Biodiversity and Conservation **14:** 1421–1432, 2005.
DOI 10.1007/s10531-004-9667-5

Have recent changes in forest structure reduced the Estonian black stork *Ciconia nigra* population?

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Received 2 September 2003; accepted in revised form 14 January 2004

Key words: Black stork, Focal species, Forest fragmentation, Habitat selection, Old growth, Population decline, Productivity

Abstract. The black stork *Ciconia nigra* is listed as a focal species for guiding forest management in Estonia, where forestry has recently intensified and the stork population has suffered a twofold decline. We explored a possible link between the decline of the population and man-induced changes in forest structure, by analysing nesting of the species in relation to forest cover, edge effects and stand structure. Although the storks had distinct habitat preferences (old remote stands near rivers and a certain distance far from ecotones in well-forested landscapes), these were hardly reflected in site re-occupancy and productivity. Therefore, changes in forest structure are probably not responsible for the population decline, although preferences for specific forest environments may limit the range of potential nest sites. The results indicated that edge avoidance cannot be considered a species-specific feature over large areas and clear habitat preferences are not necessarily related with the present success of a population. We also suggest that lists of focal species should be regularly updated and validated in the field.

Introduction

Human-caused degradation of forests has become a major issue in biodiversity conservation (e.g., Meffe and Carroll 1994; Hunter 1999). There are many ways how forest degradation affects biota, and different types of organisms that have become threatened. At the same time, conservation can only seldom take species-specific approaches, which usually are 'admissions of failure' of more general (habitat or ecosystem scale) schemes (Sutherland 2000). Major exceptions in this respect are the model species for research and focal species for management (e.g., Lambeck 1997).

The black stork is a large and rare bird, which breeds mainly in the undisturbed forests of temperate Eurasia; some southern populations are confined to mountains (Del Hoyo et al. 1992). The stork has historically gone extinct or suffered sharp declines in large areas, and forest destruction and degradation are considered its major threats (Profus 1994). The species is included in Annex 1 of the EU Directive on the Conservation of Wild Birds (EEC/79/409). The black stork has been also considered a focal forest species in the Baltic Sea region as an inhabitant of old growth (and particularly riverine) forests; that is, its status should help to guide forestry operations (Angelstam et al. in press). While the Baltic area includes the 20th century stronghold of the species in Europe (N- and E-Poland, the Baltic states and western Russia), the populations in the Baltic states are currently decreasing (Strazds et al. 1996a; BirdLife International/European Bird Census Council 2000; Sellis 2000). Ultimate causes of the decline are not known, though depressed productivity of the stork can be a proximate mechanism (Sellis 2000) and its regional occurrence points to negative changes in the breeding grounds. Such changes may be due to recently intensified forestry (e.g., Lõhmus 2002), possibly causing also desertion of nest sites and decrease in the breeding fraction of the population.

In this paper, we analyse nest site preferences and quality for the Estonian black stork population, which is the northernmost in Europe and has declined more than twofold since the late 1970s (Sellis 2000). Although breeding sites of the species have been often quantitatively described in Eastern Europe (Cieslak 1988; Ivanovsky 1990; Strazds et al. 1990; Drobelis 1993; Skuja and Budrys 1999), there are no statistical evaluations of habitat preferences, and just a preliminary note about relationships between habitat and productivity (Strazds et al. 1996b). According to the latter, breeding success may critically depend on increased disturbance by humans, but we found no support for this hypothesis in Estonia (Rosenvald and Lõhmus 2003). Here, we concentrate on three aspects of forest structure, which are strongly influenced by forest management – forest cover, edge effects and stand structure. We expect that if black storks suffer from changes in these habitat features, we should find distinct habitat preferences and relevant relationships with site re-occupancy by and productivity of the storks. Finally, we discuss the results in the light of the focal species concept.

Materials and methods

Sampling and field methods

We sampled 53 nesting territories of the black stork (about half of the national population) all over Estonia. From each territory, only the most recently occupied nest was studied. Because of technical reasons, the sample sizes for different analyses were slightly different (e.g., landscape variables have been measured in all nest sites but random plots around nests in 46 sites). Between 1994 and 2001, nests were inspected in late June or July (some also earlier in the breeding season) to record their occupancy and the number of large young. Hereafter, an occupied nest means at least some nest building in 1 year. Productivity was measured as the number of large (well feathered) young per occupancy year.

The nest sites were described at three spatial scales (landscape, stand, nest tree) in 1998 and 2001. At the landscape scale, forest area within 3 km around nest tree was measured from recent maps. This radius is close to half of the mean nearest-neighbour distance in suitable landscapes (Drobelis 1993) and has been used in other black stork studies (Pojer 1996; Strazds et al. 1996b). We also measured the distances from nest tree to the nearest forest edge, meadow or field, house, road, river, flood-plain meadow and lake. The first four distance measures were thought to reflect disturbance probability, while the remaining three are related to foraging opportunities (watercourses and lakes account for 88% of foraging sites in Estonia; Lõhmus and Sellis 2001). For comparison, the distances were measured from 53 random forest plots all over Estonia.

To study preferences for nest stands and nest trees within the home-range of the stork, we described nest sites as well as three random plots on forest land 200, 500 and 700 m from each nest site. The few plots on clear-cut areas have been omitted from this analysis, therefore sample sizes differ slightly between the distance classes. In the stands, we measured the mean height and age of overstorey trees and assessed their species composition at 5% accuracy within 30 m. For nest trees (in random plots: the largest trees), height, diameter at breast height and age were measured. Trees were aged by taking increment cores; in some partly decayed nest trees (aspens) we took the cores from other trees of the same generation nearby. We visually estimated mean canopy closure (percent cover from living overstory trees; using 10% categories) within 5 m around nest tree or random point.

Statistical methods

Two variables (forest cover within 3 km, average canopy closure at the nest tree) were independent of the others and were retained in their original form for further analyses. The remaining 21 variables were intercorrelated and their number was reduced via correlation-based principal component (PC) analysis. For this, only random points' data were used (in the nest sites, some intrinsically uncorrelated characteristics may co-occur due to the preferences of the stork). The seven PCs with eigenvalues greater than 1.0 were accepted for the further analysis, and their factor scores were calculated for both random plots and nest sites. The PCs were interpreted as follows (see Appendix 1 for details): (1) at the landscape scale, the first PC (34% of total variation) reflected forest fragmentation ('distance to ecotone') since it was positively correlated with all original distances, and particularly forest edge. The second PC ('proximity of remote river'; 22% of variation) distinguished between remote sites near rivers (high scores), and sites near roads and houses (low scores); (2) at the stand scale, four PCs (65% of total variation) were extracted. The first PC (26% of variation) was inversely correlated with the average size and age of trees as well as the abundance of fast-growing aspen; hence, this PC reflected mostly average tree size. The second PC (16% of variation) distinguished between old pine forests on poor soils (low scores) and young mixed secondary forests on former agricultural lands (high scores). The values of the third PC (14% of variation) ranged from dry boreal (particularly spruce-dominated) site types to wet deciduous stands. The dominating variable in the fourth PC (10% of variation) was the abundance of broad-leaved trees (mostly *Quercus robur, Fraxinus excelsior, Tilia cordata*) abundance; (3) height, diameter and age of the largest ('nest') tree were extracted into one PC, which accounted for 64% of total variance. This PC was strongly correlated ($r = 0.81$, $n = 132$, $P < 0.001$) with the average tree size in stand (the first PC at the stand scale), which was the only significant correlation between the final set of nine variables.

Distributions of all variables were checked for normality (Kolmogorov–Smirnov test) and transformed where appropriate (arcsine square-root transformation used for proportions; logarithmic or square-root transformation for distances). To demonstrate habitat preferences, we checked whether means and/or variances of nest-site characteristics differ from those in random plots (McCallum and Gehlbach 1988). Levene's test was used to explore the homogeneity of variances. Means were checked with parametric tests (*t*-test, ANOVA) but if variances differed significantly, we used either the *t*-test with separate variance estimates (Welch's *t*) or Kruskal–Wallis ANOVA. We did not *a priori* adjust Type I error levels due to multiple tests because these corrections severely reduce test power (Wright 1992), and at $\alpha = 0.05$, given the approximately 20 independent tests, we could reject true null-hypothesis on average just once. However, for conclusions, we treated significance levels $0.01 < P < 0.05$ only as marginal.

The effects of habitat characteristics on breeding performance were explored with two models: (1) multiple linear regression for the mean annual productivity, which had a near-normal distribution; (2) logistic regression to discriminate between unoccupied and occupied nests. For the latter, we initially used the best subsets approach to find out a few most significant combinations of variables, and then explored the model, which included the fewest variables. All statistical analyses were performed with Statistica 6.0 software (Statsoft, Inc. 1984–2001).

Results

Within 3 km around black stork nests, forest land covered on average 74 ± 16% (SD) of the landscape, which is well above the Estonian average (50%; $t = 10.4$, $df = 52$, $P < 0.0001$). Breeding storks strongly preferred remote stands near rivers and tended to nest farther from ecotones than expected by random placement (Table 1). Mean distance to ecotone differed only marginally between nests and random plots ($P = 0.049$), but we noted (1) low variance of this variable in nest sites (Table 1), even if we excluded the nine random plots having distance scores below the minimum of nest sites (Levene's $F = 6.74$, $P = 0.011$); (2) pronounced univariate difference in mean distance to forest edge (the leading original variable of the PC; Appendix 1) between nest sites (274 ± 216 m, SD; $n = 53$) and random plots (178 ± 238 m, SD; $n = 53$) ($t = 3.25$, $df = 104$, $P = 0.0015$).

Compared with those 200–700 m away, forest stands around nest sites had much larger trees and were more often in old pineries on poor soils (Table 2 and Figure 1). Both of these features as well as canopy closure were less variable in nest sites. Nest trees were also much larger than the largest trees in the surrounding stands. When the strong correlation between average tree size in stand and nest tree size was taken into account, the average tree size lost its importance ('S1 residuals' in Table 2).

Table 1. Scores of the first two PCs representing standardized distances to landscape elements from black stork nests and random forest plots (see also Appendix 1).

PC	Mean ± SD		Comparison of means[a]			Homogeneity of variances	
	Nests ($n = 53$)	Random ($n = 53$)	t	df	P	Levene's $F_{1,104}$	P
(1) Distance to ecotone	0.37 ± 0.57	0.05 ± 1.02	2.00	82.2	0.049	15.8	<0.001
(2) Proximity of remote river	0.64 ± 0.71	0.07 ± 1.01	3.34	93.1	0.001	3.9	0.051

[a] t-test with separate variance estimates (Welch t).

Table 2. Comparison of stands and largest ('nest') trees around black stork nests (A) and in random forest plots 200, 500 and 700 m from nests (B–D, respectively). (S1) to (S4) are the first four PCs of stand characteristics and (N1) is the first PC of nest tree characteristics (see Appendix 1). All tests include four groups and total $n = 179$, except for canopy closure with $n = 160$. See Figure 1 for descriptive statistics.

Variables	Comparison of means			Homogeneity of variances	
	Statistic[a]	P	Significant differences between groups[b]	Levene's F	P
Stand					
(S1) Average tree size	$H = 53.4$	<0.001	A v.s. B–D	7.93	<0.001
(S1) Residuals[c]	$F = 0.90$	0.44	–	0.50	0.68
(S2) Pine on poor soil	$H = 9.5$	0.024	A v.s. D	3.43	0.018
(S3) Deciduous trees	$F = 2.28$	0.081	–	0.50	0.68
(S4) Broad-leaved trees	$F = 0.61$	0.61	–	0.23	0.87
Canopy closure	$H = 5.91$	0.12	–	3.25	0.023
Nest					
(N1) Nest tree size	$F = 30.0$	<0.001	A v.s. B–D[b]	0.94	0.42

[a] Kruskal–Wallis ANOVA by ranks for (S1), (S2) and canopy closure; parametric ANOVA for the other variables.
[b] According to Tukey HSD *post hoc* tests; considered significant if $P < 0.05$.
[c] Residuals of the regression between (S1) (dependent variable) and (N1), showing the independent effect of (S1).

There were no significant differences between the stand and nest tree characteristics between random sites at different distances from nests.

In 43 nest sites studied, the mean annual productivity was 0.95 ± 0.93 (SD) fledged young. Neither standard (Table 3) nor stepwise multiple linear regression revealed any significant effects of habitat characteristics on the productivity.

To distinguish between unoccupied and occupied nest sites, no logistic regression model was significant at $\alpha < 0.05$ but two models had $P = 0.06$. One of these included four variables (forest cover within 3 km, the 2nd and 4th PCs of stand characteristics, and nest tree size) whereas the second model included just one (forest cover within 3 km). The latter (log-likelihood ratio $X^2 = 3.43$, df = 1, $P = 0.06$) was considered the best model and explored further. In this model,

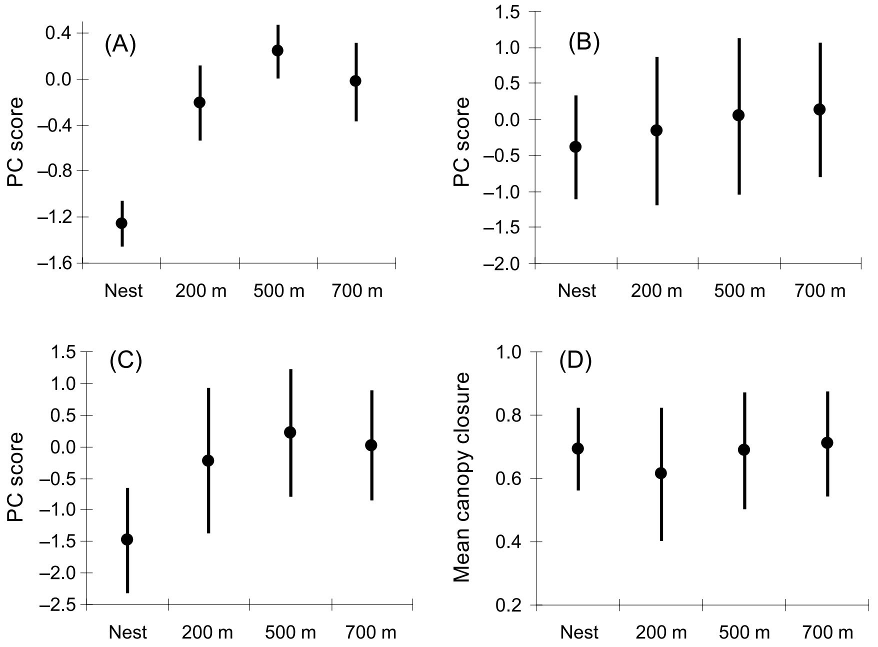

Figure 1. Stand and nest tree characteristics (mean ± 95% confidence interval), which differed significantly in black stork nest sites and in random forest plots 200, 500 and 700 m from nests: (A) average tree size in stand; (B) old pine stands on poor soils; (C) size of the largest ('nest') tree; (D) mean canopy closure around nest tree. Graphs (A–C) show standardized PC values and have reverse scales (see Appendix 1 and text for methodological details, and Table 2 for statistical tests).

Table 3. Multiple linear regression model for the annual productivity (fledged young per occupancy year) in 43 nest sites of the black stork ($R^2 = 0.16$, $F_{9,33} = 0.70$, $P = 0.70$). (S1)–(S4) are the first four PCs of stand characteristics and (N1) is the first PC of nest tree characteristics (see Appendix 1).

Independent variables	Parameter estimate		*P*
	B	SE	
Intercept	0.03	1.46	0.98
Forest cover in 3 km	−0.50	0.84	0.56
Distance to ecotone	0.06	0.32	0.85
Proximity of remote river	0.09	0.23	0.71
(S1) Average tree size	0.12	0.25	0.64
(S2) Pine on poor soil	−0.01	0.24	0.96
(S3) Deciduous trees	0.25	0.21	0.24
(S4) Broad-leaved trees	−0.28	0.21	0.18
Canopy closure	1.72	1.06	0.12
(N1) Nest tree size	0.08	0.26	0.76

intercept (-3.44 ± 2.34 SE) was not significant (Wald statistic 2.15, $P = 0.142$) and forest cover was positively related to the probability of nest site occupancy (coefficient 5.34 ± 2.44 SE for arcsine square-root transformed forest share; Wald statistic 4.77, $P = 0.029$).

Discussion

Our study showed that the threatened black stork population in Estonia had distinct habitat preferences, which were hardly reflected in the recent breeding performance of the storks. Below, we discuss the main findings and implications for conservation.

Edge avoidance

In the light of increasing anthropogenic destruction of natural forest cover, habitat specialists that avoid edges are of particular conservation concern, since they are influenced by both habitat loss and fragmentation (e.g., Askins et al. 1987; Bender et al. 1998; Villard 1998). Given that the black stork nests were on average farther from edges than expected by random, we could classify the stork as a forest-interior bird and regard it as prone to forest fragmentation. Note however, that small openings (such as treefall gaps, rides and forest roads) were not considered to create forest edge in our study, and the storks may favour the proximity of these elements (Petrinš 1986).

Importantly, this ‘average approach’ failed to recognize that rather than simply selecting for forest interior (the traditional view about interior species; Sisk and Margules 1993), the storks preferred a certain distance from edge (indicated by low variance of distance values). This may be due to a trade-off between distance to foraging sites and predation risk or disturbance at edges. Similar patterns have been recently found in the black sparrowhawk *Accipiter melanoleucus* in South Africa (Malan and Robinson 2001), and some North-American songbirds (Flashpohler et al. 2001). In such species, treating edge avoidance as a species-specific characteristic over extensive areas (e.g., McCollin 1998) is probably not correct. If areas differ in mean size of forest patches, habitat selection with respect to edges may also differ between the areas – a species may select sites further from edges in highly fragmented landscapes but prefer edges in homogeneous landscapes. We suggest that this ‘threshold of edge avoidance’ for the black stork has been reached in Estonia, where 65% of forest area is situated less than 200 m from edge and only one third of the nearest edges are natural (Lõhmus 2002). Here, continuing destruction of old forest may harm the stork more than simply due to habitat loss (cf. Bender et al. 1998), while in some remaining wilderness areas of its range, the stork may perhaps behave as an edge species and benefit from opening up the forest.

Nest site preferences of the black stork and their adaptive value

Black storks selected nest sites according to forest cover, distances to landscape elements and nest tree size. They also seemed to require a limited range of canopy closure around nests (Table 2; Figure 1), which may reflect a balance between nest accessibility and concealment (cf. Petrinš 1986). Other detected preferences were not necessarily independent. The preference for old growth could reflect availability of large nest trees in even-aged forests (see the lack of residual effect in Table 2). Several studies have shown that most black stork nests are on the largest and/or oldest trees of the stand (Drobelis 1993; Strazds et al. 1996b; Skuja and Budrys 1999), but the roles of nest stand and nest tree had not been separated so far. Our results further confirm that tree retention during forest management practices in youngish forests can improve nesting opportunities of the species (Lõhmus and Sellis in press). Also the preference for old pineries on poor soils may be related to nest tree availability, since such stands are of low silvicultural interest, often unmanaged, and may thus better retain potential nest trees than forests on fertile soils.

The only link between habitat selection and population trend of the black stork was the avoidance of sparsely forested landscapes and their desertion during population decline. Given that the area of the Estonian forest land has been increasing since the 1940s, with over 25% increase between 1975 and 2000 (Viilup 2000), the preference for well-forested landscapes cannot be the reason for the recent decline of the stork population. Moreover, we failed to show any relationships between forest structure and low productivity, which is probably the proximate cause of the decline (Sellis 2000). This result is hardly a random (Type II) or variable selection error, given the complete lack of the relationships, clear habitat preferences in the same variables, large sampling fraction (half of the population) and long-term data (8 years). It is therefore unlikely that changes in forest structure are responsible for the large decline, although preferences for specific forest environments may limit the area that can be occupied by the stork nowadays. For example, 3.5% of random 0.3-ha plots on forest land contained suitable nest trees for the stork in Estonia, but after considering stand structure and location (as described in this study), only 0.3% of forest land could be classified suitable (Lõhmus and Sellis in press).

Why should the storks be so selective if this has no apparent relationships with their reproductive success? Habitat preferences are usually assumed to result from natural selection, which means that ‘successful’ preferences, leading to the occupation of better sites, spread in the population over generations (Clark and Shutler 1999; Sergio et al. 2003). Therefore, habitat preferences in a population are a result of its evolutionary past, and pronounced preferences may be neutral or maladaptive in the short term (Clark and Shutler 1999; Lõhmus 2003). It is possible that in the modern forest landscapes, some nest site preferences of the black stork have lost their adaptive value and are retained mostly by tradition (see, e.g., Newton 1979, pp. 86–87 about traditional nest sites in some raptors). Hence, even if a threatened species occupies selectively a declining ecosystem in a changing environment (such as the black stork prefers old growth), this preference is not necessarily related with its present and future success.

The black stork as a focal species

In general, our study supported the traditional view of the black stork as a bird of large undisturbed forests (Cramp and Simmons 1977; Del Hoyo et al. 1992), which was the background of listing it as a focal species for forest management in the Baltic Sea region (Angelstam et al. 2004). At the same time, our failure to detect adaptive value of the current nest site preferences by the stork (see above) suggests that such preferences can be gradually lost. Although we lack knowledge about the rates of changes in habitat use, these changes are obvious in many taxa (e.g., urbanization). For example, in Austria, the black stork is not a forest-interior species since it breeds on average only 35 (±31 SD) m from forest edge there (Sackl 1993), that is, eight times closer to edges than in Estonia. Lesser spotted eagles *Aquila pomarina* avoid anthropogenic edges in Lithuania but prefer their proximity in Estonia (Väli et al. in press). We are *not* advocating against the use of focal species in conservation (cf. Lindenmayer et al. 2002), but our results suggest that existing lists of focal species should be regularly updated and validated in the field.

Finally, there is a question about the fate of the Estonian black stork population. We still do not know the reasons of its decline. After rejecting the disturbance (Rosenvald and Lõhmus 2003) and forest structure hypotheses (this study), the gradual loss of foraging sites (permanent water courses in forests) as a long-term impact of forest drainage (Lõhmus and Sellis 2001) seems to be a possibility that requires urgent research.

Acknowledgements

We thank Tarmo Evestus, Gunnar Sein, Ülo Väli, Riho Männik, Georg Artma, Raivo Endrekson, Rein Nellis and Toomas Talve for their help in the field. Raivo Mänd, Jukka Jokimäki, Indrikis Krams and an anonymous referee commented on early drafts of the manuscript. The study was financed by the Estonian Ministry of the Environment and the Estonian Science Foundation Grant No. 5257 to Raivo Mänd.

Appendix 1

Variable means (±95% confidence intervals) in the nest sites of the black stork and the correlations of the variables with the PCs in random plots. Sample sizes are $n = 53$ for distances, $n = 49$ for stand and tree variables in nest sites, and $n = 132$ for stand and tree variables in random plots.

	Mean in nest sites	Correlation coefficients with the PCs[a]
Distance to the nearest		
Forest edge (m)	274 ± 60	(D1) 0.77
House (m)	1205 ± 183	(D1) 0.70; (D2) 0.49
Road (m)	621 ± 99	(D1) 0.50; (D2) 0.59
River (m)	895 ± 173	(D1) 0.52; (D2) −0.64
Flood-plain meadow (m)	2341 ± 510	(D1) 0.46; (D2) −0.58
Lake (m)	3738 ± 721	(D1) 0.49

Appendix 1. Continued.

	Mean in nest sites	Correlation coefficients with the PCs[a]
Stand variables		
Scots pine *Pinus sylvestris* (%)	18.8 ± 6.9	(S2) −0.76; (S3) −0.32
Norway spruce *Picea abies* (%)	42.2 ± 8.1	(S2) 0.33; (S3) −0.66
Aspen *Populus tremula* (%)	15.5 ± 5.5	(S1) 0.70; (S3) 0.31; (S4) 0.32
Black alder *Alnus glutinosa* (%)	1.8 ± 2.3	(S3) 0.46; (S4) −0.58
Grey alder *A. incana* (%)	0	(S2) 0.39
Birch *Betula* spp. (%)	16.7 ± 5.5	(S1) 0.34; (S2) 0.47; (S3) 0.59
Broad-leaved trees (%)	4.9 ± 3.6	(S4) 0.74
Stand age (year)	97.4 ± 6.6	(S1) −0.61; (S2) −0.60
Stand height (m)	26.8 ± 1.2	(S1) −0.83
Site quality class (1 . . . 5)	2.2 ± 0.3	(S1) 0.63; (S2) −0.54
Tree dbh (cm)	38.8 ± 3.0	(S1) −0.88
Soil moisture class (1 . . . 4)	2.6 ± 0.2	(S2) −0.30; (S3) 0.57
Nest tree variables		
Nest tree age (year)	117.4 ± 11.4	(N1) −0.71
Nest tree dbh (cm)	63.9 ± 5.6	(N1) −0.92
Nest tree height (m)	25.9 ± 1.5	(N1) −0.76

[a] The PCs were extracted separately for distances (D), stand (S) and nest tree characteristics (N); their order is indicated with the number (e.g., S1 is the first PC for stand characteristics). Prior to PC extraction, distances to forest edge and house were log-transformed, the other distances square-root-transformed, and proportions arcsine-square-root transformed. Weak correlations ($r = -0.3 \dots 0.3$) are not shown.

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