

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/230043589>

Habitat requirements and foraging behaviour of the Corsican Nuthatch (*Sitta whiteheadi*)

Article in *Journal of Avian Biology* · August 2006

DOI: 10.1111/j.0908-8857.2006.03645.x

CITATIONS

21

READS

341

4 authors, including:



Roger Prodon

Ecole Pratique des Hautes Etudes

64 PUBLICATIONS 1,052 CITATIONS

[SEE PROFILE](#)



Jean-François Seguin

Parc naturel régional de Corse, France, Corte

24 PUBLICATIONS 159 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



Motorways and bird traffic casualties: the factors implied in bird mortality [View project](#)



Thesis [View project](#)

Habitat requirements and foraging behaviour of the Corsican nuthatch *Sitta whiteheadi*

Jean-Claude Thibault, Roger Prodon, Pascal Villard and Jean-François Seguin

Thibault, J.-C., Prodon, R., Villard, P. and Seguin, J.-F. 2006. Habitat requirements and foraging behaviour of the Corsican nuthatch *Sitta whiteheadi*. – J. Avian Biol. 00: 00–00.

We examined the relationship between the Corsican nuthatch *Sitta whiteheadi*, a passerine endemic to the island of Corsica and Corsican pine *Pinus nigra laricio* forest, its virtually exclusive habitat, currently restricted to inland mountains. The Corsican nuthatch prefers older Corsican pine stands with tall, large trees, and avoids younger stands, both in the breeding and wintering seasons. This preference is explained by the greater availability of pine seeds from older trees. Territorial adults are almost completely sedentary, a trait that is influenced by seed hoarding behaviour. From late autumn to early spring (i.e., when cones are mature), and during sunny weather (i.e., when cones are open), nuthatches remove pine seeds from cones and cache them on branches and under the bark of trunks. The birds retrieve the cached seeds in cold and wet weather. The presence of old Corsican pine stands appears to be a key-factor in the survival of the Corsican nuthatch, whose habitat is currently threatened by logging and fires.

J.-C. Thibault (correspondence) and J.-F. Seguin, Parc Naturel Régional de Corse, rue Major Lambroschini, B.P. 417, F-20184 Ajaccio cedex, Corsica, France. E-mail: jncldthibault@aol.com. R. Prodon and P. Villard, Biogéographie et Écologie des Vertébrés, École Pratique des Hautes Études, Université Montpellier II, c.c. 94, Place Eugène Bataillon, F-34095 Montpellier Cedex 5, France.

The Corsican nuthatch *Sitta whiteheadi* is an endemic bird to Corsica island (42°N, 9°E; western Mediterranean). It is closely related to the red-breasted nuthatch *Sitta canadensis* and to the Chinese nuthatch *Sitta villosa* (Pasquet 1998), and is probably a relict of a lineage that was formerly more widely distributed in the mid-latitudes of the Holarctic. The Corsican nuthatch is socially monogamous. It lays eggs from early April to mid-June, depending of the abundance of pine cones; the higher the number of cones available on the territories the previous winter, the earlier the breeding occurred (Thibault and Villard 2005). Its range is currently restricted to the mountain forests of Corsica, where the Corsican pine *Pinus nigra laricio*, an endemic form of the European black pine, is its main habitat (Thibault et al. 2002). The Corsican nuthatch is absent from most of the range of another pine, the maritime pine *Pinus pinaster*, which is as abundant as the Corsican pine on the island

(their stands cover 210 km² and 213 km², respectively; Anon. 1988). The main explanation for the nearly exclusive use of Corsican pine by the Corsican nuthatch is that the seeds of this tree are its main food resource; the seeds of the maritime pine are too hard to be easily eaten by the bird (Thibault et al. 2002). Individual Corsican pines may reach the age of several centuries (Conrad 1990), and stands are considered mature from at least 120 years. This pine produces its first cones at an age of 15–30 years (Anon. 1990, Lannier 1993, Saïd 2000, C. Meredieu in litt.). Cones open and release their seeds from November to March (Anon. 1990, Moneglia 2003). Although there is a peak in cone production every 2–4 years (Anon. 1990, C. Meredieu in litt.), Corsican pines produce cones every year, unlike some other pine species (Debazac 1991). There are on average 33 seeds per cone and, in a mature stand, the number of cones have been estimated as several thousands per hectare

during good crops (Moneglia 2003). Individual seeds are relatively small (mean size: 6.3×3.4 mm, mean weight: 21 mg, Thibault et al. 2002) but together represent a large potential resource for animals. However, seeds are not permanently available during winter and spring, and seed-caching behaviour has been suspected to be of crucial importance for the survival of the Corsican nuthatch (Löhrl 1960, 1988).

Although the Corsican nuthatch is not considered threatened (BirdLife International 2000), its population is very small (ca. 1400–2200 pairs), and suitable habitat – mature Corsican pine forest – is currently restricted to less than 16 000 ha (own unpubl. data). This area is still declining owing to fires (Thibault et al. 2004), forestry, and competition with maritime pine (own unpubl. data). The current range of the Corsican nuthatch is fragmented in about 70 isolated pines stands and forests, ranging from only several hectares to several thousands hectares (own unpubl. data). A better understanding of the relationship between the Corsican pine and the Corsican nuthatch is thus essential to promote appropriate conservation strategies and forestry practices.

The aims of this paper are: (i) to define the main characteristics of the pine stands used by the species, (ii) to specify to what degree Corsican nuthatches are year-round residents in mountain forests, (iii) to describe nuthatch's foraging behaviour during the critical cold season in relation to the phenology of its resource-tree, the availability of seeds, and local climate, (iv) to discuss the adaptative significance of the relationships between pine and nuthatch, as well as key-factors essential for their conservation.

Methods

Bird sampling

We estimated nuthatch abundance by point-counts at 100 sites where vegetation was also described (see below). The sites were not selected randomly. Taking into account access facilities, we attempted: (i) to select various Corsican pine stands (young, mature, or old), or more or less mixed with other tree species (beech *Fagus sylvatica*, maritime pine *Pinus pinaster*, fir *Abies alba*, or birch *Betula pendula*), but always with at least 30% of Corsican pines, (ii) to spread the sampling sites across a large part of the Corsican pine range (Anon. 1988), from 670 to 1480 m a.s.l., (iii) to minimize the risk of double counting and to prevent any edge effect by choosing points at least 150 m apart from each other, and at least 300 m from the nearest ecotone. Sampling was done in 1996, 1997 and 1998 in seven forests (from North to South: Ascu, Valdu Niellu, Casamacioli, Aitone, Corte, Venacu, and Rospa Sorba; Fig. 1). The point-count method was similar to that of Blondel et al. (1981), i.e. with unlimited distance of detection and two 20-minute

long visits to each site. Each site was visited once a year between 21 March and 30 April, when birds initiate their breeding, and the count was repeated once in another year at the same point and about the same date. As an index of relative nuthatch abundance on each point, we used the average number of territorial males heard calling during the two counts.

Checking nuthatch altitudinal movements and occupancy of territories

We looked for possible altitudinal movements of territorial nuthatches by counting the nuthatches on 11 stations along a line-transect from 400 to 1,480 m a.s.l., from Marignana to Bocca di Vergio, along the road D70. This transect ran through holm oak *Quercus ilex* and chestnut *Castanea sativa* groves, chestnut and Corsican pine groves, and pure forest of Corsican pine (from 900 m upward). The transect was sampled once in the early breeding-season (March–April), and once in the post-breeding season (August to January), during two consecutive years (1996–1997). Nuthatches respond to the calls of neighbours year round (pers. obs.) so standard recorded songs were broadcast to increase the detectability of birds.

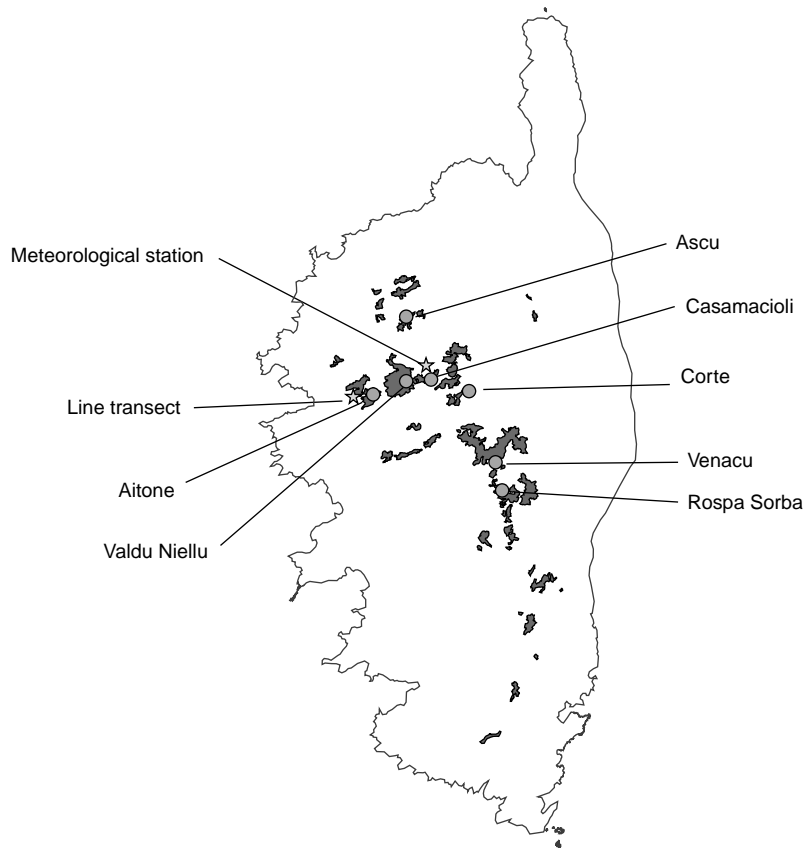
The occupancy of territories was examined by regular monitoring of the territories of colour-ringed and unringed nuthatches in the Ascu forest (from 1,020 to 1,580 m) in 1999 (19 territories), 2000 (17) and 2001 (17). Territory is defined here as including both nest-site and foraging range, occupied and defended year-round. The occupation of these territories was checked both in the breeding season (March to July) and in winter (December to January).

The aim of ringing was to verify whether breeding birds over-wintered within their own territories or not, and to look for a possible relationship between the foraging range area and the habitat quality. Territorial adults were caught in the Ascu forest with mist nets spread below the canopy (i.e., from ground level up to 8 m), and colour-ringed. Birds were lured with broadcast calls so, due to their strong territorial behaviour, more males than females were ringed. The birds were sight-recorded afterwards (from December 2000 to February 2001) with binoculars (10×42 or 8×30).

Measuring the foraging and hoarding activities of nuthatch in winter

Foraging nuthatches, colour-ringed or not, were observed in the Ascu study site during 34 days between 16 January and 28 February 2001, for about 120 h in total, by the same observer (PV). Recording was at 15-second intervals (controlled with a chronometer) from continuous observations of a given nuthatch using binoculars (10×42 or 8×30). Every 15-s, the substrate was identified as in one of the seven categories: cone, lichen, needle, twig, small branch, branch, or trunk. We

Fig. 1. Distribution map of the Corsican pine in Corsica and localities of study areas: meteorological station of Calacuccia (star), line-transect (star), census sites (dots).



recorded whether birds caught insects or extracted seeds from cones. It was difficult for a single observer to follow birds continuously when they foraged and then hoarded, so we attributed to 'hoarding' any record of bird leaving a cone with a seed in its bill to go to the trunk or branches of another tree, generally in the vicinity, then immediately coming back to forage at the same tree again.

Pine and forest stand sampling

We described the structure of the 100 sampling sites by measuring the following variables (with their abbreviations). They were measured within a 400 square metres area, i.e., within a radius of 11.3–14.0 m (depending on slope) around the sample point: ALTI: elevation in metres, measured with an altimeter daily calibrated, or read directly from maps (Institut Géographique National; scale: 1:25 000; 10 m intervals between contour lines), CV4, CV8, CV16, CV32, CV64: canopy cover (%), visually estimated by comparison with a reference chart (cf. Prodon and Lebreton 1981) within a series of five layers with limits in geometrical progression, i.e., 2–4 m above the ground, 4–8 m, 8–16 m, 16–32 m, and 32–64 m, FV: index of foliage volume; this estimation

of the volume of the canopy was calculated from the above cover values ($FV = CV4 \times 2 + CV8 \times 4 + CV16 \times 8 + CV32 \times 16 + CV64 \times 32$), then log-transformed, HP: height (m) of the highest Corsican pine, measured with a dendrometer (Suunto®), NP: number (log-transformed) of Corsican pine stems of any diameter, including saplings, DP: mean diameter (cm) of Corsican pines 20 cm or more in diameter at breast height (DBH); in calculations, DP was arbitrarily fixed at 10 cm when there was no pine >20 cm DBH, AP: basal area at DBH of the Corsican pine, i.e., sum of the areas of cross section of the pines >20 cm DBH, DX and AX: mean diameter and basal area, respectively, of trees (>20 cm DBH) other than Corsican pine, and X%: proportion of tree species other than the Corsican pine (mainly beeches), calculated from the ratio of the basal area of the non-Corsican pine trees to the basal area of all the trees ($X\% = 100 \times AX / (AP + AX)$).

In the Ascu forest, from October to December 2000, 2001 and 2002, we measured cone production in pines by counting – with a 10 × 42 binocular – the number of cones per tree on the 10 Corsican pines (DBH ≥ 20 cm) nearest to a nuthatch nest-site that had been occupied during the previous breeding season. We counted closed cones that became mature a few weeks later and thus represented the crop of the year. This measure is

accurate because the foliage of Corsican pines is sparse and cones relatively few.

Estimating habitat quality and foraging surface area in winter

From December 2000 to February 2001, we monitored 15 color-ringed adults in the Ascu forest. The birds were located daily and plotted on a 1:10.000-map divided into 1-ha grid squares. Each square was scored 1, 2 or 3, according to the following scale of putative habitat quality for the nuthatch (in decreasing order): 1 = old forest (>160-year old), 2 = mature forest (\approx 120–160-year old), 3 = pines erratically scattered among rocky grassland or shrubland. The *a priori* scoring was done using aerial colour photograph (scale 1:10.000) from the Institut Géographique National. A crude estimate of the surface area of the home range of a given individual was obtained by counting the number of different 1-ha squares in which this individual was observed. The mean 'quality' of a given range was calculated *a posteriori* by averaging the scores of the used squares within this home range.

Climatic data

The temperatures (daily minima and maxima) were recorded under shelter in a standard way at the Ascu study site (1,420 m a.s.l.). Some missing data were extrapolated, with a slight altitudinal correction, from the nearby station of Calacuccia (900 m; Fig. 1).

Statistical methods

The relationship between forest stand characteristics and nuthatch abundance was first investigated by simple linear regression, testing significance by an analysis of variance procedure (F test), and by PCA to get a synthetic view of the data set. We then quantified the relationship between relative abundance of Corsican nuthatch and the habitat variables using upward step-wise multiple regression, after having factored out the influence of altitude. The correlation between the diameter of pine trunks and the production of cones

was measured by simple linear regression on log-transformed data (to normalise variances). The relationship between winter foraging range and habitat quality was tested using non-parametric correlation (Spearman or Kendall correlation coefficient) and that between foraging substrate and temperature was modelled by logistic regression. We used ADE-4 (Thioulouse et al. 1997), Statistica 6 (Statsoft 2002), and SAS 8.0 statistical package software. Means are reported \pm 1 SD.

Results

Sedentariness and territoriality of the Corsican nuthatch

No evidence of any altitudinal movement was detected along our line-transect during the two years of the study. Both in spring and outside the breeding season, the nuthatches were present only from 900 m a.s.l. (i.e., the lower limits of the Corsican pine forest along the transect) upwards.

Most territories (i.e., 95% in 1999–2000; 88% in 2000–2001; 94% in 2001–2002) were occupied year-round by males, but fewer were occupied year-round by females (Table 1). Some colour-ringed breeding males retained their territories from one winter to the next. The situation for females may have been similar, but our sample was too small to test this hypothesis. Unoccupied territories in winter were situated within the altitudinal range of occupied territories, so the proportion of occupied sites did not seem to be related to the altitude. We assumed that the colour-ringed birds we observed again later were located on their own territories, but we did not know to what extent the boundaries of territories changed between the breeding and wintering seasons.

Nuthatch abundance and forest characteristics

Zero to four nuthatches were recorded during a single count. The average number of nuthatches recorded during the two visits on a same point in the breeding season (NN) varied from 0 to 3.5 (mean 1.03) in the different sites.

Table 1. Occupancy of territories by adult Corsican nuthatches in the Ascu forest during the breeding season and the following winter. The number of ringed birds during winter is indicated in brackets.

Occupied territories during breeding				Occupied territories during the following winter			
Year	No. of territories	Ringed birds		Year	No. of territories	No. of birds	
		Male	Female			Male	Female
1999	19	17	5	2000	18	18 (10)	15 (2)
2000	17	14	6	2001	15	15 (10)	12 (4)
2001	17	9	8	2002	16	16 (6)	15 (4)

The first axis of the PCA of 10 pine stand descriptors was positively correlated with the height, diameter, and canopy cover (above 16 m) of the pines and negatively related to the number of pine stems (large numbers of stems correspond to numerous saplings); this axis clearly corresponds to the age of the stands. The second axis is related to the density of the undergrowth, i.e., to the canopy cover between 2 and 16 m, which can be effected by trees other than pines (Fig. 2a). Projecting NN values on the 100 point-counts corresponding to the sampling sites in the first plane of PCA shows that nuthatches were more numerous in the sites where the pines were tallest, had large diameter and high canopy cover (in the upper layers, 16–32 m and 32–64 m; Fig. 2b). Nuthatch numbers were lower where the vegetative cover of the lower layer (between 2 and 16 m) was high, and/or the proportion of non-pine trees was relatively high. Nuthatches were generally absent in young pine stands with numerous saplings. Certain vegetation descriptors were inter-correlated. The highest positive correlations were observed between HP and DP ($r=0.77$), and between $\log(FV)$ on the one hand and HP, CV32, and CV16 on the other ($r=0.85, 0.84$ and 0.77 , respectively). The highest negative correlations were observed between NP on the one hand, and FV and DP on the other ($r=-0.66$ and -0.63 , respectively; $P<0.001$ in all cases).

As the number of nuthatches NN slightly increased with altitude in the data set ($r=0.17$, $P=0.088$), this variable was factored out before quantifying the influence of pine stand characteristics on NN. The number of nuthatches NN was significantly and positively correlated with (in decreasing order) the height of the Corsican pines ($r=0.54$), their diameter ($r=0.49$), the foliage volume index ($r=0.48$, $P<0.001$ in all cases), and negatively correlated with the number of pines (including saplings) per area ($r=-0.33$; $P<0.001$). No nuthatches were recorded when the height of the Corsican pine was lower than 15 m (or their diameter less than 28 cm), and the counts were always positive when this height was equal or greater than 32 m (or the diameter greater than 58 cm). Although there seemed to be no direct correlation between NN and the percentage of non-Corsican pine trees ($r=-0.12$, $P=0.25$), the maximum numbers of nuthatches recorded (i.e., the greatest census values) were 3.5, 2, 1.5, and 1, when this percentage was 0%, 10%, 35%, and 70%, respectively. This apparent lack of correlation may be related to the fact that the proportion of Corsican pine was never lower than $\approx 30\%$ in our data set. As regards the five variables of the foliage profile (canopy cover), the best correlation with NN was found with the 16–32m layer ($r=0.45$, $P<0.001$).

From five dendrometric variables considered together (HP, NP, DP, $\log FV$, X%), a step-up multiple-correlation procedure retained the maximum height of the Corsican pines (HP) and the percentage of non-Corsican pine

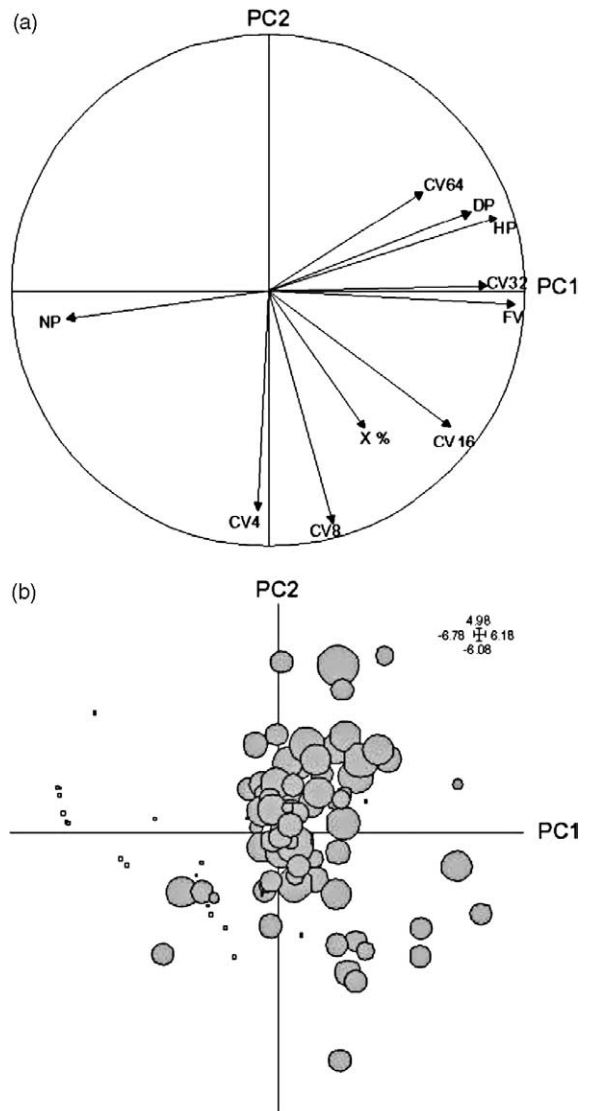


Fig. 2. Principal Component Analysis of 10 descriptors of pine stands, using data from 100 census plots: (a) Correlation circle in the PC1-PC2 plane, with the 5 variables of foliage cover (CV4=2–4 m layer; CV8=4–8 m layer; CV16=8–16 m layer; CV32=16–32 m layer; CV64=32–64 m layer) and the 5 dendrometric descriptors (HP: height of the highest Corsican pine; NP: number of Corsican pine stems; DP: mean diameter of Corsican pines; FV: index of foliage volume, X%: proportion of non-Corsican pine trees; see text). (b) Scores of the 100 sampling plots on the PC1-PC2 plane. The surface of a given dot is proportional to the number of nuthatches recorded on the corresponding plot (top right: maximum values of abscissa and ordinates).

trees (X%) as significantly correlated – the former positively, the latter negatively – with nuthatch abundance (Table 2, first model). From the five cover values of the stratification profile, the same procedure retained only the 16–32 m layer and, marginally, the 4–8 m layer, the former positively, the latter negatively (Table 2,

Table 2. Multiple correlation between the average number of nuthatches recorded during the counts (after the influence of altitude has been factored out) and two sets of pine stand descriptors, as resulting from a step-up procedure. The first model corresponds to the selection of two variables among five dendrometric descriptors. The second model corresponds to the selection of two variables among five variables of foliage cover (see Fig. 2 for the abbreviations of the variables).

First model	HP	X%
Partial regression coefficient	0.446	-0.201
P-level	<0.001	0.018
Multiple correlation coefficient R = 0.59		
Second model	CV32	CV8
Partial regression coefficient	0.484	-0.17
P-level	<0.001	0.07
Multiple correlation coefficient R = 0.48		

second model). However, the selection of the variables should be considered with caution due to multi-colinearity among variables.

Productivity of cones as a function of the diameter of the tree

The production of cones was considerably lower in 2000 than in 2001 and 2002 (mean number of cones per tree: in 2000 = 20 ± 36 , $n = 160$; in 2001 = 122 ± 114 , $n = 120$; in 2002 = 103 ± 160 , $n = 142$). Nevertheless, within each of the three years, the number of cones on a pine tree was significantly correlated with the diameter of its trunk: year 2000 ($r_{158} = 0.17$, $P < 0.05$), year 2001 ($r_{118} = 0.65$, $P < 0.0001$), year 2002 ($r_{140} = 0.36$, $P < 0.0001$); the larger the tree, the more numerous the cones.

Nuthatch foraging behaviour in winter

Relationships between home range surface area and habitat quality in winter

During the three months of the study, the 135 visits enabled us to map the ranges of fifteen adults nuthatches (11 males, 4 females). Range areas varied from roughly 1 to 8 ha. There was a highly significant correlation between the home range areas and their mean "quality" estimated by the average of the quality scores of their constituent squares (Spearman correlation coefficient $r_s = 0.90$, $P < 0.001$).

Foraging and seed hoarding

We obtained 3086 sight records of foraging activity from 46 different nuthatches (28 males and 18 females). The nuthatches foraged mainly on Corsican pines (98.5%). Only 1.5% of the records were on birches. On the pines, the birds foraged mostly on open cones (62%, $n = 1,911$) extracting the seed by the wing with their bill, and less

frequently on other substrates i.e. lichen, needle, twig, branch and trunk (38%, $n = 1,175$). We could not identify the food items – arthropods or retrieved seeds – gathered by nuthatches when foraging in bark crevices. Nuthatches were rarely seen eating seeds when foraging on cones (0.04%, $n = 11$) and about half of the records of foraging on open cones were followed by hoarding activity (51.4%, $n = 982$), suggesting that most of the seeds picked from cones were hoarded. Birds hoarded under bark or in bark crevices on pines, often on the undersides of main horizontal branches, and generally in the upper part of the tree. Hoarding was usually at less than 50 meters from the foraging tree. There were several observations of birds putting a small piece of bark on the crevice and of birds shifting a seed to another place.

Switching of foraging behaviour as a function of temperature

We examined the daily variation in the proportion of the total observed foraging time that was spent on cones (total foraging time was 3086 15-second time units, within 1911 foraging events, from 34 days). During the study period, temperatures on different observation days ranged from -10°C to $+16.5^\circ \text{C}$. Within this range, the relative use of cones by foraging nuthatches increased with temperature (Fig. 3). The probability that nuthatches foraged on the cones according to temperature was fitted to logistic models, taking into account either the daily minima, or the daily maxima, or both (with or without interaction; Fig. 3, Table 3). The probability that nuthatches foraged on the cones according to temperature was fitted to logistic models, taking into account either the daily minima, or the daily maxima, or both (with or without interaction; Fig. 3, Table 3). Although the effect of the daily minima was

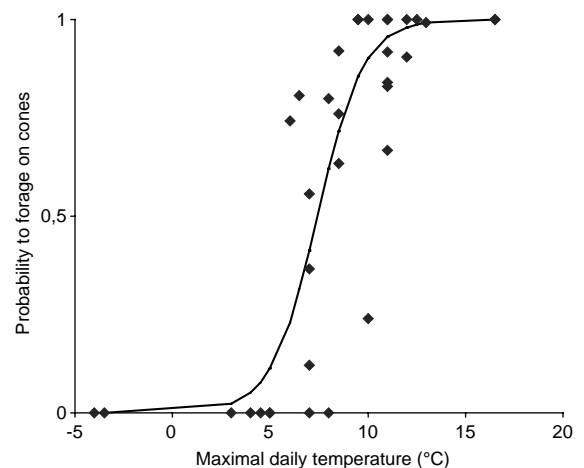


Fig. 3. The probability of Corsican nuthatches foraging on pine cones (ordinate) as a function of the daily maximum temperature (abscissa). The fitted curve corresponds to a logistic model whose linear predictor is $-6.33 + 0.854 \times T_{\text{max}}$. Goodness of fit: $\text{Pr} > \text{Log Ratio } \chi^2 < 0.0001$ (see Table 3).

Table 3. Correlation between the use of the pine cones by the Corsican nuthatch as substrate for foraging, and the daily temperature (minimum Tmin, or maximum Tmax). Selection of a logistic model (AIC: Akaike Information Criterion).

Model	Log ratio Pr > χ^2	Scaled deviance	Number of parameters	AIC
Tmin	0.82	28.68	4	36.7
Tmax	<0.0001			
Tmin × Tmax	0.97			
Tmin	0.59	29.64	3	35.6
Tmax	<0.001			
Tmin	<0.001	35.29	2	39.3
Tmax	<0.001	29.4	2	33.4

significant when considered alone, the best fit and the most parsimonious model was obtained with the daily maxima alone, with an inflexion point at $\sim 7.4^\circ\text{C}$ (curve on Fig. 3). However the distribution of the events around this point was not symmetrical, as no bird was observed foraging on cones when the maximal temperature was lower than 6°C , and none was observed foraging on trunks or branches when the maximal temperature was higher than 13°C .

Discussion

Food and seasonal cycle of the Corsican nuthatch in the pine forest

Nuthatch sedentariness

Although there are occasional sightings of birds outside the Corsican pine range (Thibault and Bonaccorsi 1999) during the non breeding season, the Corsican nuthatch appears to be strictly sedentary. Matthysen and Adriaensen (1989) have suggested that the social system of the Corsican nuthatch is based on permanent pairs defending their territories throughout the year. Our monitoring of a set of marked birds in the Ascu forest during three consecutive years confirmed that most breeding pairs maintained their territories throughout the winter. A similar pattern has been observed with other species of nuthatch in temperate zones (Matthysen 1998).

Nuthatch home range size and pine productivity in seeds

Nuthatch territories are smaller when pines are larger (i.e., more productive). In young stands and clearings, birds must forage over a larger area than in old stands. Conner et al. (2001) reported that the home range area of the red-cockaded woodpecker *Picoides borealis* was inversely correlated with the habitat quality measured by the density and age of the pines. A positive relationship between the age of trees and productivity in seeds has been shown in several conifers species, both in temperate and tropical climates (Holimon et al. 1998, Latta et al. 2000).

Nuthatch diet through the annual cycle

During the breeding season, nuthatches catch arthropods on trees (trunk and canopy), as well as in flight (Villard et al. 2003). At that time, the cones are still closed (Anon. 1990, unpubl. data), and the seeds of the year are not yet available. Field observations during incubation and brood rearing periods confirm that adults bring mainly insects to the nest, although adults recover some seeds hoarded in caches or on open cones when cone crops are abundant (unpubl. data). From late autumn to early spring (i.e., when the cones are mature), nuthatches can collect seeds but only during sunny weather when the cones are open because they still close on cold and humid days. In the field, it is difficult to see when nuthatches eat seeds, but the large proportion of time spent by birds hoarding when the cones are open strongly suggests that seeds constitute an important if not the virtually exclusive resource for nuthatches during winter. Remains of seeds and the occurrence of very small stones in faeces, support this view (unpubl. data). The birds also take advantage of the sunny periods (when cones are dehiscent) to hoard seeds in bark crevices. These cached seeds are retrieved in cold and wet weather by birds foraging on branches and trunks.

Adaptive value of seed hoarding

Seed hoarding by animals is an adaptive strategy that has two functions: accumulating food reserves, and removing food surplus from competitors (Källander and Smith 1990, Brodin and Ekman 1994). Most of the nuthatch species whose biology is known store food (Nilsson et al. 1993, Harrap and Quinn 1996). The related red-breasted nuthatch stores food (mainly conifers seed) during fall and winter (Grubb and Waite 1987, Ghalambor and Martin 1999), but in years of low cone production, the birds disperse various distances to compensate for the scarcity of resources (Ghalambor and Martin 1999). The strict sedentariness of the Corsican nuthatch in the Corsican pine forest is facilitated both by the long period of cone opening (4–5 months) of this pine, and by the absence of years with no cone production (Debazac 1991). Sedentariness of a large fraction of the avifauna in the Pyrenean pine forests, and particularly of the common crossbill *Loxia curvirostra*, has also been related to the relative stability in pine seed production (Génard and Lescourret 1987, Senar et al. 1993, Clouet 2000). In Scotland, ‘large-billed’ crossbills (*L. scotica* and *L. pytyopsittacus*) also exploit annual seed crops of Scots pine *P. sylvestris* and are largely sedentary, in contrast to ‘small-billed’ crossbills that exploit sporadic crops of spruce *Abies* and are itinerant (Marquiss and Rae 2002). In Northern Europe, both the European nuthatch *Sitta europaea* and the willow tit *Parus montanus* hoard seeds during autumn for the winter months (Nilsson et al. 1993, Brodin 1994, Brodin and Clark 1997). In southern Europe, coal tits

Parus ater seem to hoard seeds to provide against food scarcity during the short periods of bad weather (Brotons and Haftorn, 1999), a behaviour similar to that recorded in the Corsican nuthatch.

Sedentariness in high altitude forests implies the ability to cope with the adverse conditions of the cold season, when food resources become scarce or hardly accessible. In the supra-Mediterranean and montane levels of Corsica, the mean number of days below freezing, and with snowfall, are ca. 20–30, and 90, respectively (Bruno et al. 2001). Seed hoarding seems an adaptative trait enabling Corsican nuthatches to stay on their territories in the mountains even during such cold and snowy periods, when most other bird species have moved downhill to warmer areas. Climatic conditions were even more severe than today in Corsica during the cold periods of the Pleistocene, when conditions were about 7–9°C cooler (Prodon et al. 2002). Nevertheless, the Corsican nuthatch is clearly a paleo-endemic that could not have re-colonized Corsica after the last glacial maximum. Although the presence of Corsican pine on the island during the last glacial maximum has sometimes been questioned (Reille et al. 1997), it is very likely that the persistence of this tree, at least at low altitudes, and the hoarding behaviour of the nuthatch, together enabled the survival of this island endemic during this critical period.

Is there coevolution between the Corsican nuthatch and the Corsican pine?

The study of co-evolution between some conifers and corvids has shown that birds could be the main dispersal agent of seeds (Ligon 1978, Vander Wall and Balda 1981, Tomback and Linhart 1990). As regards the case of the Krüper's nuthatch *Sitta krueperi* and the Turkish pine *Pinus brutia*, a co-adaptation has been suggested, on the basis of the complete coincidence of the ranges of the bird and of the pine, and of the fact that the Krüper's nuthatch stores the seeds in sites *a priori* suitable for their germination (Frankis 1992). However, the case of the Corsican nuthatch and the Corsican pine is different. Among the different agents responsible for the dispersal of pine seeds (Lanner 1998), the wind seems the main factor for the dispersal of the light winged seeds (Benkman 1995) of the Corsican pine (Saïd 2000). Moreover, Corsican nuthatches hoard seeds under the bark of trunks or living branches. Since we have no evidence of bird caching seeds in the ground, the hoarding activity of the nuthatch does not seem to have any positive effect on seed dispersal. Thus, although the Corsican nuthatch depends on the Corsican pine for food, the reproduction of the pine seems independent of the nuthatch.

Nevertheless, coevolution could be involved in the reciprocal morphological selection in both bill of birds and cone of pines, as has been established for crossbills (Benkman 1999, Benkman et al. 2003). The Corsican nuthatch is a seed predator unable to open cones like crossbills, but has a long and thin bill that seems to be a tool perfectly adapted to extract seeds by their wing when the cone is open. We could verify with a living bird that the shape and length of nuthatch's bill exactly fits the spaces between the scales of open cones, suggesting these may select for nuthatch bill morphology. But conversely we do not know if the nuthatch, by its predation, has driven selection for the morphology of cones and seeds. Seeds are periodically overabundant, attracting large numbers of seed-eating birds such as siskins *Carduelis spinus* and chaffinches *Fringilla coelebs* (pers. obs.), but during the years of low seed production, sedentary birds, as great spotted woodpecker *Dendrocopos major*, coal tit, and Corsican nuthatch are the only seed-eater species in Laricio pine forests, where they are likely to exert severe predation on seeds. The same situation pertains after wildfire when cones opened by the heat of the fire have attracted numerous seed-eating birds (Thibault and Prodon 2006). In this case, the postfire regeneration of pines completely depends on the seeds surviving in the cones, so we cannot exclude a negative effect of seed predation by birds on tree recruitment.

Habitat selection and conservation issues

We have here shown the preference of the Corsican nuthatch for older stands with tall large Corsican pines, and its avoidance of younger stands, both in the breeding and wintering seasons. We have also shown that this preference is probably related to a greater availability of seeds for birds on tall trees during the cold season. An increase in the productivity of seeds with the age of the trees has previously been shown for several conifer species, both in temperate and tropical climates (Holimon et al. 1998, Latta et al. 2000). Structural features of the trees may also play a role in nuthatch feeding preference, as the thick bark of older Corsican pines – being deeply fissured – offers more potential caches for hoarding seeds and searching for arthropods than the bark of younger trees. Lastly, older pine stands are more likely to offer dead snags favourable for digging nest holes. Thus, the presence of old Corsican pine stands is a key-factor for the survival of the Corsican nuthatch. This bird, as well as other species that exploit conifer seeds, may be threatened if logging and/or fires lead to the replacement of older stands by younger ones (Benkman 1993).

The Corsican pine forest is considered as a habitat of European concern (Annex I of the Habitat Directive,

Anon. 2001). The surface area of the Corsican pine forest is currently ca. 21,000 ha, i.e., no more than 2.4% of the island area, and less than 16 000 ha are considered as “mature forest” (own unpubl. data). Moreover, the old stands have a fragmented distribution, as a consequence of both forestry practice and repeated fires. Old pine stands are mostly confined to less accessible areas where they are often classified by foresters as “out category” or “ecological series”. Therefore, the strict conservation of these old stands is essential for the survival of Corsican nuthatch in the long-term. In this context, large forest fires like those of the summers 2000 and 2003 in the Corsican mountains represent a major threat to the survival of this endemic species (Thibault et al. 2004).

Acknowledgements – We express our gratitude to Alice Cibois, Mick Marquiss, Diana Tomback, and an anonymous referee for improving a first draft of the manuscript, to Céline Méredieu (INRA) and Jean-Pierre Palauqui (MTO-France, Bastia-Poretta) for providing unpublished data, to Mick Marquiss and Corinne Faure for improving the English, and to Aurélien Besnard (EPHE) for his help in data processing. This study was granted by the DIREN-Corse (Ministry of Environment) and by the Office de l'Environnement de la Corse, and represents also a part of a «personal program» of the “Centre de Recherches sur la Biologie des Populations d'Oiseaux” (Muséum National d'Histoire Naturelle, Paris).

References

Anon. 1988. Inventaire forestier national. Départements de Haute-Corse et de Corse du Sud. – Ministère de l'Agriculture et Développement Rural, Direction de l'Espace Rural et Forestier, Paris, France.

Anon. 1990. ConsGuide technique du forestier méditerranéen français. – CEMAGREF, Grenoble, France.

Anon. 2001. Connaissance et gestion des habitats et des espèces d'intérêt communautaire. Tome 1, Habitats forestiers, vol. 2. Cahiers d'habitats Natura 2000. La documentation française, Paris.

Benkman, C. W. 1993. Logging, conifers, and the conservation of crossbills. – *Cons. Biol.* 7: 473–479.

Benkman, C. W. 1995. Wind dispersal capacity of pine seeds and the evolution of different seed dispersal modes in pines. – *Oikos* 73: 221–224.

Benkman, C. W. 1999. The selection mosaic and diversifying coevolution between crossbills and lodgepole pine. – *Am. Nat.* 153 (suppl.): 75–91.

Benkman, C. W., Parchman, T. L., Favis, A. and Siepielski, A. M. 2003. Reciprocal selection causes a coevolutionary arms race between crossbills and lodgepole pine. – *Am. Nat.* 162: 182–194.

BirdLife International 2000. Threatened birds of the world. – Lynx Edicions and BirdLife International, Barcelona and Cambridge, UK.

Blondel, J., Ferry, C. and Frochot, B. 1981. Points counts with unlimited distance. – *Stud. Avian Biol.* 6: 414–420.

Brodin, A. 1994. The role of naturally stored food supplies in the winter diet of the boreal willow tit *Parus montanus*. – *Ornis Svecica* 4: 31–40.

Brodin, A. and Clark, C. 1997. Long-term hoarding in the *Paridae*: a dynamic model. – *Behav. Ecol.* 8: 178–185.

Brodin, A. and Ekman, J. 1994. Benefits of food hoarding. – *Nature* 372: 510.

Brotons, L. and Haftorn, S. 1999. Geographic variation of the storing behaviour in the coal tit *Parus ater*: role of winter residency and environmental conditions. – *Ibis* 141: 587–595.

Bruno, C., Dupré, G., Giorgetti, G., Giorgetti, J.-P. and Alessandri, J. 2001. Chi tempu face? Météorologie, climat et microclimats de la Corse. – Centre Régional de la Documentation Pédagogique, Ajaccio, France.

Clouet, M. 2000. The breeding biology of the common crossbill *Loxia curvirostra* in the Central Pyrenees. – *Bird Study* 47: 186–194.

Conner, R. N., Rudolph, D. C. and Walters, J. R. 2001. The red-cockaded woodpecker. Surviving in a fire-maintained ecosystem. – University of Texas Press, Austin.

Conrad, M. 1990. Les monuments végétaux de la Corse. – *Le Monde des Plantes* 438: 10–11.

Debazac, E.-F. 1991. Manuel des conifères, 2nd ed. – ENGREF, Nancy, France.

Frankis, M. P. 1992. Krüper's nuthatch *Sitta krueperi* and Turkish pine *Pinus brutia*: an evolving association? – *Sandgrouse* 13: 92–97.

Génard, M. and Lescourret, F. 1987. The common crossbill (*Loxia curvirostra*) in the Pyrenees: some observations on its habitats and on its relation with conifer seeds. – *Bird Study* 34: 52–63.

Ghalambor, C. K. and Martin, T. E. 1999. Red-breasted nuthatch (*Sitta canadensis*). – In: Poole, A. and Gill, F. (eds). The birds of North America, no.459. The Birds of North America, Inc, Philadelphia, USA.

Grubb, T. C., Jr. and Waite, T. A. 1987. Caching by red-breasted nuthatches. – *Wilson Bull.* 99: 696–699.

Harrap, S. and Quinn, D. 1996. Tits, nuthatches and treecreepers. – Helm Identification Guides. A. and C. Black, London, UK.

Holimon, W. C., Benkman, C. W. and Willson, M. F. 1998. The importance of mature conifers to red crossbills in southeast Alaska. – *Forest Ecol Manage.* 102: 167–172.

Källander, H. and Smith, H. G. 1990. Food storage in birds. An evolutionary perspective. – *Curr. Ornithol.* 7: 147–207.

Lanner, R. M. 1998. Seed dispersal in *Pinus*. Ecology and Biogeography of *Pinus*. – In: Richardson, D. M. (ed.). Cambridge University Press, Cambridge, UK, pp. 281–295.

Lannier, L. 1993. Précis de sylviculture. – ENGREF, Nancy.

Latta, S. C., Sondreal, M. L. and Brown, C. R. 2000. A hierarchical analysis of nesting and foraging habitat for the conservation of the Hispaniolan white-winged crossbill (*Loxia leucoptera megapalaga*). – *Biol. Cons.* 96: 139–150.

Ligon, J. D. 1978. Reproductive interdependence of piñon jays and piñon pines. – *Ecol. Monogr.* 48: 111–126.

Löhrl, H. 1960. Vergleichende Studien über Brutbiologie und Verhalten der Kleiber *Sitta whiteheadi* Sharpe und *Sitta canadensis* L. – *J. Ornithol.* 101: 245–264.

Löhrl, H. 1988. Etho-ökologische Untersuchungen an verschiedenen Kleiberarten (Sittidae). Eine vergleichende Zusammenstellung. – *Bonner Zool. Monogr.* 26: 1–208.

Marquiss, M. and Rae, R. 2002. Ecological differentiation in relation to bill size amongst sympatric, genetically undifferentiated crossbills *Loxia* spp. – *Ibis* 144: 494–508.

Matthysen, E. 1998. The Nuthatches. – T & AD Poyser, London.

Matthysen, E. and Adriaensen, F. 1989. Notes on winter territoriality and social behaviour in the Corsican nuthatch *Sitta whiteheadi* Sharpe. – *Alauda* 57: 155–168.

Moneglia, P. 2003. Etude sur la fructification du Pin laricio (*Pinus nigra laricio*) comme ressource alimentaire hivernale de la Sittelle corse (*Sitta whiteheadi*). – Mémoire DEA, Université de Corse, Corte, France.

Nilsson, J.-Å., Källander, H. and Persson, O. 1993. A prudent hoarder: effects of long-term hoarding in the European nuthatch, *Sitta europaea*. – *Behav. Ecol.* 4: 369–373.

Pasquet, E. 1998. Phylogeny of the nuthatches of the *Sitta canadensis* group and its evolutionary and biogeographic implications. – *Ibis* 140: 150–156.

- Prodon, R. and Lebreton, J.-D. 1981. Breeding avifauna of a Mediterranean succession: the holm oak and cork oak series in the eastern Pyrénées. 1 Analysis and modelling of the structure gradient. – *Oikos* 37: 21–38.
- Prodon, R., Thibault, J.-C. and Dejafve, P.-A. 2002. Expansions vs. compression of bird altitudinal ranges on a Mediterranean island. – *Ecology* 83: 1294–1306.
- Reille, M., Gamisans, J., Beaulieu de, J.-L. and Andrieu, V. 1997. The late-glacial at Lac de Creno (Corsica, France): a key site in the western Mediterranean basin. – *New Phytol.* 135: 547–559.
- Saïd, S. 2000. Modélisation spatio-temporelle de la dynamique de la végétation dans l'aire naturelle du pin laricio en Corse. – Thesis, Université de Corse, Corte, France.
- Senar, J. C., Borrás, A., Cabrera, T. and Cabrera, J. 1993. Testing for the relationship between coniferous crop stability and common crossbill residence. – *J. Field Ornithol.* 64: 464–469.
- Statsoft 2002. Statistica, version 6. – Tulsa, USA.
- Thibault, J.-C. and Bonaccorsi, G. 1999. The Birds of Corsica. An annotated check-list. No17. – BOU, Tring, UK.
- Thibault, J.-C. and Prodon, R. 2006. Seed harvesting by birds shortly after a wildfire in a Corsican pine forest. – *Int. J. Wildland Fire.* 15: 81–86.
- Thibault, J.-C., Prodon, R. and Moneglia, P. 2004. Impact des incendies de l'été 2000 sur l'effectif d'une espèce endémique menacée: la Sittelle corse (*Sitta whiteheadi*). – *Ecol. Mediterr.* 30: 63–71.
- Thibault, J.-C., Seguin, J.-F., Villard, P. and Prodon, R. 2002. Le Pin laricio (*Pinus nigra*) est-il une espèce-clé pour la Sittelle corse (*Sitta whiteheadi*)? – *Revue d'écologie (Terre Vie)* 57: 329–341.
- Thibault, J.-C. and Villard, P. 2005. Reproductive ecology of the Corsican nuthatch. – *Bird Study* 52: 282–288.
- Thioulouse, J., Chessel, D., Dolédec, S. and Olivier, J. M. 1997. ADE-4: a multivariate analysis and graphical display software. – *Stat. Comp.* 7: 75–83.
- Tomback, D. F. and Linhart, Y. B. 1990. The evolution of bird-dispersed pines. – *Evol. Ecol.* 4: 185–219.
- Vander Wall, S. B. and Balda, R. P. 1981. Ecology and evolution of food-storage behaviour in conifer-seed-caching corvids. – *Z. Tierpsychol.* 56: 217–242.
- Villard, P., Bichelberger, S., Seguin, J.-F. and Thibault, J.-C. 2003. La quête alimentaire de la Sittelle corse (*Sitta whiteheadi*) dans les Pins laricio (*Pinus nigra laricio*). – *Vie & Milieu* 53: 27–32.

(Received 7 February 2005, revised 26 August 2005, accepted 12 September 2005.)