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The importance of landscape structure for nest defence in the Eurasian Treecreeper *Certhia familiaris*

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Forest loss and fragmentation induces harmful ecological effects especially for species preferring mature forests. The Eurasian Treecreeper, *Certhia familiaris*, is highly specialised in foraging on large tree trunks and can only occasionally forage outside of mature forests. We quantified nest defence behaviour of Treecreeper parents toward a stuffed model of Great Spotted Woodpecker *Dendrocopos major* in central Finland. We used a Geographical Information System (GIS) to measure the landscape structure within a 200 m radius around the nest. We found that females with more fledged offspring gave alarm calls from farther away from the predator model than did females with fewer fledged offspring. The alarming distance of females was longer when the forest patch around the nest was larger. In males, however, alarming distance decreased with increasing home patch size. It seems that forest loss may influence parental nest defence behaviour, which is one of the fundamental life-history traits in birds. The association between habitat characteristics and nest defence behaviour of birds need more attention to understand how human modified habitats affect bird breeding success.

1. Introduction

Destruction of natural habitats results in habitat loss, edge effects, and habitat isolation. The last two elements have been termed habitat fragmentation (Andrén 1994, Fahrig 1997, Schmiegelow & Mönkkönen 2002), and may have several harmful biological and ecological effects (Andrén 1994). In fragmented environments, behaviour, breeding success and other fitness-related consequences are committed to follow the constraints set by patch size, habitat within patches, variable food supply, and inter-specific interactions, and changes in vegetation structure and climatic conditions close to the edge (Gates & Gysel 1978, Møller 1988 & 1991, Robinson *et al*. 1995, Burke & Nol 2000, Zanette *et al*. 2000). Bird species often show variable responses to forest loss and fragmentation

(Schmiegelow & Mönkkönen 2002), but in this study we concentrate on a bird species which is strongly associated with old growth forests. The reproductive performance of mature forest birds has been shown to decrease with an increasing level of habitat fragmentation (Gates & Gysel 1978, Robinson *et al.* 1995, Kurki *et al*. 2000).

Modern forestry usually diminishes the quality of forested environments as a living habitat for forest-dwelling species. It especially causes the loss of mature forest habitats, particularly in the boreal forest ecosystems. As a result of this rational forest planning, forest blocks are fragmented and separated by large clear-cuts and dense sapling stands (Mykrä *et al.* 2000). This environmental alteration increases the harmful effects on species that are dependent on continuous and homogeneous wood and forest cover (Niemelä 1999, Kouki & Väänänen 2000). These species may have restricted ability to disperse between suitable habitat patches (Hansson 1992), and the energy expenditure of food and mate searching may fail in strongly fragmented landscapes (e.g. Rolstad & Wegge 1989). Also, increased predation pressure in fragmented forest landscapes is exhaustively documented (e.g. Kuitunen & Helle 1988, Andrén 1992, Kurki & Linden 1995, Huhta 1995, Huhta *et al.* 2003, 2004). A general interest in associations between forest habitat loss and fragmentation and forest bird communities has led to the publication of several studies from all over the world (Haila *et al.* 1993, Faaborg *et al.* 1995, Freemark *et al*. 1995, Greenberg *et al.* 1997, Boulinier *et al*. 2001). In several studies, it has also been shown that forest fragmentation due to timber production has deleterious effects on forest birds (e. g. Askins *et al.* 1987, Jokimäki & Huhta 1996, Schmiegelow *et al.* 1997, Luck 2002). For species experiencing strong habitat fragmentation, both empirical data (Doncaster *et al.* 1996, Jansson & Angelstam 1999) and theoretical models predict that there are critical thresholds of habitat proportions within a landscape at which various ecological processes change abruptly (O'Neill *et al.* 1989, Dytham 1995, With & Crist 1995, Bascompte & Solé 1996).

Nest defence is one of the most important life-history traits in the reproductive investment of birds and it increases the probability of successful breeding (Blancher & Robertson 1982). The main benefit of nest defence is increased brood survival, but nest defence also has costs like energy expenditure and a risk of injury or even death (Montgomerie & Weatherhead 1988). It could also decrease the future reproductive life of the parents (Wallin 1987). The intensity of nest defence may be affected by many factors such as clutch and brood size, offspring age, parental age, laying date, weather and predator type and food conditions (Knight & Temple 1986, Winkler & Wilkinson 1988, Clutton-Brock 1991, Hakkarainen & Korpimäki 1994).

We examined the effects of landscape structure on nest-defence behaviour in the Eurasian Treecreeper *Certhia familiaris* (hereafter "Treecreeper"). The Treecreeper is an excellent study object for forest fragmentation studies because it breeds in old-growth spruce (*Picea abies*) and mixed spruce and pine (*Pinus sylvestris*) coniferous forests (Kuitunen 1987, Kuitunen & Helle 1988, Aho *et al*. 1999). Further, its breeding densities are three times higher in old-growth forests than in managed forests (Virkkala *et al*. 1994, Haila *et al.* 1989). Also, this species is known to be extremely sensitive to forest fragmentation, because it is absent from clear-cuts and saplings (Kuitunen & Helle 1988). Treecreepers breed in specially designed nest boxes in managed forests (Kuitunen 1987). Breeding parents need large trees for foraging (Suhonen & Kuitunen 1991a, Aho *et al*. 1997 a, b, Jäntti *et al.* 2001) where they search for arthropods for their nestlings (Kuitunen & Törmälä 1983, Suhonen & Kuitunen 1991b). The Treecreeper is a monogamous passerine bird showing biparental offspring care (Kuitunen & Suhonen 1989, Kuitunen et al. 1996) and nest defence, especially during the first brood (Jäntti *et al.* 2003). Potential nest predators for Treecreepers in our study area are the Great Spotted Woodpecker *Dendrocopos major*, Least Weasel *Mustela nivalis* and Stoat *Mustela erminea (*Kuitunen & Aleknonis 1992).

In this study we had two aims. First, we studied whether parent Treecreeper nest defence behaviour was related to number of nestlings and laying date, since the number of nestlings is an important life-history trait. Second, because habitat loss and landscape fragmentation has often been associated with poor habitat quality we aimed to study possible associations between forest loss and fragmentation and parental nest defence behaviour. No study so far has documented the effects of landscape structure on the nest defence behaviour of birds.

2. Material and methods

2.1. Study area and general methods

This study was conducted in 60–100 year old coniferous and mixed managed forests in the vicinity of Konnevesi Research Station in central Finland (62º37' N, 26º20' E) during the summer of 1991. There were about 60 forests with two special nest boxes for Treecreepers, one for the first clutch and one for the second clutch (Kuitunen 1987). We used mist nets to trap breeding females at the nest near the end of egg incubation, and males were trapped when they were feeding their offspring. The birds were individually marked both with aluminium and coloured rings. The throat of each parent was coloured to distinguish the females from the males. The adult birds were sexed by morphological criteria, e.g. bill length, and the presence of a brood patch in females (Suhonen & Kuitunen 1991a, b, Kuitunen unpublished data).

2.2. Quantification of nest defence

We used 18 early brood pairs of Treecreepers to study nest defence (17 May–3 June, 1991). Nest defence measurements were done when the nestlings were 13–15 days old, i.e. a couple of days before fledging. At this age nestlings are quite vulnerable to predators because they are generally noisy (see Jäntti *et al*. 2003). We used a stuffed Great Spotted Woodpecker as a predator model. The model was wired to a 1 m long wood stick, which was put up at the front of the nest box about 20 cm away from the two side entrance holes. Observations were made with binoculars from a shelter at a distance of 10–40 m from the nest on sunny or cloudy days, but not on rainy days. Data were recorded into a dictaphone and later transcribed.

We started each measurement period (later called trial) as soon as we saw or heard one of the parents calling; to be sure that it had noticed the predator. The tape-recorded measurement period lasted for five minutes. Generally, the arrival time was different for the male and female, so the trial was performed separately for each parent. Arrival time was the time from setting up the predator model until the parent arrived and started to display (Jäntti *et al.* 2003).

Mobbing rate was the attack or fluttering behaviour of the Treecreeper towards the predator model during the five minute period. The distances of parents from the predator were measured during the trial, and after the trial the mean, minimum, and maximum distances from the predator model were recorded. The mean distance from the predator was the mean value of the bird to predator distances recorded every fifteen seconds during the trial. The minimum distance was defined as the shortest recorded distance of the Treecreeper to the model during the trial. The maximum distance was the longest observed distance of the parent from the model during the trial. We also recorded the number of parental visits into the nest box (Jäntti *et al.* 2003).

The call rate was the mean number of tjii warning calls per minute during the five minute period. At each nest, we waited for about 20 minutes to make sure the parents were present or absent. During the trial, we also observed the level of quieting that resulted after the parents' alarm call to address whether the high-pitched calls are enough to silence the offspring in the nest. Generally, the two week old nestlings made some noises (chirr) in the nest box. In our observations, offspring in all nests made some chirr sounds before the parents were present and made alarm calls (Jäntti *et al.* 2003).

2.3. Landscape data analyses

Land use and forest data for the study area as well as the location of each Treecreeper territory were imported into a Geographical Information System (GIS). We measured the forest structure within 200 m radii around each of the nest-boxes (12.75 ha), which was the maximum observed foraging distance of breeding parents from the nest (Suhonen & Kuitunen unpublished data).

We used classified Landsat TM 5 satellite images produced by the National Land Survey of Finland (NLS) from the year 1990 as the land-use and forest-resource data (Vuorela 1997). Pixels

Table 1. Spearman rank correlations between the mean distance of the female and male Treecreeper and separate landscape indices at a radius of 200 m from the nest (Number of observation in females n = 15 and in male n = 18).

Index	Female		Male	
	r_s	P	r_s	P
Number of patches (no/200 m radii)	–0.54	0.038	0.27	0.274
Total edge length (m/200m radii)	–0.46	0.082	0.05	0.845
Area of home patch (ha)	0.77	0.001	–0.48	0.044

originally measuring 30 m × 30 m were re-sampled to measure 25 m × 25 m by NLS. Digital maps of roads, agricultural land etc. were used to separate forest from non-forest land. Each pixel in an NLS classification can initially belong to one of 50 land use and forest classes. In the case of forested areas, each pixel was classified according to the total timber volume (mainly applying 50 m^3/ha intervals) before being further classified according to the main tree species or mixed species composition.

Clear cuts and sapling stands were separated as distinct classes by allowing a maximum timber volume of 4 m^3/ha for clear-cuts and 12 m^3/ha for sapling stands (Vuorela 1997). According to the national forest inventory, this definition refers to sapling stands of 1–20 years old (Tomppo *et al.* 1999). Mature forest area was calculated by combining the area of forest land where total timber volume was > 151 $m^{3/}$ha (Tomppo *et al.* 1999). Thus, the identification of mature forest stands is based on the timber volume and not, for example, on the management status of the stand. However, we find this criterion reasonable since, according to the national forest inventory, forests in the age class of 101–120 years have on average a timber volume of 211.3 m^3/ha in the study area. Further, intensive forest management in this area with clear-cutting as the main regeneration method mainly concerns forests > 100 m^3/ha in timber volume.

The habitat classes (means in parentheses) used in the analyses to describe the landscape structure at the radii of 200 m were lake (3.5%), open mire (0.0%), agricultural field (11.1%), clear-cut (4.8%), open land (combined with unforested habitat, 22.8%), wet spruce forest (1.3%), pine mires (0.7%), sapling stands (3.3%), pine forest (14.5%), spruce forest (34.8%), deciduous forest (2.1%) and mixed forest (20.5%). We also measured the number of forest patches, total length of forest-open land edge within 200 m radii, and the size of a home patch (forest patch where nest boxes were situated) using FRAGSTATS (McGarigal & Marks 1995).

2.4. Statistical analyses

Spearman correlations were calculated between the mean distance of males and females and fledgling number, laying date and habitat quality variables including number of patches, total edge length, and area of the home patch (Table 1). We used the Mann-Whitney U-test to find differences in the distance from the woodpecker model, minimum distance from the woodpecker model, mobbing rate and alarm call rate in female and male Treecreepers in small (< 10 ha) and large (at least 10 ha) home patches (Table 2). There were no differences between age and quality of males and females between small and large home patches. We performed a regression analysis to examine relationships between the mean distance of females and males as dependent variables and habitat quality variables, number of nestlings and laying date as predictors (Table 3). Colinearity analysis revealed significant correlations between several habitat variables and behavioural variables. Due to these correlations, we only included in our final regression model mean distance of males and females from the stuffed woodpecker, fledgling number, laying date and habitat quality variables including number of patches, total edge length, and area of the home patch and omitted most of the habitat variables from the model. Finally, we used

Table 2. Mean (SD) distance from the nest, minimum distance distance from the nest, mobbing rate and alarm call rate in the female and male Treecreeper in small (< 10 ha) and large (at least 10 ha) home patch. Test statistics refers to Mann-Whitney U-test.

Variable	Small home patch		Large home patch			
Female	n = 6		n = 9			
	Mean	SD	Mean	SD	U	P
Mean distance	2.5	0.2	5.9	3.2	3	0.003
Minimum distance	0.4	0.2	0.7	1.2	20.5	0.46
Mobbing rate	0.2	0.4	0.8	1.5	21	0.53
Alarm call rate	33.2	18.6	41.1	18.0	20	0.46
Male	n = 8		n = 10			
	Mean	SD	Mean	SD	U	P
Mean distance	13.6	9.8	6.4	6.8	12	0.012
Minimum distance	0.5	0.4	0.5	0.2	37.5	0.83
Mobbing rate	1.0	1.4	2.1	3.0	31	0.46
Alarm call rate	37.3	17.3	49.5	17.2	23	0.15

Table 3. Final stepwise regression model (adjusted $R^2 = 0.482$) to explain the mean distance of female Treecreeper from the Woodpecker model for the first broods ($F_{2, 12} = 7.52$, P = 0.008).

	B	SE	$t_{2,12}$	P
Constant	–9.46	3.73	–2.54	0.026
Number of Fledglings	1.42	0.56	2.55	0.025
Home Patch Size	0.77	0.32	2.38	0.035

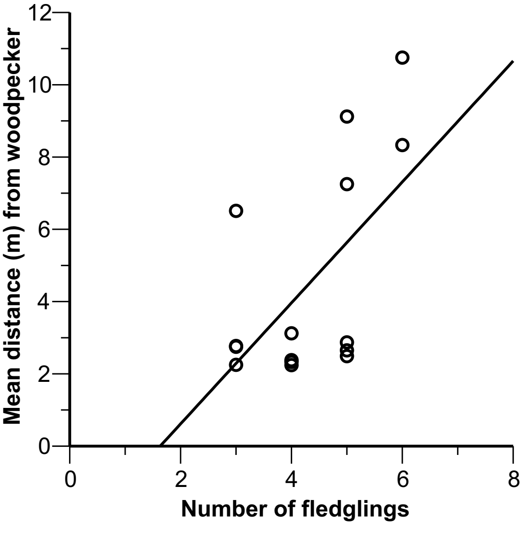

Fig. 1 Number of fledglings in relation to the mean distance (m) of female Treecreeper from the stuffed Woodpecker during the five minute trial.

a stepwise linear regression to fit the final model. The statistical analyses were conducted in SPSS version 12.0.1 for Windows.

3. Results

We found that female Treecrepers with more fledged offspring gave alarm calls from farther away from the stuffed woodpecker than did females with fewer fledged offspring ($r_s = 0.52$, n = 15, P = 0.049; Fig. 1). In contrast to females, the number of fledged offspring was not associated with male Treecreeper distance from the stuffed woodpecker ($r_s = –0.24$, n = 18, P = 0.35). Mean distances of females and males from the stuffed woodpecker did not depend on laying dates (r_s = 0.49, n = 15, P = 0.064 r_s = –0.18, n = 18, P = 0.47, respectively).

Because habitat loss has often been associated with poor habitat quality, we tested separate variables measuring the structure of the breeding landscape. Only the mean distance of parents from the stuffed woodpecker was associated with landscape indices (Table 1, 2; Fig. 2). In females the mean distance was longer when the home patch size was larger and in males it was opposite (Table 1, 2, Fig. 2). However, because most of the landscape indices or habitat variables did not correlate significantly with the mean distance of females and males from the stuffed woodpecker (Table 1), we performed a stepwise regression analysis to estimate the most important variables in explaining the mean distance of females from the stuffed woodpecker (Table 3).

Both the number of fledglings and size of home patch were statistically significant predictors for mean alarming distance of females (Table 3) and number of patches in 200 m radii, total edge length was omitted from the final stepwise linear regression model. No measured variable explained the mean male distance from the stuffed Woodpecker.

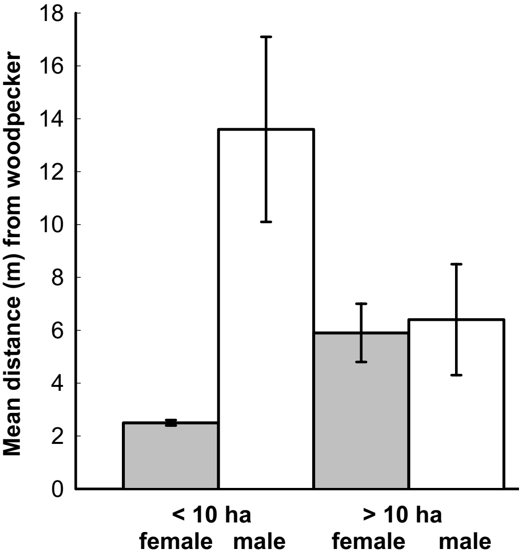

Fig. 2 The size of the home patch (ha) in relation to the mean distance of female and male Treecreeper from the stuffed Woodpecker during the five minute trial.

4. Discussion

Treecreeper females have a longer alarming distance in larger forest patches, and when there were more fledged offspring. This longer distance seems to be dependent on laying date. Treecreepers use warning calls to silence the nestlings in the nest (Jäntti *et al.* 2001). Possibly, noiseless, well-fed nestlings in larger forest environments may be easier to silence by a Treecreeper parent, even from longer distances from the nest, than in poor quality, small forest fragments with hungry and stressed nestlings (see also Suorsa *et al.* 2003). As we expected, parents seem to take more risks in their nest defence in smaller forest patches to keep the hungry nestlings quiet because they must be close to the nest for noisy offspring to hear their alarm-calls.

Many large, old-growth forest-dwelling bird species, for example Goshawk *Accipiter gentiles* and Black Woodpecker *Dryocopus martius*, can survive in fragmented fine-grained habitats by having large territories with many patches of forest per territory (Widen 1989, Tjernberg *et al.* 1993, see also Forsman *et al*. 1984, Wegge & Rolstad 1986). Treecreepers, however, seldom fly over wide open areas (> 100 m) during the breeding season, and large territories could be very costly to control and protect, especially for males, in fragmented, fine-grained forest habitats (Jäntti *et al.* 2001, Suorsa *et al.* 2003, Huhta *et al.* 2003 & 2004).

Within populations of passerine Ovenbird *Seiurus aurocapillus*, males paired better in a contiguous forest farther from edges than in fragments created by agriculture and forestry (Bayne & Hobson 2001). Female Ovenbirds seem to avoid pairing with males near edges, because rates of nest predation and brood parasitism near edges in small farm land fragments were higher (van Horn *et al.*1995, Burke & Nol 1998, Bayne 2000, Hobson & Bayne 2000). Also, the earliest-arriving male Pied Flycatchers *Ficedula hypoleuca* consistently avoid experimental breeding sites at the edge between forest stands and clear-cuts, and prefer nest boxes 50–100 m from the edge (Huhta *et al*. 1999).

Our nest defence study was done during the nestling phase when nest defence activity was assumed to be strongest and nestlings are most valuable because of their age (Andersson *et al.* 1980, Grieg-Smith 1980, Montgomerie & Weatherhead 1988). Two week old Treecreeper nestlings are very noisy and almost ready to fledge. Consequently, they are vulnerable to predators like Stoat, Least Weasel, and Great Spotted Woodpecker at this age. Thus, in this phase of breeding effective nest defence by parents is required.

The Treecreeper nest is normally quite cryptically located in a crevice of a tree or between the bark and the tree trunk, and consequently it could be assumed that birds with cryptic nests should defend their offspring less than birds with open nests (Montgomerie & Weatherhead 1988). Treecreeper nest defence consists of alarm calls that are high-pitched and narrow frequency (tjii). These calls are difficult to locate, and Treecreepers are hard to observe in thick spruce forests. Furthermore, at the same time, the nestlings in the cryptic nests become quiet (Jäntti *et al.* 2003). Treecreepers use these alarm calls to silence nestlings, like many other bird species (Grieg-Smith 1980, East 1981, Knight & Temple 1986, Jäntti *et al.* 2003), rather than immediately engaging in active nest defence. Parents with high-pitched alarm calls do not expose the nest or themselves to the nearby predator.

This could explain the nest defence behaviour of Treecreepers, which does not appear to be very active. We have earlier shown that over 90% of nests were silenced by one or both parent Treecreepers (Jäntti *et al.* 2003). Thus, parents have done enough to defend their nest if they can silence their offspring from far away before a predator gets too close to locate the nest. This could partly explain why landscape structure had only minor effects on direct nest defence actions of the Treecreeper.

To conclude, it seems that forest loss as measured by forest patch size is associated with parents nest defence behaviour, which is one of the fundamental life-history traits in birds. The association between habitat characteristics and nest defence behaviour of birds needs more attention to understand how human modified habitats affect the breeding success of birds.

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Puukiipijän pesänpuolustuskäyttäytyminen ja maisemarakenne

Maisemarakenteen pirstoutuminen ja elinympäristöjen huonontuminen on etenkin boreaalisten havumetsien osalta osoitettu viimeaikaisissa tutkimuksissa lintujen pesintätulosta merkittävästi heikentäviksi tekijöiksi. Sen sijaan maisemarakenteen merkitystä lintujen pesänpuolustuskäyttäytymiseen ei ole aiemmin tutkittu. Testasimme puukiipijä emojen pesänpuolustusaktiivisuutta käyttäen petomallina täytettyä käpytikkaa. Käpytikka on puukiipijälle todellinen peto, koska se syö sen munia ja poikasia, ja se voi tuhota niin luonnonpesiä kuin pesäpönttöjäkin.

Tutkimus toteutettiin Keski-Suomessa Konneveden tutkimusaseman ympäristössä. Pesänpuolustuskokeet tehtiin kevään ensimmäisen poikueen ollessa vajaa kaksiviikkoisia ennen pesästä lähtöä touko–kesäkuun vaihteessa, jolloin poikaset ovat vielä haavoittuvia ja nälkäisinä ne helposti paljastavat olinpaikkansa pedoille. Käpytikkamalli asetettiin puolentoista metrin mittaiseen keppiin pesäpönttöä vasten, minkä jälkeen odotettiin emojen saapumista pesälle. Emojen saavuttua keräsimme käyttäytymistietoja noin viiden minuutin ajan: saapumisaika puolustukseen, varoitusten määrä per minuutti, emojen etäisyys pesästä ja hyökkäysten määrä kokeen aikana. Tutkimuksessa käytettiin vain aikaisia pesintöjä sekä koirasta ja naarasta seurattiin. Maisemarakenne määritettiin maankäyttö- ja puustotulkitusta Landsat-satelliitin tuottamasta aineistosta, josta Fragstat-ohjelmalla ajettiin maisemaindeksit: metsälaikkujen määrä, keskimääräinen laikun koko, laikun koon CV, reunan pituus ja tiheys pinta-alayksikköä kohden, keskimääräinen muoto indeksi, keskimääräinen etäisyys lähimpään naapuriin ja puukiipijän pesimälaikun koko.

Puukiipijän pesänpuolustus koostuu pääosin korkeista *tjii*-varoitusäänistä, joiden tarkoitus on hiljentää poikaset pesässä. Maisemarakenteen pirstoutuneisuus näkyi puukiipijän pesänpuolustuksessa siten, että varoittavan naaraan keskimääräinen etäisyys täytetystä käpytykasta oli lyhyempi ja koiraan pidempi pienissä metsäsaarekkeissa kuin suurissa yli 10 ha metsäsaarekkeissa. Muutoin maisematekijöillä, kuten metsälaikkujen määrällä, reunan pituudella ei ollut vaikutusta pesänpuolustukseen.

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