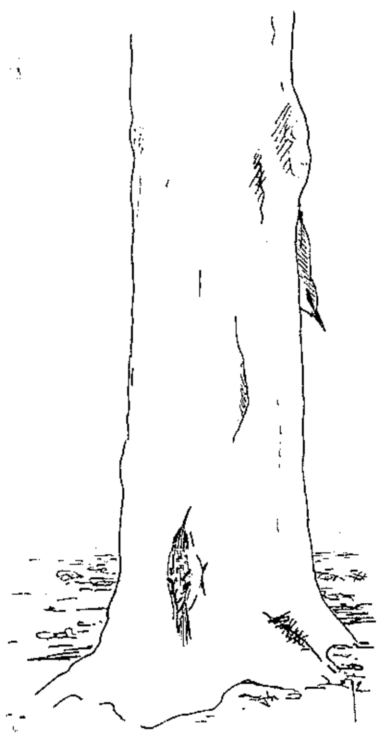
DOES THE DOMINANT NUTHATCH *SITTA EUROPAEA* AFFECT THE FORAGING BEHAVIOUR OF THE SUBORDINATE TREECREEPER *CERTHIA BRACHYDACTYLA* IN SMALL FOREST FRAGMENTS?

NADIA NOUR[1], JUKKA SUHONEN[2], RAOUL VAN DAMME[1], ERIK MATTHYSEN[1] & ANDRÉ A. DHONDT[3]



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We studied the winter foraging behaviour of Short-toed Treecreeper *Certhia brachydactyla* and Nuthatch *Sitta europaea* in 18 deciduous forest fragments varying in size between 1 and 30 ha and in one forest of about 200 ha in order to examine how forest area and the presence/absence of the dominant Nuthatch affect the foraging behaviour of the subordinate Treecreeper. The Treecreeper occurred in 14 out of 18 forest fragments while the Nuthatch was only observed in seven, mainly in fragments exceeding 4 ha We found no effect of forest size on any of the components of the foraging niches of either Treecreeper or Nuthatch, and Treecreeper foraging niches did not become broader in the smaller fragments in which Nuthatches were absent. The significant niche change we did observe was opposite to the expected direction We conclude that winter foraging niches of small insectivorous birds do not necessarily expand in the absence of close competitors in island-like situations.

Key words: *Sitta europaea* - *Certhia brachydactyla* - interaction - niche overlap - competitive release

[1]Department of Biology, University of Antwerp (UIA), B-2610 Antwerp, Belgium; E-mail: nour@uia.ua.ac.be; [2]Department of Biological and Environmental Science, University of Jyväskylä, P.O. Box 35, FIN-40351 Jyväskylä, Finland; [3]Cornell Laboratory of Ornithology, 159 Sapsucker Woods Road, Ithaca NY 14850, USA.

INTRODUCTION

The effects of habitat fragmentation have become a major item in ecology and conservation biology (for reviews, see Wilcox & Murphy 1985, Soulé 1986, Opdam 1991, Saunders *et al.* 1991). Most studies on birds have focused on effects at the species level, i.e. they examine whether fragmentation affects the probability of occurrence, abundance or demographic characteristics of a single species, or of several species but independently of each other (Martin 1980, Lynch & Whigham 1984, Blake & Karr 1987, Van Dorp & Opdam 1987). However, habitat fragmentation is also likely to affect the behaviour of individuals and interactions between species. For instance, in field-forest ecotones, species that benefit from habitat fragmentation have been shown to cause substantial damage to other species, through competition, predation or nest parasitism (Brittingham & Temple 1983, Andrén & Angelstam 1988, Nour *et al* 1993, Robinson *et al* 1995). Examples of such effects mainly come from studies on interspecific interactions between species that primarily inhabit forests and species that live in the surrounding agricultural matrix. The effects of forest fragmentation on mutual interactions among forest birds have been documented far less. This is surprising, because the effects of fragmentation on one species are likely to affect the life of other members of the community. For instance, interspecific competition may be harsher in smaller fragments if resources are in short supply. On the other hand, the absence of a fragmentation-sensitive species may allow competing species to expand their foraging niches in smaller forest fragments, as has been described in real island situations (Diamond 1970, Terborgh & Faaborg 1973, Alerstam *et al.* 1974).

In this study, we compare the winter foraging behaviour of two forest-inhabiting passerines, the Nuthatch *Sitta europaea* and the Short-toed Treecreeper *Certhia brachydactyla* in a suite of forest fragments differing in size and in degree of isolation. Although this has never been tested explicitly, the similarity of their foraging behaviour and diet suggests that these species, when co-occurring, might be competing for food. Both bird species show specialized morphological adaptations that allow them to forage on tree trunks and both feed mainly on spiders and insects (Bilcke *et al.* 1986, Kristin 1990 & 1992, Cramp & Perrins 1993). The niche overlap between Nuthatch and Treecreeper, two members of the Pariform guild, is among the highest in that guild (Moreno 1981, Bilcke *et al.* 1986, Székely 1987, Nour *et al.* 1997). Frequent field observations (pers. obs.) show that the larger Nuthatch frequently chases the smaller Treecreeper, suggesting that interference is intense, with the Nuthatch being the dominant actor. Although both Nuthatch and Treecreeper suffer from forest fragmentation (Kuitunen & Helle 1988, Opdam 1991, Verboom *et al.* 1991), the former seems most sensitive (Opdam & Schotman 1987, Nour *et al.* unpubl. data) and is thus more likely to be absent from smaller fragments.

In this paper we examine how (1) forest area and (2) the presence or absence of the dominant Nuthatch, affect the foraging behaviour of the subordinate Treecreeper. If interspecific competition is important, we predict that in small forest fragments the Treecreeper will have a narrower foraging niche when the Nuthatch is present, but an expanded one in the absence of the Nuthatch, because of competitive release.

METHODS

Selection of forest fragments

Seventeen patches of mature woodland (1 to 30 ha) and one larger forested area (200 ha) were selected in the vicinity of Antwerp (Belgium). Forest fragments are dispersed in a mainly agricultural landscape and are isolated from one another by meadows, fields and residential areas (cf. map in Matthysen *et al.* 1995). All study sites are covered with mature deciduous trees, mainly Common Oak *Quercus robur* (70-90%), and few (10-30%) other trees, such as Beech *Fagus sylvatica*, Larch *Larix decidua*, Birch *Betula* spp. and Sycamore *Acer pseudoplatanus*. The understory is dominated by Bird Cherry *Prunus padus*, Alder *Alnus glutinosa*, Hazel *Coryllus avellana* and *Rhododendron ponticum*. The herb layer consists mainly of Bracken *Pteridium aquilinum* and Bramble *Rubus fruticosos*. Woodlots are separated from one another by at least 200 m of open area.

Foraging behaviour

As part of a study on the foraging behaviour of species belonging to the Pariform guild in the 18 forest patches described above (Nour *et al.* 1997) we recorded the foraging activity of Nuthatch and Short-toed Treecreeper. From early December 1993 to late February 1994 each woodlot was visited approximately every two weeks between 7.30 and 11.00 a.m. Since the same forest fragments were visited repeatedly, and given that both Nuthatches and Treecreepers are resident in winter, the same individuals were observed more than once. For that reason we analysed the data by combining the average values per forest patch, rather than by using individual observations. Our sample sizes are, therefore, the number of forest patches in which the species were observed

Four niche dimensions were considered: substrate, height, time spent on a tree and tree size visited. The foraging substrates were divided into trunk, large branches (with a diameter larger than that of the bird), and small branches (with a diameter smaller than that of the bird) (Bilcke *et al.* 1986) The feeding stations were assigned to one of four height categories: first, second, third and fourth quarter of the tree. We collected at least 15 foraging observations (for height and substrate) per forest fragment per species The time an individual remained on a tree was measured in seconds, using a stop watch, starting at the time it arrived on a tree. For each species and in each woodlot we recorded at least five such observations The size of trees on which the birds foraged was recorded, using three size categories: small (trunk diameter 26-40 cm), medium (diameter 41-55 cm) and large (diameter 56-70 cm). The frequency (in %) of each tree size category in each forest fragment was obtained by walking through the forest and noting the size category of randomly chosen trees.

To compare groups we calculated a mean tree size index, a mean foraging height index and a mean foraging substrate index (Suhonen *et al.* 1994) from all records based on the categories mentioned above. For instance, a high index value for substrate indicates frequent foraging on small branches and less on trunks and large branches.

Niche breadths (B_i) for each of the three niche components (substrate, height and tree size), were calculated using Levin's formula:

$$B_i = 1/\sum P_i^2 \times n,$$

where P_i is the proportion of observations in the i^{th} unit of the resource set and n equals the number of resource states (Hurlbert 1978) To simplify the comparison of niche breadth values where different numbers of categories were involved, we scaled the values so that $B_{max} = 1$ and $B_{min} \times = 0$. Niche overlaps (P_{jk}) between the two species for use of substrate, height and tree size, were calculated using a measure of proportional overlap $P_{jk} = \sum$minimum P_{ij}, P_{ik}, which is the sum of the minima of the relative frequencies over all categories (Hurlbert 1978).

RESULTS

In 4 of the 18 forest fragments, neither Nuthatch nor Treecreeper was observed during the study period. The remaining 14 fragments all contained Treecreepers, and seven of these patches also held Nuthatches Nuthatches were absent from all patches smaller than 4 ha except one (1 ha) The total number of foraging observations was 254 for the Nuthatch and 464 for the Treecreeper.

Foraging behaviour and forest size

To study possible variation of foraging behaviour in relation to fragment size, we calculated correlation coefficients between forest patch size (log-transformed) and the various components of the foraging niche we measured (foraging time per tree, tree size index, foraging height index, foraging substrate index, and niche breadths for use of substrate, of height and size of tree). None of the correlation coefficients in either species was statistically significant (Table 1; all $P > 0.1$)

Table 1. Correlation of forest fragment size (after $\log_{10}$ transformation) with the foraging behaviour measures of Treecreeper ($n = 14$) and Nuthatch ($n = 7$). No significant differences were found

	Treecreeper		Nuthatch	
	r	*P*	*r*	*P*
Time per tree, s	0 04	0 89	0 50	0 26
Tree size index	-0 15	0 62	-0 27	0 56
Height index	0 26	0 37	0 34	0 46
Substrate index	0 40	0 16	0 04	0 98
Niche breadth				
Tree size	0 40	0 15	-0 24	0 60
Height	0 27	0 35	-0 42	0 35
Substrate	0 44	0 12	-0 68	0 10

Table 2. Comparison of foraging behaviour of Treecreeper and Nuthatch when both species occurred in the same forest fragments ($n = 7$). Bold: significant difference

	Treecreeper		Nuthatch		Test		
	$\bar{x}$	SD	$\bar{x}$	SD	t	df	P
Time per tree, s	82	38	88	32	-0.37	6	0.72
Tree size index	1.7	0.2	1.8	0.4	-0.93	6	0.4
Height index	2.3	0.3	2.8	0.5	-1.86	6	0.12
Substrate index	**1.7**	0.2	**2.2**	0.2	**-4.03**	6	**0.006**
Niche breadth							
Tree size	0.55	0.07	0.45	0.25	0.10	6	0.9
Height	0.51	0.23	0.56	0.16	-0.44	6	0.7
Substrate	0.77	0.30	0.76	0.17	1.03	6	0.3

Foraging behaviour of Treecreeper and Nuthatch in forest fragments where both species occurred

In the seven fragments in which they co-occurred, Treecreepers and Nuthatches differed in substrate use (paired t-test, $P = 0.006$, Bonferroni adjustment for multiple testing $\alpha = 0.007$; Table 2). While Treecreepers prefer to forage on trunks, Nuthatches favour small branches (Fig. 1). Nuthatches and Treecreepers spent a similar amount of time per tree, and had comparable tree size and height indices (Table 2; all $P > 0.1$). Their niche breadths for tree size, height and substrate did not differ either (all $P > 0.3$).

Foraging behaviour of Treecreeper in presence/absence of Nuthatch

We also compared the foraging parameters of the Treecreeper between forest fragments where Nuthatches were present ($n = 7$) and absent ($n = 7$). The only difference found was that the Treecreeper's niche breadth for tree size was significantly narrower in the absence of Nuthatches (Table 3; $P < 0.001$; Bonferroni adjustment for multiple testing $\alpha = 0.007$), a non-intuitive result. However, tree size distribution differed between fragments containing both Nuthatch and Treecreeper and fragments containing only Teecreeper ($\chi^2 = 56.6$, $P < 0.001$). There were fewer large trees in fragments that were not inhabited by Nuthatches (Fig. 2). This difference in tree size distribution has to be taken into account when comparing the niche breadth of the Treecreeper between both types of fragments. The observed change in niche breadth may reflect the change in tree availability rather than a change in competition pressure. The tree size index for Nuthatches (Table 4) was not significantly different from the mean tree size index of the forest fragments ($P = 0.07$), indicating that these birds have no special preference for trees of a certain size class. In contrast, Treecreepers foraged more on trees with diameters smaller than average, irrespective of the presence or absence of the Nuthatch (Table 4), both $P < 0.05$).

In an attempt to separate the habitat-effect and the competitor-effect, we deduced the 'preference' of the Treecreeper for all tree size classes when it was foraging in the absence of the Nuthatch. These preferences were obtained by dividing the number of birds observed in tree class i by the number of trees of class i present (i varies between 1 and 3). This resulted in a preference of 1.45 for small trees, 0.96 for medium trees, and 0.02 for large trees. We then predicted the numbers of observations in each tree size class for fragments in which Nuthatches were present by multiplying the preferences with the actual numbers of trees of each size class. The values thus obtained predict where Treecreepers would for-

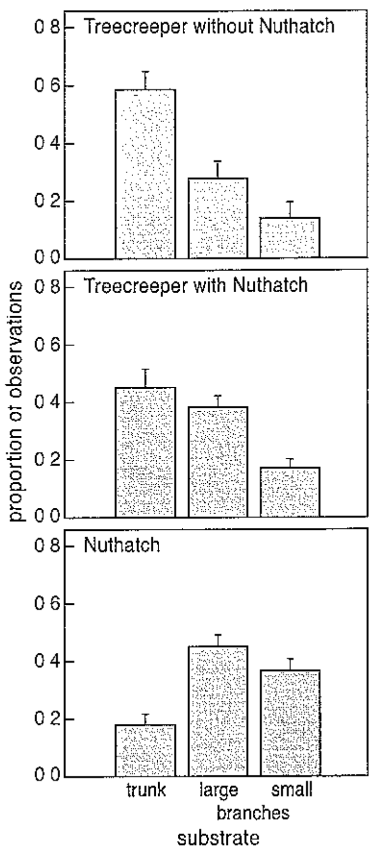

Fig. 1 Substrate use by Treecreeper in the presence/absence of Nuthatch, and by Nuthatch in the presence of Treecreeper (seven fragments in each case). SE indicated

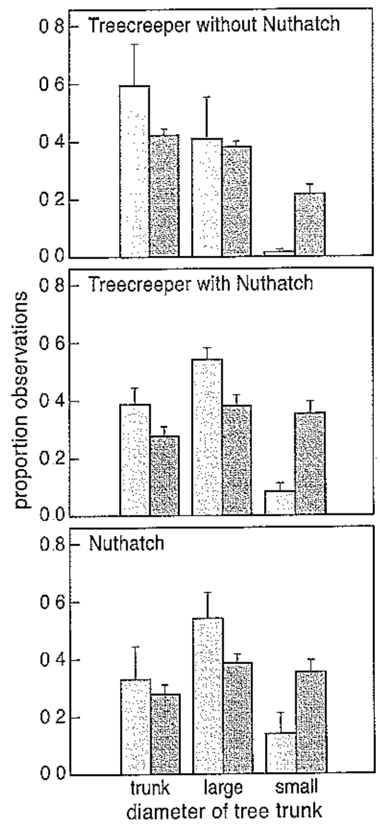

Fig. 2 Proportion of foraging observations of the Treecreeper and the Nuthatch on tree size categories in forest fragments in which the Nuthatch was absent or present (open bars), and availability of each tree size category in the same forest fragments (closed bars). SE indicated

age in fragments with a given tree size distribution, provided they do not change their tree size selection in response to the Nuthatch. From these 'virtual' data we recalculated niche breadth. We found no difference between the virtual (mean ± SD: 0.60 ± 0.005, $n = 7$) and the observed mean niche breadths (0.55 ± 0.07, $n = 7$; paired t-test, $t_6 = -1.22$, $P = 0.27$). This suggests that the narrowing of the Treecreeper's niche in the smallest fragments is not a response to the absence of the Nuthatch, but merely reflects the different tree size distribution in these habitats.

Niche overlaps and direction of niche changes

Another way of assessing the effects of the presence/absence of the Nuthatch on the Treecreeper's foraging behaviour is by comparing the 'actual' niche overlap between the two species (when co-occurring) and the 'expected' niche overlap (that would arise if Treecreeper had foraged as it did in the absence of the Nuthatch) (Alatalo 1981, Alatalo *et al.* 1986). The difference between these two measures estimates the effect of a foraging-site change by Treecreepers on the niche overlap between the two species. If the sign of the

Table 3 Foraging behaviour of Treecreeper in the presence/absence of Nuthatch in forest fragments (each $n = 7$). Bold: significant difference.

	Absence of Nuthatch		Presence of Nuthatch		Test		
	$\bar{x}$	SD	$\bar{x}$	SD	t	df	P
Time per tree, s	61	18	82	38	-1 32	12	0 21
Tree size index	1 4	0 4	1 7	0 2	-1 63	12	0 13
Height index	2 0	05	2 3	0 3	-1 45	12	0 17
Substrate index	1 6	0 3	1 7	0 2	-1 22	12	0 3
Niche breadth							
Tree size	**0 19**	0 15	**0 55**	0.07	**-5 56**	12	**0.0001**
Height	0.47	0 17	0 51	0.23	-0 35	12	0 73
Substrate	0 59	0.29	0 77	0.24	-1 30	12	0 21

Table 4 Comparison of use and availability of tree size categories for Nuthatch and for Treecreeper in presence/absence of Nuthatch (each $n = 7$) Bold: significant difference.

	Tree size index used		Tree size index available		Test		
	$\bar{x}$	SD	$\bar{x}$	SD	t	df	P
Nuthatch	1 8	0 4	2.1	0.2	-1 58	6	0 17
Treecreeper with Nuthatch	**1.7**	0 2	**2.1**	0.2	**-2.97**	6	**0 03**
Treecreeper alone	**1.4**	0 4	**1.8**	0.1	**-2.55**	6	**0.04**

Table 5 Mean actual and expected niche overlaps between Treecreeper and Nuthatch (for use of tree size, height and substrate) If the sign of the difference is positive, niche change is convergent (Treecreepers increase their use of foraging sites of the Nuthatch in its presence) Bold: significant difference

	Actual		Expected		Test		
	$\bar{x}$	SD	$\bar{x}$	SD	t	df	P
Tree size	**0.76**	0 10	**0.46**	0 29	**2.47**	6	**0.04**
Height	0 59	0 17	0.60	0 19	-0 32	6	0 80
Substrate	0.68	0 19	0.58	0.15	1 32	6	0 23

difference is negative, the niche change is divergent and the Treecreeper reduces its use of foraging sites of the Nuthatch We calculated actual and expected niche overlaps for each of the seven fragments in which both species were present. We found non-significant changes in overlap for foraging height and substrate (Table 5; $P > 0.1$) The change in overlap for foraging tree size was significant and positive, suggesting niche convergence (Table 5; paired t-test, $t_6 = 2.47$, $P = 0.04$) The Treecreeper seems to increase the use of Nuthatch-like foraging sites in its presence

DISCUSSION

The aim of this study was to investigate (1) whether components of the foraging niches of two passerine birds change with forest fragment size, and (2) to what extent the absence of a fragmentation-sensitive species (the Nuthatch) affects the foraging behaviour of a close competitor (the Treecreeper) that is less sensitive to fragmentation Our results show no effect of fragment size on the foraging behaviour of Nuthatch or Treecreeper. This suggests that the foraging environment of both species remains unaffected, or that the birds do not respond to the changes (see also Nour *et al* 1997). Habitat fragmentation may affect a bird's foraging environment in a variety of ways. Physical parameters such as temperature and wind speed that are likely to influence both predator and prey populations have been shown to vary with fragment size (Saunders *et al* 1991) Prey density, predation pressure and the degree of intra- and interspecific competition rate probably also depend on fragment size It therefore seems unlikely that the foraging environment of both bird species does not change with fragment size, although we lack the data to document this premise Alternatively, birds may show insufficient plasticity in their foraging behaviour to respond to the environmental changes. This would imply that birds are foraging suboptimally in some environments These suggestions may be considered as hypotheses for further investigations.

Several experimental and non-experimental studies have shown that birds restrict their foraging sites in the presence of close competitors and that the local absence of some species is associated with niche expansion of the remaining ones (for reviews, see Suhonen *et al*. 1993, Cimprich & Grubb 1994). Comparable expansion on the feeding niches has also been observed on species-poor islands, with reduced interspecific competition (Diamond 1970, Terborgh & Faaborg 1973, Alerstam *et al* 1974).

High foraging overlap values between Nuthatch and Treecreeper have been reported in several studies (Moreno 1981, Bilcke *et al* 1986, Székely 1987, Nour *et al* 1997). The two genera are assumed to avoid competition to some degree by foraging on different substrates and/or by differences in the size of prey consumed. Our results also show that Treecreepers forage more on tree-trunks and less on small branches than Nuthatches (Fig. 1) Morse (1974) predicted that if an interspecific dominance hierarchy exists, subordinates should shift their use of resources so as to decrease their overlap with dominants. We therefore expected the subordinate Treecreeper to restrict its foraging niche in forest fragments that also house the dominant Nuthatch Our results do not follow this expectation; Treecreeper foraging niches are not broader in Nuthatch-free fragments For the tree size dimension, we even found an opposite shift, with narrower niches for the Treecreeper in the absence of the Nuthatch. However, this shift was largely due to differences in tree size distribution Similar results were obtained through the analysis of niche overlaps The Treecreeper's niche did not diverge from that of the Nuthatch in its presence, indicating that Treecreepers did not reduce the amount of overlap for resource use with the Nuthatch. Niche overlap was even significantly larger than expected for the tree size dimension. As in the analysis of niche breadths, this result could be explained by the variation in tree size distribution among plots.

How can we explain these results? Firstly, our analyses on foraging behaviour were restricted to height and substrate use; possibly niche shifts in other dimensions (e.g prey size and prey type) may have gone unnoticed (but see below) Secondly, there may be no need to switch. Changes in foraging behaviour may reflect a response to changes in food availability If food is not limiting in any of the forest fragments studied, competition between Nuthatch and Treecreeper is not expected The absence, in either species, of any niche shift in relation to fragment size, could reflect an overall similarity of habitat conditions among fragments This also suggests that even in the smallest fragments occupied, food conditions during mid-winter are still adequate We know, for instance, that Nuthatch survival is not lower in these fragments compared to that in a nearby large forest (Matthysen unpubl. data). Thirdly, social learning and copying can also lead to convergence in the foraging niches of birds in multispecific flocks (Alatalo *et al* 1986). Henderson (1989) and Hogstad (1990) showed that Treecreepers could reduce their vigilance, and consequently forage more efficiently, by living in mixed-species flocks. In small fragments, bird density is reduced, and flocks are either absent or small In such a case, associating more closely with Nuthatches could be beneficial for the Treecreeper.

Alternatively, the intensity of competition between Treecreepers and Nuthatches may be overestimated by the amount of overlap in substrate use as measured by us, because the two species might select different prey during winter The Treecreeper has a short, soft decurved bill, whereas the Nuthatch has a thicker, stronger chisel like bill. Furthermore, the Nuthatch often forages head down, and uses stored food (Cramp & Perrins 1993) Another possibility, finally, is that competition actually is higher in smaller fragments, but that birds are unable to avoid it by shifting their foraging niche Such a lack of response may occur if foraging habits are somehow fixed, or if the space towards which animals can move is limited, for instance because it is already occupied by other species, not considered in this study.

In conclusion, our results show that winter foraging niches of small insectivorous birds do not always change in small and isolated forest fragments, and do not always expand in the absence of close competitors in island-like situations. In the future such hypotheses can be tested by the experimental removal of the socially dominant species (Nuthatch) in some forest fragments.

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SAMENVATTING

We bestudeerden het foerageergedrag van de Boomkruiper *Certhia brachydactyla* en de Boomklever *Sitta europaea* in de winter in 18 loofbosfragmenten (oppervlakte tussen 1 en 30 ha) en 1 loofbos (200 ha) om de invloed van bosfragmentatie op de interacties tussen de twee soorten na te gaan. Er werd met name verwacht dat de aan- of afwezigheid van de dominante Boomklever een invloed zou hebben op het foerageergedrag van de kleinere en ondergeschikte Boomkruiper Gedurende de winter 1993-1994 werd elk bosfragment een zestal keer bezocht, en van de waargenomen individuen het volgende genoteerd: foerageersubstraat (stam, dikke of dunne tak), hoogte, stamdiameter (drie grotteklassen) en de tijd doorgebracht op elke boom. Omdat het aantal individuen per bosfragment zeer klein is werden alle analyses uitgevoerd op gemiddelde waarden per fragment

De Boomkruiper kwam voor in 14 van de 18 bosfragmenten terwijl de Boomklever slechts in zeven fragmenten, voornamelijk groter dan 4 ha, voorkwam We vonden geen relaties tussen fragmentoppervlakte en het foerageergedrag van de beide soorten. Boomkruipers gebruikten een breder aanbod aan grootteklassen van bomen in aanwezigheid van Boomklevers, waardoor de overlap tussen de twee soorten groter was dan kon worden verwacht op basis van waarnemingen in fragmenten zonder Boomklevers. Dit is in tegenstelling tot de verwachtingen op basis van een mogelijk competitie-effect en lijkt eerder te verklaren door een verschil in boomgrootte tussen fragmenten met en zonder Boomklevers Er waren geen effecten op gebruik van substraat- of hoogteklassen We besluiten dat in kleine habitateilanden de foerageerniches van kleine insectivore vogels in de winter niet noodzakelijk uitbreiden in afwezigheid van de naaste concurrenten

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Corresponding editor Mardik F. Leopold