (edge density, patch density, mean patch size, mean nearest-neighbour distance and nesting forest patch size) and percentage of old forest, uncorrelated patch and edge densities were used as a measure of fragmentation in the analyses at both the b and c spatial scales.

We modelled the relationship between primary brood sex ratio and habitat characteristics first by using linear stepwise forward regression analyses in GLM (SPSS v. 11.0) to select the significant explanatory variables. A probability of 0.05 was used as the criterion for a variable to be entered into the model, and a probability of 0.1 for it to be removed. The arcsine-transformed proportion of males was treated as a dependent variable and the log-transformed habitat variables from a–c spatial scales and timing of breeding were used simultaneously as independent variables in the analyses. The habitat variables included the mean density of the tree trunks and the percentages of pine, birch and other deciduous trees on spatial scale a. The variables for spatial scales b and c included the percentages of pine and spruce mires, pine, deciduous and mixed forests and saplings in addition to the forest patch and edge densities. The timing of breeding was categorized according to the Julian date of egg laying as follows: 1 April = 1 and 1 May = 31, etc.

Finally, the selected explanatory variables (covariates) and the territory as a random factor were modelled simultaneously using logistic regression in generalized linear mixed models (glimmix-macro in SAS 8.2) allowing the analysis of the binomial error variance (Krackow & Tkadlec 2001; Wilson & Hardy 2002). The mean distance between nearest-neighbour territory centres was 1374 ± 122 m (mean ± s.e.m.), thus spatial autocorrelation did not confound the landscape variables measured. In § 3 the means are given with the standard errors of the means.

3. RESULTS

The ratio of the sexes did not differ from unity either in the first (176 males versus 174 females) or in the second (82 males versus 91 females) broods (binomial test: $p = 0.957$ and $p = 0.543$, respectively). However, the proportion of male young within a brood ranged among the territories from 0% to 100%.

(a) *Sex-related variation in survival and body size of nestlings*

The mortality of male nestlings (9.3% out of 247 chicks) was higher than that of females (4.0% out of 252 chicks; Pearson $\chi^2 = 5.77$, d.f. = 1, $p = 0.016$). In the middle of the nestling period, the 9-day-old chicks were already sexually dimorphic with respect to size as the males weighed 5.5% more than the females (table 2). At the fledging phase the males weighed 6.6% more and had 1.1% longer wings and 1.8% longer tarsi than the females (table 2). The total brood mass of the male-biased broods was also higher than that of the female-biased broods at

Table 1. The number of nests used in the sex-ratio analyses of the treecreeper broods.

	1999			2000			
	first	second	Σ	first	second	Σ	total
complete broods	21	8	29	45	23	68	97
incomplete broods with unhatched eggs	0	6	6	16	0	16	22
broods with nestling mortality before sexing	1	2	3	3	0	3	6
total	22	16	38	64	23	87	125

Table 2. Size dimorphism in the 9- and 14-day-old treecreeper nestlings.
(t, t-test; Z, Mann–Whitney U-test; $n = 457$.)

	males mean ± s.e.	females mean ± s.e.	test$_{\text{d.f.}}$	p
9 days				
mass (g)	8.4 ± 0.1	7.9 ± 0.1	(t_{239}) 4.63	< 0.001
wing (mm)	30.6 ± 0.4	29.9 ± 0.5	(t_{265}) 1.14	0.256
14 days				
mass (g)	8.9 ± 0.1	8.4 ± 0.04	(t_{438}) 8.73	< 0.001
wing (mm)	43.3 ± 0.4	42.8 ± 0.3	(Z) −2.73	0.006
tarsus (mm)	15.7 ± 0.03	15.4 ± 0.03	(t_{434}) 6.40	< 0.001

the age of 14 days (analysis of covariance factor: number of nestlings $F_{3,59} = 90.57$, $p < 0.001$, covariate: proportion of males $F_{1,59} = 4.99$, $p = 0.029$).

(b) *Body size and condition of parents*

Body sizes as measured by tarsus length of male and female parents did not influence the primary proportion of male chicks in either the first or the second broods (male parents: logistic regression: $\chi^2 = 0.83$, d.f. = 1, $p = 0.362$ and $\chi^2 = 0.714$, d.f. = 1, $p = 0.714$, respectively; female parents: $\chi^2 = 1.32$, d.f. = 1, $p = 0.251$ and $\chi^2 = 0.03$, d.f. = 1, $p = 0.853$, respectively). Primary brood sex ratio did not affect the residual body mass of male parents (linear regression: $t_{1,60} = 0.12$, $p = 0.907$ in the first broods, $t_{1,5} = -0.27$, $p = 0.800$ in the second broods). In female parents no effects were found in the first broods ($t_{1,63} = -0.98$, $p = 0.330$). In the second broods, however, the rearing of male-biased broods was related to a lowered residual body mass in the female parents (figure 1). Visible subcutaneous fat reserves in the abdomen and tracheal pit explained 30.8% of the variation in the residual body mass in the female parents (analysis of variance: $F_{2,14} = 4.56$, $p = 0.030$).

(c) *Food abundance on main tree species and provisioning rates*

In the first broods the density of spiders was 38.3% higher on the spruce trunks (4.5 ± 0.2 individuals per m^2, $n = 805$ trunks) than on pines (3.2 ± 0.4 individuals per m^2, $n = 119$; Mann–Whitney U-test $Z = -2.337$, $p = 0.019$). In addition, the total densities of all the invertebrate specimens seemed to differ between the spruce and pine trunks (Mann–Whitney U-test: $Z = -1.77$, $p = 0.076$). In support of this, the feeding frequencies were lower in nests surrounded by a high proportion of pine forests at spatial scale c (radius of 500 m; $b = 0.300 \pm 0.147$, $t_{2,50} = -2.03$, $p = 0.047$). The mean volume indices of spiders ($Z = -0.07$, $n = 708$, $p = 0.939$) and all invertebrates ($Z = -0.11$, $n = 781$, $p = 0.917$) did not differ between the spruces and pines.

Parents fed male-biased broods at a higher frequency than female-biased broods (figure 2). In general, the feeding frequency explained 59.1% of the total amount of food delivered per hour, and inclusion of the load size improved the model by 29.7% ($_{\text{Adj.}}r^2 = 0.89$, $F_{2,50} = 207.45$, $p < 0.001$). In the second broods, the feeding frequency was no longer related to the sex ratio ($t_{1,11} = 0.40$, $p = 0.694$).

(d) *Effects of habitat structure on the primary brood sex ratio*

In the first broods, a high edge density at spatial scale b (radius of 200 m) and a high proportion of pine forests at spatial scale c (radius of 500 m) were negatively related to the proportion of male young (table 3). In the second broods, a high forest patch density at spatial scale c decreased the proportion of male young, whereas a high proportion of deciduous trees at the territory core area (radius of 30 m) and a high proportion of mixed forests at spatial scale c increased male production. The results were similar in both of the study years (see the two-factor interactions in table 3).

4. DISCUSSION

This research is among the very few studies showing an association between sex ratio and habitat characteristics (see Dhondt 1970; reviewed in Sheldon 1998). Our findings support the idea that birds might be capable of adjusting their progeny in relation to their own circum-

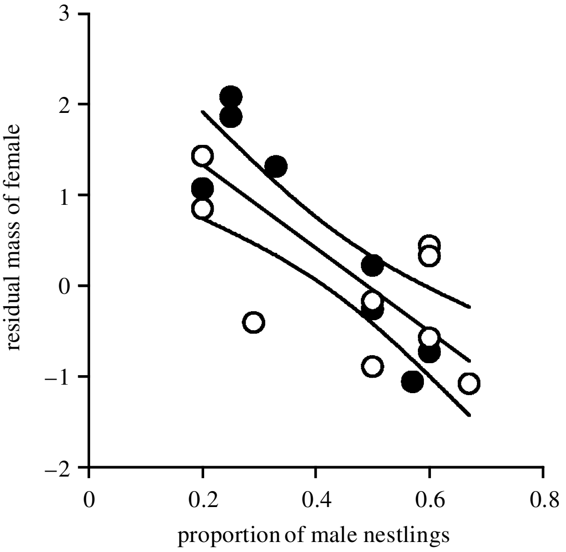

Figure 1. The effects of primary brood sex ratio on the residual body mass (from the regression between wing and body mass) of female parents during the second broods in 1999 (filled circles) and 2000 (open circles) (linear regression: $b = -4.375 \pm 0.959$, $_{\text{Adj.}}\,r^2 = 0.55$, $t_{1,15} = -4.56$, $p < 0.001$).

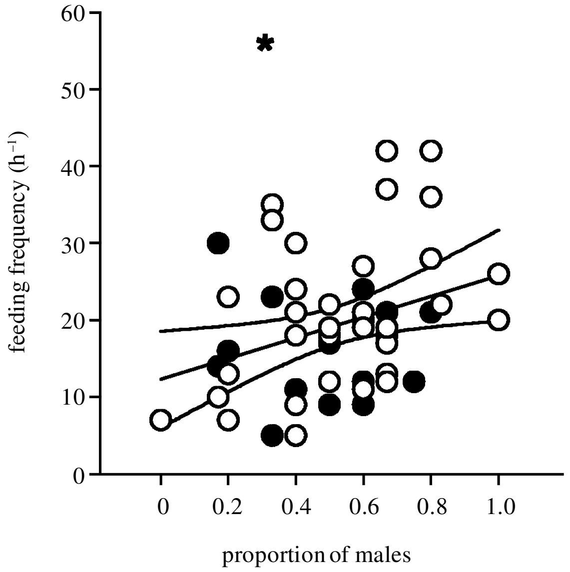

Figure 2. The effects of sex ratio on the feeding frequency per hour during the first broods in 1999 (filled circles) and 2000 (open circles). The asterisk depicts the outlier. Without the outlier, linear regression: $b = 10.765 \pm 4.554$, $t_{1,50} = 2.364$, $_{\text{Adj.}}\,r^2 = 0.083$, $p = 0.022$. With the outlier, $b = 8.803 \pm 5.293$, $t_{1,51} = 1.663$, $p = 0.102$.

stances (Komdeur *et al.* 1997; Bradbury & Blakey 1998; Sheldon 1998). In the treecreeper forest, fragmentation in terms of increased edge density and forest patch density was related to the lowered production of the larger sex, i.e. males. Furthermore, parents dwelling in low-quality territories (characterized by a high proportion of pine forests) produced female-biased broods, whereas a male bias was found in high-quality territories with a large amount of deciduous trees and mixed forests.

Parents are expected to adjust their investment in the sexes to maximize their own lifetime reproductive success, provided that the fitness return of each sex differs (Trivers & Willard 1973). When resources are plentiful parents should produce a greater number of the sex that is more dependent on the parents' resources (Trivers & Willard 1973). Accordingly, studies have found sex ratios skewed towards large offspring corresponding to a high amount of resources available to parents (Methrel & Ryder 1987; Wiebe & Bortolotti 1992; Appleby *et al.* 1997). Adjusting the sex ratio of progeny in relation to environmental conditions may also be beneficial to females because it allows for the maximization of the number of young produced in the current breeding attempt (Myers 1978). The maximization of the number of young per breeding attempt may have considerable fitness consequences in a short-lived passerine, in which most birds surviving the first winter may not breed more than once in their entire lifetime. For example, in our nest-box population only 17.6% (out of 142) of breeding female treecreepers in 2000 were caught in the next breeding season (P. Suorsa and H. Hakkarainen, unpublished data).

As a forest-dwelling species, the treecreeper strictly avoids open habitats. Individual birds forage exclusively on tree trunks and branches, where invertebrates are scarce especially during the first broods (Kuitunen *et al.* 1996). Adults may even deplete their food sources by almost 0.5 in the vicinity of their nest during the breeding season (Jäntti *et al.* 2001). In this study fragmented habitats may have elevated the foraging costs to adults by way of increased provisioning distances and enlarged foraging areas (see Huhta *et al.* 1999). In our study area pines contained fewer spiders than spruces (spiders are the main food specimen of the treecreeper; Kuitunen 1989). In agreement with this the feeding frequency was lower in territories with a high proportion of pine forests than in those with a low amount of pine forests. We suggest that the low food abundance may have induced female parents to produce the cheaper sex (i.e. females) in poor pine-dominated forests. By contrast, the high-quality territories (characterized by a high amount of deciduous trees and mixed forests) might have been richer in resources enabling the production of the more costly sex (i.e. males).

Male nestlings in the treecreeper had larger body sizes and suffered from higher nestling mortality than female nestlings suggesting that male chicks had higher nutritional requirements than females (Fiala & Congdon 1983; Slagsvold *et al.* 1986; Sheldon *et al.* 1998). Furthermore, a male-biased primary brood sex ratio was positively related to the provisioning rates and negatively associated with the residual body mass of female parents. The latter was observed only during the second broods, when male parents had abandoned the female parents who consequently had to rear the chicks alone. The parents' measurements took place in the mid-nestling phase, at the peak of chick feeding (Perrins 1979). Therefore, the decrease in body mass of the abandoned females may have resulted from increased parental effort (Askenmo 1977; Martins & Wright 1993; Tinbergen & Dietz 1994; but see Wright *et al.* 1998). Alternatively, the mass loss of females rearing male-biased broods may be adaptive in terms of decreasing power consumption in flights delivering food to young (reviewed in Breitwisch 1989).

The quality of male parenting as measured by ornaments may be related to sex ratio in birds (Burley 1986;

Table 3. The glimmix-based likelihoods of brood sex ratios (males per [males + females]) in relation to habitat characteristics in the first and second broods.
(Abbreviations used: (+) (–), direction of the effect; CB, primary sex-ratio data of complete broods; CIB, pooled sex-ratio data of complete and incomplete broods.)

		CB		CIB	
		$F_{\mathrm{d.f.}}$	p	$F_{\mathrm{d.f.}}$	p
first broods					
edge density (m ha^{-1})[b]	(–)	$6.82_{1,63}$	0.0112	$2.97_{1,83}$	0.0887
pine forests (%)[c]	(–)	$7.27_{1,63}$	0.0090	$6.57_{1,83}$	0.0122
interaction terms					
year × edge density (m ha^{-1})[b]		$0.30_{1,60}$	0.5848	$0.06_{1,80}$	0.8075
year × % pine forests[c]		$0.73_{1,60}$	0.3952	$0.34_{1,80}$	0.5634
second broods					
patch density (number per 100 ha)[c]	(–)	$10.59_{1,24.5}$	0.0033	$6.53_{1,35}$	0.0151
other deciduous trees (%)[a]	(+)	$7.38_{1,24.4}$	0.0120	$5.38_{1,35}$	0.0263
mixed forests (%)[c]	(+)	$4.82_{1,24.5}$	0.0379	$2.34_{1,35}$	0.1350
interaction terms					
year × patch density (number per 100 ha)[c]		$0.96_{1,17.3}$	0.3414	$0.00_{1,30.9}$	0.9983
year × % other deciduous trees[a]		$0.52_{1,17.2}$	0.4819	$0.44_{1,27}$	0.5143
year × % mixed forests[c]		$0.00_{1,17.3}$	0.9563	$0.59_{1,27.1}$	0.4500

[a] Territory core scale a (radius of 30 m).
[b] Territory scale b (radius of 200 m).
[c] Large scale c (radius of 500 m).

Ellegren *et al.* 1996; Sheldon *et al.* 1999). Treecreepers lack clear secondary sexual traits that could serve as ornaments and are visible to human beings and all the traits of the male parents measured were unrelated to any variations in the sex ratio. It is thought that sex ratio can also change over the breeding season (Dijkstra *et al.* 1990; Bednarz & Hayden 1991; Olsen & Cockburn 1991; Zijlstra *et al.* 1992; Daan *et al.* 1996); however, in our data such a relationship was not found.

In summary, we found that habitat quality as measured by habitat structure was associated with a high level of variation in the primary brood sex ratio. The smaller sex with the higher nestling survival was produced in fragmented and pine-dominated low-quality territories. Our results suggest that treecreepers may maximize the number of offspring per breeding attempt by adjusting the sex ratio of the progeny in relation to habitat quality. This is assumed to be a reasonable strategy for a short-lived passerine characterized by a low number of subsequent breeding attempts. Habitat quality, in general, may play an important role in determining essential life-history traits in forest-dwelling species.

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