

Population trend and status of the endangered White-backed Woodpecker *Dendrocopos leucotos* in Finland

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White-backed Woodpecker *Dendrocopos leucotos* is an endangered specialist of mature deciduous forest in many European countries, including Finland. The Finnish population declined severely during the 20th century. We studied the population development and demographic parameters in Finland during recent decades. According to winter counts, the population has been the lowest in 1980–1990s before the recent population increase. Both breeding success (study years 1991–2010) and the number of migrants (1979–2010) arriving from the east, have recently increased significantly. The sex ratio of migrants was female biased. The probability of detected occupancy of breeding pairs, other pairs and occupied territories (at least one individual observed) increased strongly during 1991–2010 especially in the eastern part of the country. Thus, the ca. 300–400% increase in numbers observed is not solely due to the increased number of monitored sites. The proportion of detected occupancy was also higher on territories considered as high-quality habitat. Number of autumn migrants positively affected the territory occupancy in the following spring, but not the occupancy of pairs or confirmed breeders. Nevertheless, despite the positive trend in the intensity of irruptions, there was a strong additional positive trend in occupancy that was independent from the effect of immigration.



1. Introduction

White-backed Woodpecker *Dendrocopos leucotos* is a widespread resident species breeding from Spain and France to Korea and Japan (Cramp 1985). Nevertheless, in Europe the species is rare and patchily distributed outside Eastern Europe (Spiridinov & Virkkala 1997, BirdLife International 2004). The species is specialized on sapro-

xylic invertebrates (e.g., insect larvae), which live in dead trees (Aulén 1991). In most of its breeding range, including Finland, the species is a clear specialist of deciduous forests (e.g., Cramp 1985, Virkkala *et al.* 1993), although the species occurs in coniferous forests in some regions (e.g., Cramp 1985, Gjerde *et al.* 2005). Hence, old-growth deciduous forests with abundant dead wood represent key habitat for the species (Gjerde *et al.* 2005,

Table 1. Annual numbers of confirmed breeding occasions, additional pairs and additional territories (only one bird observed) in White-backed Woodpeckers in Finland in 1985–2010 including number of visited sites and their quality status if known.

Year	Breeding	Pairs	Territories	Occupied	No. sites	High quality	Low quality
2010	91	41	123	255	518	38	380
2009	87	74	105	266	481	38	399
2008	71	42	67	180	467	38	388
2007	62	27	23	112	450	37	380
2006	54	34	28	116	428	37	358
2005	53	30	68	151	413	36	351
2004	48	18	50	116	403	36	345
2003	34	20	27	81	395	38	338
2002	25	27	36	88	332	38	282
2001	26	26	22	74	326	38	279
2000	22	20	9	51	330	38	283
1999	22	12	13	47	269	35	229
1998	18	13	13	44	244	35	206
1997	23	4	21	48	235	37	195
1996	17	4	14	35	194	31	160
1995	16	6	14	36	263	32	223
1994	10	15	28	53	282	32	243
1993	16	5	9	30	273	33	235
1992	18	6	9	33	263	33	229
1991	24	6	10	40	274	33	237
1990	14	2	7	23	237	32	202
1989	11	1	6	18	193	27	161
1988	8	3	13	24	128	25	101
1987	6	1	7	14	110	24	85
1986	6	1	4	11	107	24	82
1985	3	1	5	9	101	21	79

Löhmus *et al.* 2010), and it typically requires $\geq 1.4\text{m}^2/\text{ha}$ of deciduous snags for its territory (Roberge *et al.* 2008a).

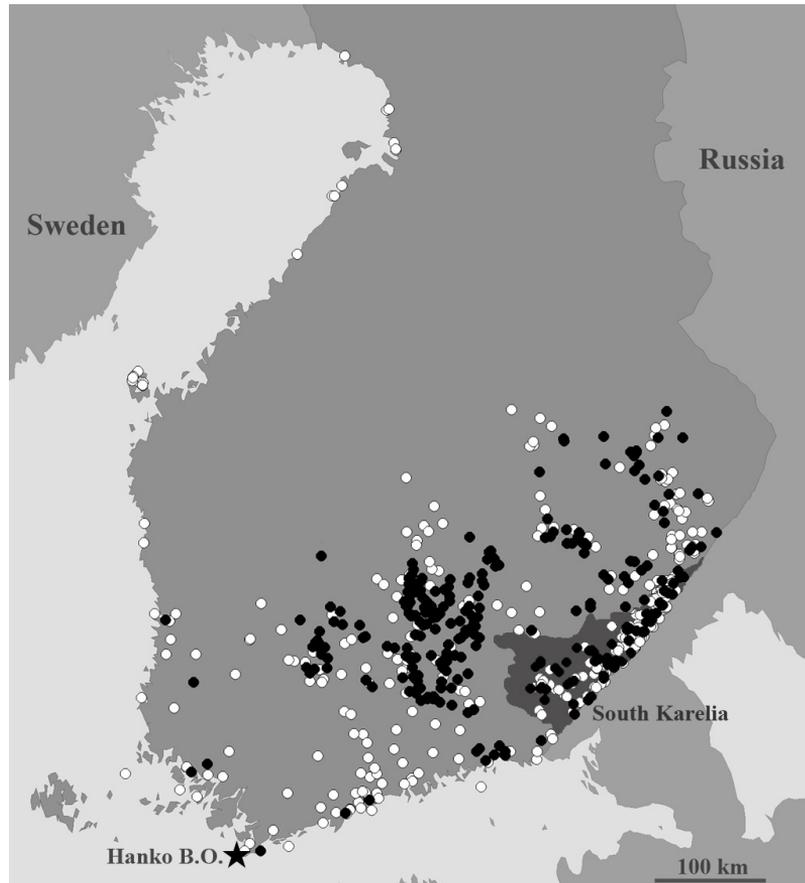
White-backed Woodpecker is considered an umbrella species (Martikainen *et al.* 1998, Roberge *et al.* 2008b), and its occurrence indicates high forest-bird diversity and presence of some endangered polypore and beetle species (Martikainen *et al.* 1998, Roberge *et al.* 2008b, Halme *et al.* 2009).

Despite the status of the species having been classified as secure in Europe, several local populations have declined during recent decades (BirdLife International 2004). Forest management has been suggested to be the main reason for these declines (Virkkala *et al.* 1993, Carlson 2000, Garmendia *et al.* 2006), as a decrease in dead wood decreases the occurrence probability of the species (Czeszczewik & Walankiewicz 2006). In Sweden, for instance, the population has declined throughout the 20th century and the species nearly

went extinct in the 2000s. The Swedish population is currently dependent on introduced individuals brought from Norway. In 2003, only three pairs were found (Mild & Stighäll 2005). In 2006, the only pair, which consisted of introduced Norwegian birds, failed in their breeding attempt (Sveriges Ornitologiska Förening 2007). In 2009, two pairs consisting of one native and three introduced individuals produced three young (Sveriges Ornitologiska Förening 2010). In Finland, the species has faced a steep decline since the 1950s (Virkkala *et al.* 1993). The negative trend continued until mid-1990s, when the population size was no more than 30 pairs (14 nests found; Laine *et al.* 1995).

According to surveys of White-backed Woodpeckers, the number of observed individuals has recently increased (Laine 2010), but it is not well known how much of this is due to increased observation activity in terms of increased number of investigated, potential breeding sites (Konttiokorpi

Fig. 1. The distribution of monitored White-backed Woodpecker sites in 1991–2010 in Finland. Black dots show the sites monitored in 1991, and white dots represent sites that have been added during monitoring afterwards. South Karelia in south-eastern Finland is shown in dark grey, and the black star shows the location of the Hanko Bird Observatory.



2007a). Therefore, possible temporal and spatial trends in the population density remain obscure.

The purpose of this paper was to summarize the knowledge of the population status of Finnish White-backed Woodpeckers, especially after early 1990s (Virkkala *et al.* 1993). The increased number of woodpecker observations can potentially be due to (a) increased observation activity expressed as higher number of monitored sites, (b) higher breeding success in the Finnish population, (c) increased immigration (see Pasinelli 2006), (d) higher survival, or (e) a combination of these. We attempted to evaluate the relative significance of these reasons. Using breeding monitoring and migration data, we modeled the sighting rate of breeding and territory-holding birds at potential sites, and assess the plausibility of the three first reasons (a–c). We also studied the breeding success and sex ratio, acknowledging that endangered populations often show sex-ratio bias (Donald 2007).

2. Material and methods

2.1. Breeding data

WWF Finland coordinated the monitoring of White-backed Woodpecker sites in 1987–2002, and Metsähallitus (Natural Heritage Services) has continued the follow-up since then. The number of monitored sites increased from 101 in 1985 to 518 in 2010 (Table 1). We selected 1991 as a reference year (starting point), because the number of sites checked was fairly high (274 sites) from that year onwards, compared to the low numbers of sites explored in the 1980s. The distribution of monitored sites is shown in Fig. 1. Furthermore, Virkkala *et al.* (1993) reviewed the status of the population until the beginning of early 1990s, so the chosen time window of the present study only slightly overlaps with that study.

We used the longitudinal coordinate of the ter-

ritory site (Finnish Uniform Coordinate System) in our models to control for the spatial location of the population, because the Finnish White-backed Woodpecker population has traditionally been divided into ‘western’ and ‘eastern’ populations (Virkkala *et al.* 1993, Laine 2007). We used the coordinate as a continuous variable, because the border between the eastern and western populations is not clear and birds are known to migrate from east to west (Kontio Korpi 2007b, Laine 2010). In further analyses the variable was centered and scaled such that one unit corresponded to 100 km.

Because the monitoring of Finnish White-backed Woodpeckers has largely been based on voluntary work, all sites have not been monitored every year, which needs to be taken into account in the analysis (see section 2.3.). All sites included in the analysis had been visited at least once during early spring, at the time when woodpeckers are displaying. These visits are conducted between March and May by quietly walking through a given forest patch. To increase observation efficiency playback calls were used to attract territory-holding birds. In addition to observing individuals, experienced volunteers can confirm the presence of these woodpeckers fairly easily based on fresh species-specific foraging signs on trees (Alanko & Müller 1987, Müller & Virkkala 1988). If a territory was reported to be occupied by a pair, a nest search was conducted. However, even if the species breeds at a given site, the nest can remain undetected, but whenever the nest was found, chicks were usually ringed.

For the analyses purposes, sites for potential territories were classified each year as follows: (a) not visited, (b) visited but the species was not observed, (c) at least one bird observed (territory), (d) male and female seen (a pair) and (e) confirmed breeding (nest found). Most of the data, used here, had been collected by the same few persons, which makes annual comparisons more reliable. Annual breeding success was quantified as the number of ringed chicks per pair and the sex of chicks has been identified in order to assess the sex ratio.

Most of the potential territories (98% of all sites) were classified based on their quality: (a) high-quality sites ($n = 33$; Table 1): large uniform patches of open, light old-growth birch-dominated forest with abundant dead wood, near water bodies or moist areas, or (b) lower-quality sites ($n = 237$;

Table 1): smaller, more fragmented, or younger forest. This classification is subjective, but was done by one person (TL) for all sites. Therefore, we are convinced that these data allow an evaluation of how precisely this site classification reflects the site quality from the point of view of the White-backed Woodpecker.

2.2. Non-breeding data

Non-breeding data included autumn-migration observation records and winter-bird counts. Migration data were from two locations: the eastern border of Finland (South Karelia from 1980–2009; data of the Ornithological Society of South Karelia; Kontio Korpi 2007b) and south-western Finland (the Hanko Bird Observatory 1979–2009; Lehtikoinen *et al.* 2008). In South Karelia, birds observed in direct flight during autumn were classified as migrants, and their flight direction was recorded for most cases. At Hanko, also staging birds were included, because the observatory is geographically situated outside the breeding area of the White-backed Woodpecker and hence every observed bird indicates immigration. As the numbers of migrating woodpeckers at the two sites were positively correlated, we combined these two datasets (total number of migrants) for analysing potential effects of large-scale immigration on site-occupancy rate in the population during 1991–2010 (see Statistical analyses). We also examined the sex and age ratio of individuals that had been ringed in Finnish bird observatories that are situated outside the species breeding areas during autumn migration (September–October).

The Finnish winter-bird route-count scheme has been running since the winter of 1956/57, when mid-winter counts were initiated. This scheme was complemented with late-winter counts (done between 21 Feb and 7 Mar) in 1966 and with early-winter counts (1–14 Nov) in 1976 (Hildén *et al.* 1991). The same individuals can be potentially observed in all three counts in a given winter, which can lead to pseudo-replication and biased results. Therefore we chose the maximum number of observed individuals for each route and year (9.9% of the observations were excluded). These were used to calculate a minimum estimate for the number of observed individuals per 1,000

km, based on the lengths of the routes in the most popular mid-winter count (Väisänen & Solonen 1997, Väisänen 2003). Because different winters may include one, two or three counts, only years with similar number of counts are comparable. Hence, we presented results separately for three periods, i.e., 1956/57–1965/66 (mid-winter only; 119–595 routes each year) 1966/67–1974/75 (mid-winter and late-winter; 531–670 routes) and 1975/76–2009/10 (all counts; 459–656 routes). The data were standardized to individuals per 1,000 route-km.

2.3. Statistical analyses

To study the spatio-temporal variation in site occupancy and possible effects of immigration on this variation, we used logistic regression with detected occupancy as the response variable (binary variable; no = 0, yes = 1). Separate analyses were done for territories occupied by (i) breeding pairs (nest found), (ii) pairs, and (iii) territories (at least one bird observed). In logistic regression, the model expectation equals the estimated probability of success. In this case, the probability of observing an occupied nest, pair or territory ($p_{t,i}$) in year t at site i is

$$p_{t,i} = \exp[a + Z_{t,i}] / (1 + \exp[a + Z_{t,i}]), \quad (1)$$

where $Z_{t,i}$ is a linear combination of the year- and site-specific explanatory variables included in the model (see Eq. 3), and each data point ($y_{t,i}$) is assumed to be a binomially distributed random variable with one trial and probability $p_{t,i}$ (i.e., a Bernoulli process).

$$y_{t,i} \sim \text{Bino}(1, p_{t,i}). \quad (2)$$

The explanatory variables and their role in the model (the interpretation of possible effects) are described below.

T_t = year of observation. This variable accounts for the temporal trend in the model. It is scaled such that $T_{1991} = 0$.

Q_i = site quality (see breeding data). This variable is coded such that “high quality” = 1 and “lower quality” = 0.

E_i = east coordinate. The site-specific east coordinate controls for the possible west-east gradient in occupancy probability. The variable was scaled to the unit 100 km and centered to 3504416 (between Kouvola and Mikkeli), which is the mean of all sites.

M_{t-1} = total number of migrants at Hanko and South-Karelia in the fall prior to the breeding season. This variable potentially affects the occupancy rate through immigration.

M_{t-2} = total number of migrants at Hanko and South-Karelia two falls before the focal breeding season. This variable is included because most irruptive birds are young and pair formation/breeding is often delayed over the first breeding season (Laine *ym.* 1995).

$M_{t-1}E_i$ = interaction between immigration and east coordinate. This variable explicitly allows a west-east gradient in the effect of migration on occupancy probability. Because the source of immigration is in the east, its effect should be stronger towards the east.

T_tE_i = interaction between year and east coordinate. This variable allows a west-east gradient in the temporal trend.

For the full model with all explanatory variables included, the relevant linear combination ($Z_{t,i}$) in Eq. 1 is

$$Z_{t,i} = b_1 T_t + b_2 Q_i + b_3 E_i + b_4 M_{t-1} + b_5 M_{t-2} + b_6 M_{t-1} E_i + b_7 T_t E_i. \quad (3)$$

Due to the scaling of variables T_t , Q_i , and E_i , the constant (a) alone, will (if applied to Eq. 1) describe the average sighting probability in year 1991 in lower quality sites in the middle point of the whole study area.

As the observation probability is modelled explicitly, the results are independent of the temporally increased number of monitored sites, which is merely a matter of temporally heterogeneous sample size. However, this modelling approach does not explicitly separate site-specific detection probability and actual occupancy rate. Therefore, we assume that the former show little temporal and spatial variation and that most of the variation in observed birds is actually due to variation in occupancy rate.

Ten competing models with different potential

Table 2. Explanatory variables used in the 10 candidate models for probability of detected occupancy. T_t is the focal year (starting from 0), Q_i is the quality class of site i , E_i is the site location expressed as the centred longitude coordinate, and M_t is the total number of observed irruptive autumn migrants in year t .

Model #	Variables in the model									
#1	T_t	Q_i	E_i							
#2	T_t	Q_i	E_i	M_{t-1}						
#3	T_t	Q_i	E_i	M_{t-1}	M_{t-2}					
#4	T_t	Q_i	E_i	M_{t-1}		$M_{t-1}E_i$				
#5	T_t	Q_i	E_i	M_{t-1}	M_{t-2}	$M_{t-1}E_i$				
#6	T_t	Q_i	E_i						T_tE_i	
#7	T_t	Q_i	E_i	M_{t-1}					T_tE_i	
#8	T_t	Q_i	E_i	M_{t-1}	M_{t-2}				T_tE_i	
#9	T_t	Q_i	E_i	M_{t-1}		$M_{t-1}E_i$			T_tE_i	
#10	T_t	Q_i	E_i	M_{t-1}	M_{t-2}	$M_{t-1}E_i$			T_tE_i	

effects of irruptive migration and potentially spatially variable trends were compared and evaluated using information-theoretical model selection (Table 2; Burnham & Anderson 2002). In this procedure, model averaging is applied to make multimodel inference if several models perform equally well. All the ten competing models included year of observation (T_t), site quality (Q_i) and the east coordinate (E_i) as explanatory variables, because these are highly likely to affect the response. The winter-count data were not included in these models, because they are affected by irruption and potentially hamper the identification of immigration effects.

Fitting the logistic regressions is done in the environment Matlab, using function glmfit.m. Standard errors are adjusted for potential overdispersion. Comparison of the models is based on Akaike information criterion corrected for overdispersion; QAIC (Burnham & Anderson 2002).

$$QAIC = -2\ln L / \hat{c} + 2K, \tag{4}$$

where L is the model likelihood at the maximum likelihood estimate, \hat{c} is an estimated variance-inflation factor obtained from the most complex model (#10), and K is the number of estimated parameters in the model.

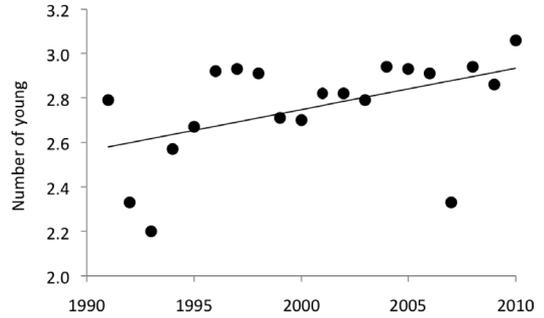


Fig. 2. Annual mean numbers of young in nests of White-backed Woodpeckers at the time of ringing in Finland in 1991–2010.

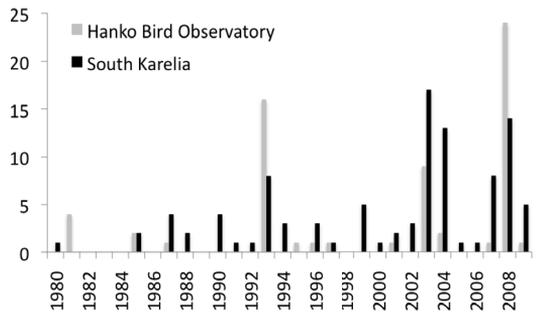


Fig. 3. Annual numbers of migrating White-backed Woodpeckers at the Hanko Bird Observatory ($n = 64$) and South Karelia ($n = 100$) in 1980–2009.

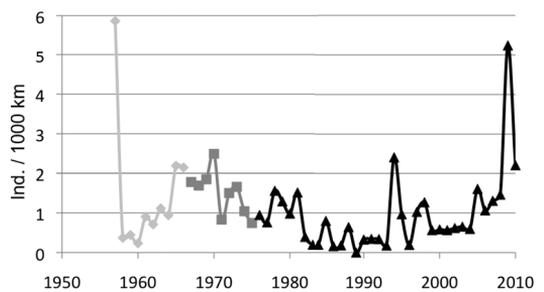


Fig. 4. Densities of the White-backed Woodpecker in the southern part of Finland between the winters of 1956/57 and 2009/10 based on winter bird counts. The densities are divided into three periods that are not directly comparable. Light grey diamonds, dark grey squares and black triangles represent the periods 1956/57–1965/66, 1966/67–1974/75 and 1975/76–2009/10, respectively (see Material and methods). Year 1960 on the x-axis indicates winter 1959/60.

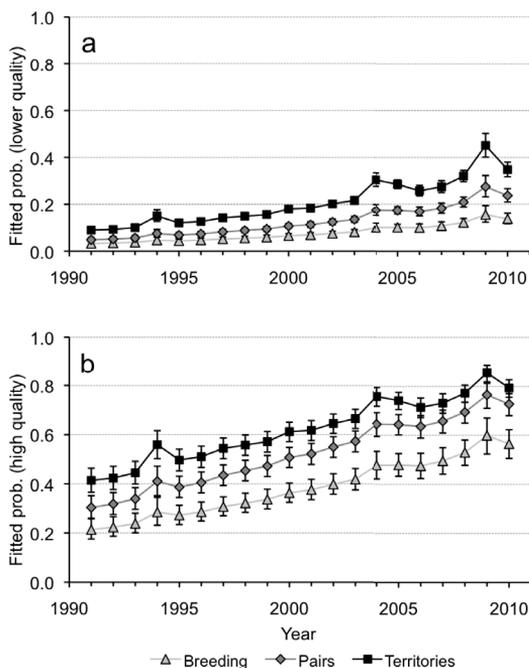


Fig. 5. Model predictions of the probabilities of detecting White-backed Woodpecker nests, pairs and territories in (a) low- and (b) high-quality sites. The fitted probabilities and their 95% confidence intervals (whiskers) are based on the most parsimonious models, with the spatial variable (E_s) fixed to the middle point of the study area.

3. Results

3.1. Breeding parameters and demography

The annual mean breeding success (2.76 ± 0.23 SD), measured as the number of ringed chicks per nest, increased significantly during 1991–2010 (annual change 0.019 ± 0.008 , $F_{1,18} = 5.16$, $P = 0.035$; Fig. 2). However, the annual mean number of nestlings at the time of ringing did not differ between high- and lower-quality sites during 2000–2010 (high quality 2.78 ± 0.76 SD, $n = 25$; lower quality 2.78 ± 0.73 , $n = 70$; t test, $t = -0.02$, $df = 93$, $P = 0.99$). The sex ratio of nestlings during 1988–2009 did not differ from unity ($\chi^2_1 = 0.16$, $P = 0.69$).

3.2. Migration and wintering

One hundred migrating White-backed Woodpeckers were observed in South Karelia (1980–2009)

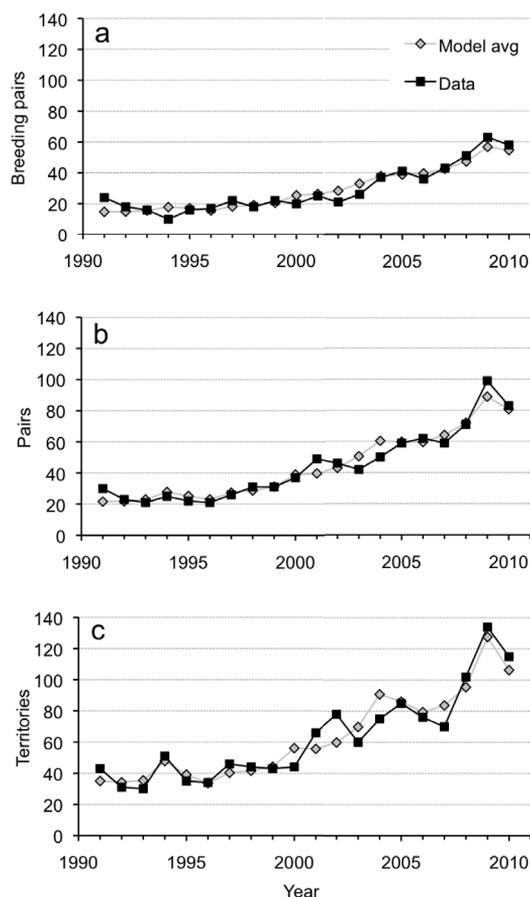


Fig. 6. Total numbers of observed (a) nests, (b) pairs, and (c) territories of the White-backed Woodpecker included in the analysis (black symbols), and model-averaged predictions (grey symbols). Model expectations of annual totals are gained by summing together the expected probabilities for all potential sites. Thus, the total numbers are affected by the number of monitored sites.

and 68 at the Hanko Bird Observatory (1979–2010). There was large variation between years. Nevertheless, the annual migration numbers of the two sites were significantly and positively correlated ($r_s = 0.52$, $df = 28$, $P = 0.003$; Fig. 3). The migration numbers increased significantly in South Karelia ($r_s = 0.57$, $df = 28$, $P = 0.001$) and at the Hanko Bird Observatory ($r_s = 0.35$, $df = 29$, $P = 0.048$). The annual mean migration numbers at Hanko and South Karelia were not significantly associated with the annual mean breeding success at Finnish breeding sites during 1991–2009 ($r_s = 0.04$, $df = 17$, $P = 0.86$).

Table 3. Ranked hypothesized models used to explain detected occupancy of confirmed breeders, pairs and territories in Finnish White-backed Woodpeckers. For each model we present the negative log likelihood ($-\ln L$), the number of free model parameters (K), the estimated variance inflation factor (\hat{c}), QAIC, the difference in QAIC compared to the most parsimonious model (Δ), and the Akaike weight (w).

Model #	$\text{logit}(Y_{i,t}) = a + b_1T_t + b_2Q_i + b_3E_i$	$-\ln L$	K	\hat{c}	QAIC	Δ	w
Confirmed breeding							
#7	$b_4M_{t-1} + b_7T_tE_i$	1474.7	7	1.006	2947.0	0.0	0.333
#6	$b_7T_tE_i$	1475.9	6	1.006	2947.4	0.4	0.276
#8	$b_4M_{t-1} + b_5M_{t-2} + b_7T_tE_i$	1474.3	8	1.006	2948.1	1.1	0.195
#9	$b_4M_{t-1} + b_5M_{t-1}E_i + b_7T_tE_i$	1474.7	8	1.006	2949.0	2.0	0.123
#10	$b_4M_{t-1} + b_5M_{t-2} + b_6M_{t-1}E_i + b_7T_tE_i$	1474.3	9	1.006	2950.1	3.1	0.072
#4	$b_4M_{t-1} + b_6M_{t-1}E_i$	1486.1	7	1.006	2969.7	22.7	0.000
#5	$b_4M_{t-1} + b_5M_{t-2} + b_6M_{t-1}E_i$	1485.6	8	1.006	2970.6	23.6	0.000
#2	b_4M_{t-1}	1487.9	6	1.006	2971.1	24.1	0.000
#1	0	1489.2	5	1.006	2971.7	24.7	0.000
#3	$b_4M_{t-1} + b_5M_{t-2}$	1487.4	7	1.006	2972.1	25.1	0.000
Pairs							
#7	$b_4M_{t-1} + b_7T_tE_i$	1867.5	7	1.003	2947.0	0.0	0.463
#8	$b_4M_{t-1} + b_5M_{t-2} + b_7T_tE_i$	1867.3	8	1.003	2948.1	1.6	0.209
#9	$b_4M_{t-1} + b_6M_{t-1}E_i + b_7T_tE_i$	1867.5	8	1.003	2949.0	2.0	0.170
#6	$b_7T_tE_i$	1870.3	6	1.003	2947.4	3.5	0.081
#10	$b_4M_{t-1} + b_5M_{t-2} + b_6M_{t-1}E_i + b_7T_tE_i$	1867.3	9	1.003	2950.1	3.6	0.077
#4	$b_4M_{t-1} + b_6M_{t-1}E_i$	1875.8	7	1.003	2969.7	16.5	0.000
#2	b_4M_{t-1}	1876.9	6	1.003	2971.1	16.7	0.000
#5	$b_4M_{t-1} + b_5M_{t-2} + b_6M_{t-1}E_i$	1875.6	8	1.003	2970.6	18.1	0.000
#3	$b_4M_{t-1} + b_5M_{t-2}$	1876.7	7	1.003	2972.1	18.3	0.000
#1	0	1879.7	5	1.003	2971.7	20.2	0.000
Territories							
#7	$b_4M_{t-1} + b_7T_tE_i$	2319.4	7	1.005	4627.6	0.0	0.282
#9	$b_4M_{t-1} + b_6M_{t-1}E_i + b_7T_tE_i$	2318.5	8	1.005	4627.9	0.2	0.251
#8	$b_4M_{t-1} + b_5M_{t-2} + b_7T_tE_i$	2318.5	8	1.005	4627.9	0.3	0.245
#10	$b_4M_{t-1} + b_5M_{t-2} + b_6M_{t-1}E_i + b_7T_tE_i$	2317.6	9	1.005	4628.1	0.5	0.222
#2	b_4M_{t-1}	2330.1	6	1.005	4646.9	19.2	0.000
#6	$b_7T_tE_i$	2330.2	6	1.005	4647.2	19.5	0.000
#3	$b_4M_{t-1} + b_5M_{t-2}$	2329.3	7	1.005	4647.3	19.6	0.000
#4	$b_4M_{t-1} + b_6M_{t-1}E_i$	2330.0	7	1.005	4648.8	21.1	0.000
#5	$b_4M_{t-1} + b_5M_{t-2} + b_6M_{t-1}E_i$	2329.2	8	1.005	4649.2	21.6	0.000
#1	0	2340.7	5	1.005	4666.1	38.5	0.000

The sex ratio of migrating birds, trapped at bird observatories in Finland outside breeding areas, was strongly female biased during 1979–2010 (2.1 times more females than males; $n = 72$, $\chi^2_1 = 9.39$, $P = 0.002$). All the individuals ringed at Hanko Bird Observatory ($n = 17$) were young, i.e., first-year, birds.

A total of 354 White-backed Woodpeckers were observed in winter-bird counts during winters 1956/1957–2009/2010 in Finland. The annual winter densities are shown in Fig. 4 for three periods that differed from each other slightly in terms of counting effort. The densities were lowest in the late 1980s and early 1990s (Fig. 4).

3.3. Population development

The number of checked potential breeding sites, observed territories, pairs and confirmed nests are shown in Table 1. Among the competing logistic regression models evaluated there were no models that were clearly superior to the others (Table 3). Therefore, we applied model averaging for inference.

The analyses showed trends of increased observation frequency for confirmed breeding records ($b_1 = 0.082 \pm 0.010$ SE), pairs ($b_1 = 0.094 \pm 0.009$ SE) and territories ($b_1 = 0.085 \pm 0.008$ SE) during 1991–2010 (Fig. 5). This increase was

Table 4. Parameter estimates and their standard errors (in parentheses) for models explaining the detected occupancy of recorded breeding birds, pairs and territory observations. The left-hand column shows results for the best model (in all cases Model #7), while the right-hand column presents model-averaged values (see Table 3). Estimates that differ significantly from zero are bolded.

Estimates	Breeding			Pairs		Territories
a (Intercept)	-3.425 (0.123)	-3.421 (0.123)	-3.017 (0.105)	-3.015 (0.105)	-2.387 (0.086)	-2.386 (0.086)
b_1 (T_t)	0.082 (0.009)	0.082 (0.010)	0.094 (0.008)	0.094 (0.009)	0.088 (0.007)	0.085 (0.008)
b_2 (Q_t)	2.093 (0.107)	2.092 (0.107)	2.150 (0.100)	2.150 (0.100)	1.974 (0.096)	1.975 (0.096)
b_3 (E_t)	-0.108 (0.120)	-0.109 (0.120)	0.134 (0.103)	0.134 (0.103)	0.048 (0.085)	0.053 (0.085)
b_4 (M_{t-1})	0.069 (0.045)	0.051 (0.050)	0.092 (0.039)	0.085 (0.045)	0.162 (0.035)	0.166 (0.035)
b_4 (M_{t-2})	0	0.012 (0.031)	0	0.007 (0.025)	0	0.022 ± 0.035
b_6 ($E_t M_{t-1}$)	0	0.001 (0.022)	0	0.000 (0.022)	0	-0.024 (0.036)
b_7 ($T_t E_t$)	0.048 (0.010)	0.048 (0.010)	0.035 (0.008)	0.035 (0.008)	0.032 (0.007)	0.033 (0.007)

more rapid towards the east (Table 3; parameter b_7 in Table 4). These effects were strong also in all the models including irruptive migration, indicating that the increase was independent from the effect of migration (which also showed a weak increasing trend). Thus, much of the increase of approximately 300–400% in total numbers of nests, pairs and territories (Fig. 6) was due to an increased probability of detecting occupancy, not only due to an increase in the number of monitored sites.

Individuals were observed more frequently in high-quality than in lower-quality sites in all three observation classes (Table 3, parameter b_2 in Table 4, Fig. 5). Effects of immigration, measured as autumn migration numbers in previous autumn, improved the observation probability of territories ($b_4 = 0.166 \pm 0.035$ SE), and was indicative also for pairs ($b_4 = 0.085 \pm 0.045$ SE). Migration two years earlier and the west–east gradient did not significantly affect migration.

4. Discussion

The winter bird counts demonstrate the decline of the White-backed Woodpecker since mid-1950s until 1980s, as shown earlier by Virkkala *et al.* (1993), but they also reflect the recent increase since the early 1990s (e.g., Laine 2010). However, the observed densities in the early years of winter-bird counts are not necessarily directly comparable to densities in more recent years, because winter feeding has become increasingly popular during the last three decades (e.g., Väisänen 2008). White-backed Woodpeckers visit feeders, making

them easier to observe (e.g., Virkkala *et al.* 1993, Kontiokorpi 2007a). Another source of potential bias is the rapid increase in internet-based databases where birders can submit their observations; see www.tiira.fi for a Finnish example. Due to databases, birdwatchers are better aware of recent records along their census routes and, if the species has recently been reported nearby, may be tempted to intentionally search the known individual(s). Further, some of the birds seen during winter counts are likely to be migrants that have established winter territories and may migrate back eastwards in spring. For these reasons population trends may be more reliably monitored based on breeding-season records.

The results on detected breeding-site occupancy showed that the national population of the White-backed Woodpecker has indisputably increased, and that the number of monitored sites alone cannot explain the increased total numbers of observed individuals. Also the intensity of migration during previous autumn positively affected the proportion of occupied territories and, to some extent, pairs. Despite the weak positive trend in the intensity of irruptions, there was a strong additional positive trend in occupancy that was independent from the effect of immigration. The main migration direction in South Karelia was westwards (about 80%; Kontiokorpi 2007b), confirming that large numbers of White-backed Woodpeckers immigrate from the Russian Federation in some years. Our results suggest that at least some of these establish territories in Finland and contribute to the national population dynamics.

The detected site-occupancy rate suggested

spatial variation, as the increase was considerably more rapid towards the eastern parts of the population, compared to the western parts. As such, this is not surprising, because immigration positively impacts the population, and immigrants mostly arrive from the east. However, the models with interaction effects of longitude and autumn-migration intensity showed only marginal effects pointing in that direction, possibly because the migration data were small and imprecise. The immigrant influence is likely less in the west, even though ringing recoveries suggest that first-year birds can migrate more than 1,000 km during their first autumn (Laine 2010). Also the severely female-biased sex ratio of the immigrants, typical for many bird species (Greenwood 1980), can cause especially females to have more difficulties to find mates in the west than in the east. Dale (2001) demonstrated that small and isolated bird populations with strong sex biased dispersal are particularly vulnerable for extinction.

Also increased breeding success may partly explain the observed positive population trend. However, the increase during the last 10–15 years has not been remarkable, and there were several low-productivity years in the early 1990s (Fig. 2). The reason for the general increase in reproduction is not known. Perhaps breeding success had declined due to inbreeding depression at the time when the population was the smallest and most isolated (e.g., Crnokrak & Roff 1999, Keller & Waller 2002). For example, the small and isolated population of the Middle Spotted Woodpecker *Dendrocopos medius* in Sweden had poor productivity during the last years before extinction in 1980s, which was linked with inbreeding depression (Petterson 1985).

Another potential explanation for the improved breeding success could be that higher reproduction is climate-driven. Indeed, an increase in winter temperature improves the pre-breeding condition of White-backed Woodpecker females (Högstad & Stenberg 2005), which may be reflected in the clutch size and general reproduction output. Cold and wet weather during nestling period negatively affects breeding success of Middle Spotted Woodpeckers (Pasinelli 2001). The importance of climatic variables for the breeding performance of the White-backed Woodpecker should be studied in the future.

Conservation efforts since the early 1990s may have improved the quality of the breeding sites for the White-backed Woodpecker, although we did not find site quality to directly affect annual breeding success. The mean fledging success per nest in the stable Norwegian White-backed Woodpecker population was 2.4 (Högstad & Stenberg 1997). This can indicate that Finnish birds are reproducing rather well (on average 2.76 young at the time of ringing), although these two measures of breeding success are not directly comparable. Nevertheless, based on national monitoring schemes of the Finnish Forest Research Institute (Metsäntutkimuslaitos 2010), the proportion of deciduous forests has increased from 1988–1991 to 2004–2008 with about 40% in the central and eastern parts of Finland. Even though most of the additional forests are highly managed or young with low amount of dead wood, this may have added some new habitat for the White-backed Woodpecker. Climate change has also been predicted to increase the volume of deciduous wood in Finland during the 21st century (Kellomäki *et al.* 2005).

The survival of adult Finnish White-backed Woodpeckers was estimated to be 0.80 in 1988–1991 (Virkkala *et al.* 1993), which is not worryingly low. Unfortunately, there are no recent estimates of survival of Finnish birds. We can therefore not quantify the role of first-year or adult survival in the population development. In Sweden, winter mortality of the Middle Spotted Woodpecker increased during cold days (Petterson 1985). Because the White-backed Woodpeckers occupying Finland are at the northern edge of the species' distribution, their winter survival may have improved due to the ongoing global warming. Alternatively, the survival may have improved due to the increased winter feeding (Väisänen 2008). A recent study on Blue Tits *Parus caeruleus* showed that winter feeding can improve also the subsequent breeding success even if the feeding would be ceased before breeding season (Robb *et al.* 2008).

Although the Finnish White-backed Woodpecker population seems to do rather well at the moment and the population has increased during the last ten years, the species is still considered nationally endangered in the latest Red List of Finland (Rassi *et al.* 2010). The species has improved

one category since the previous evaluation (cf. Rassi *et al.* 2000). In Finland, White-backed Woodpeckers are highly dependent on old-growth forest, and as our results show, the species breeds and occurs more frequently in deciduous sites with abundant dead wood, which are traditionally regarded to be high-quality sites for the species. Based on studying growth bars of feathers, Carlson (1998) suggested that individuals living in high-quality breeding sites were more frequently in good body condition than individuals occupying low quality sites.

Our findings highlight the crucial impact of immigration on the population development, as measured by detected occupancy rate of territories. This can be one of the reasons why the Finnish population has been persisting in a landscape where the amount of suitable habitat seems to be below the threshold for persistence (Carlson 2000). It is also noticeable that the isolated Swedish population would have gone extinct without recently-introduced individuals from Norway (e.g., Sveriges Ornitologiska Förening 2007). Nevertheless, it is not a wise conservation strategy to assume that the immigration from east will continue as strongly as in recent years, and even if it will, the effect may not necessarily be sufficient for the maintenance of a sustainable population in a poor breeding environment (but see Metsäntutkimuslaitos 2010, Kellomäki *et al.* 2005). A self-maintaining Finnish population would – most importantly – require developing of a conservation-area network in southern Finland (Virkkala *et al.* 1993). Also a survival analysis, including both young and adult birds, would be useful to thoroughly assess the ability of the current breeding performance to maintain the Finnish White-backed Woodpecker population.

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Suomen valkoselkätikkojen kannankehitys ja nykytila

Valkoselkätikka (*Dendrocopos leucotos*) on uhanalainen vanhojen lehtimetsien laji monissa Euroopan maissa, kuten Suomessa. Suomen kanta kutistui voimakkaasti 1900-luvun aikana. Selvittimme Suomen kannan kehitystä ja rakennetta viime vuosikymmeninä. Talvilintulaskentojen mukaan valkoselkätikkakanta on ollut aallonpohjassa 1980–90-luvuilla, ennen viimeaikaista runsastumistaan. Sekä pesimämenestys (vuodet 1991–2010) että idästä tulevien vaeltavien yksilöiden määrät (1979–2010) ovat kasvaneet viime vuosina merkitsevästi. Valtaosa vaeltavista valkoselkätikoista oli naaraita.

Todennäköisyys havaita pesimäpari reviiirilään, muu pari tai vähintään yhden yksilön reviiiri kasvoivat voimakkaasti 1991–2010 eritoten maamme itäosassa. Siten havaittu 300–400 % havaittujen yksilöiden määrän kasvu ei johdu yksinomaan seurattujen metsiköiden määrän kasvusta. Asuttujen reviiirien määrä oli korkeampi hyväkuin huonompilaatusissa metsiköissä. Syysmuuttajien määrä vaikutti positiivisesti seuraavan kevään asuttujen reviiirien määrään, muttei parien tai varmistettujen pesintöjen määrään. Huolimatta maahamme muuttavien tikkojen määrän positiivisesta kehityksestä osa maamme valkoselkätikkakannan kasvusta johtuu muista syistä.

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