



Uphill shifts in the distribution of the white stork *Ciconia ciconia* in southern Poland: the importance of nest quality

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ABSTRACT

The aim of this paper is to explain the altitudinal changes that have occurred during the 20th century to the white stork distribution in the Podhale region of the uplands of the Tatra mountains, southern Poland. We analysed both historical data from the white stork censuses and detailed yearly records from 1974 to 2003 on population size, distribution and breeding success.

A white stork nest was first recorded at Podhale in 1931 and numbers increased to seven nests in 1933, all located below 650 m altitude. During the 30-years, 1974–2003, both the maximum and upper-quartile altitudes of nests increased significantly. In 1974 the highest nest was at an altitude of 770 m, and the maximum reached 890 m in 1999. In the same period, the breeding population increased significantly. The minimum and lower-quartile altitudes of nests decreased significantly following initial occupation of suitable lower altitude sites before uphill expansion. We noted the positive association between nest occupancy over the study period and breeding performance. As a result, long-occupied nests contributed most of the young produced in the population and chicks from these nests probably colonized new areas. We believe this is the first well-documented evidence of, and mechanism for, a particular bird species to ascend to higher elevations and that the altitudinal shifts reported for butterflies, plants and whole biomes can be detected in birds as well.

Keywords

Altitudinal gradient, Central Europe, climate change, foraging areas, historical records, uplands, white stork.

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INTRODUCTION

There is evidence of changes in the distribution of terrestrial species throughout the World (Parmesan *et al.*, 1999; Walther *et al.*, 2002) consistent with recent global warming, although reported increases in altitudinal ranges are rare (Grabherr *et al.*, 1994; Pounds *et al.*, 1999). Reports of altitudinal shifts in birds are strictly limited and, except for an extension of Costa Rican pre-montane species (Pounds *et al.*, 1999), have only been anecdotal and/or have shown inconsistent responses (Archaux, 2004).

Evidence for distributional change is often derived from two surveys at discrete points in time. Species' behaviour at those specific time points can affect conclusions, because changes in the distribution of species are connected not only with climatological events, but also with major changes in habitats (Pounds *et al.*, 1999; Warren *et al.*, 2001; Konvicka *et al.*, 2004). Therefore uphill shifts can be a possible response to the influence of both factors. However, evidence of such shifts, in contrast to latitudinal or longitudinal range changes, are not easy to obtain, because

only the highest-quality data on both historical and recent distribution can reveal these changes (Parmesan, 1996; Hill *et al.*, 2002; Konvicka *et al.*, 2004; Archaux, 2004). This may be the reason why altitudinal changes have been investigated in only a few studies, sometimes without clear results (Pounds *et al.*, 1999; Archaux, 2004 and references therein).

Among European birds the white stork *Ciconia ciconia* is a useful species in which to examine altitudinal shifts. It is an easily detected charismatic species, associated with human habitation, that has been subject to long-term studies during recent decades and with historical data for comparison (Janota, 1876; Wodzicki, 1933; Indyk *et al.*, 1979; Profus & Mielczarek, 1981; Schulz, 1998; and data provided in the current paper). A significant proportion of the world's breeding population inhabits Eastern and Central Europe (Schulz, 1998). In the current paper we concentrate on part of the important Polish population of white storks (25% of the world population — Jakubiec & Guziak, 1998; Schulz, 1998). In contrast to white stork populations in Western Europe, the Central European ones are stable, or even increasing, in numbers,

mainly in previously unoccupied upland areas (Wuczyński, 1997; Jakubiec & Guziak, 1998; Schulz, 1998; Ćwikowski & Profus, 2000). Previous explanations of this phenomenon have only been speculative, and anecdotal, and linked with various factors such as changes in habitat structure, food supply and climate (Wuczyński, 1997; Jakubiec & Guziak, 1998; Ćwikowski & Profus, 2000).

However, the occupation of new uphill areas can be achieved in two ways. Firstly, by the species systematically increasing its altitudinal limit; secondly by multidirectional expansion from previously optimal habitat to include higher nesting sites. The second scenario can play an important role for white stork, because this species needs at least two important elements to breed successfully: a suitable nest site and foraging habitats providing a rich food supply (Profus & Mielczarek, 1981; Schulz, 1998). At the population level, habitat (including nest) heterogeneity, coupled with an ideal despotic process of settlement, results in two predictions: (1) the percentage of low-quality territories that are occupied increases with population density; and (2) such progressive increase in use of low-quality territories causes a decline in mean per capita productivity, resulting in density-dependent reproduction which may act to regulate the population (Newton, 1998; Sergio & Newton, 2003). In support of this theory we would expect that more consistently occupied nests would be characterized by higher fledgling success.

Here we present data obtained during a long-term study conducted over a large study area. In contrast to many of the studies cited above, that focus on distributional pattern at two or three time points, we present results for both differences in historical white stork distribution in the uplands of the Tatra Mountains, southern Poland, and detailed population study results for the years 1974–2003.

STUDY AREA AND METHODS

The study area covers 950 km², and is located in the Podhale region, in the uphill Tatra Mountains. The proportions of different habitats in the study period averaged: arable fields 49%, pastures 28%, forests 14%, and 9% inhabited areas, roads, etc. (for further details, see Profus & Mielczarek, 1981; Profus & Cichocki, 2002).

Studies of white stork distribution have a long tradition in the Podhale region. The study area was first checked for white stork nests in the second half of the 19th century during a regional census in the North Carpathians (Janota, 1876). Subsequently, the distribution was checked in 1931–3 during a regional census (Wodzicki, 1933). The next census took place as part of the International Year of White Stork in 1974 (Indyk *et al.*, 1979; Profus & Mielczarek, 1981) and since then the white stork distribution and population fecundity has been studied annually (more details below).

The white stork builds nests mainly on roofs, trees and electric poles (Profus & Mielczarek, 1981; Profus & Cichocki, 2002). Large obvious nests of the white stork are associated with human settlements and it is highly unlikely that any nests were missed. The population size and fecundity of the local population were

established, for each year 1974–2003, by standard methods used during the International Census of White Stork (Profus & Mielczarek, 1981; Creutz, 1985; Schulz, 1998). All active nests in the region were found and breeding success was established by counting fledglings, including zero counts, in the nests during July. Nest positions were marked on a detailed geographical map from which altitude was recorded (to an accuracy of 10 m, measured at ground level under the nest). For analysis, nest sites were allocated to three altitude bands by divisions approximating to the lower and upper quartiles, namely: under 580 m, between 580 m and 680 m and over 680 m.

Data on land use, especially percentage of pasture (the main foraging habitat of breeding storks here — Profus & Mielczarek, 1981) were obtained from local landowner agencies in Zakopane and Nowy Targ.

Mean monthly air temperature for March and April in the period 1974–2003 was obtained from the Nowy Targ meteorological station (altitude 585 m).

Nest occupancy as a measure of the nest quality (*sensu* Sergio & Newton, 2003) was derived in two ways; as a continuous nest occupancy index (CNOI) and as the number of years when the nest was occupied over the whole study period. The CNOI indicates how many consecutive years a nest has been occupied. The first year of occupancy counts as one, the second as two and so on. A gap in the continuity of occupation resets the index to zero. For nests already occupied in 1974 (our first year) we do not know how long they had been previously occupied, so they are excluded from the analysis unless a subsequent gap year is encountered.

Throughout the text, values are reported as means \pm SE. Calculations were conducted using the *SPSS* for Windows package. All basic statistical analyses were applied according to the recommendations of Zar (1999). Multiple regression models report partial (Type III) coefficients and *P*-values.

RESULTS

Historical records

The first white stork census in southern Poland in 1876 did not record breeding in the study area which elsewhere was restricted to altitudes below 300 m (Janota, 1876). In the first three decades of the 20th century the study area was still unoccupied; the first nest was recorded in 1931, increasing to seven nests in 1933 and all were located below 650 m altitude (Wodzicki, 1933) (Fig. 1).

Recent changes in altitudes and population size

During the 30 years, 1974–2003, both the maximum and upper-quartile altitudes of nests increased significantly ($r = 0.725$, $P < 0.001$ and $r = 0.469$, $P < 0.01$, respectively). In 1974 the highest nest was at an altitude of 770 m, and the maximum reached 890 m in 1999. In the same period, the breeding population increased significantly ($r = 0.942$, $P < 0.001$) as did both the extent of pasture ($r = 0.975$, $P < 0.001$) and April temperatures ($r = 0.503$, $P < 0.01$) — Fig. 2, but not March temperatures

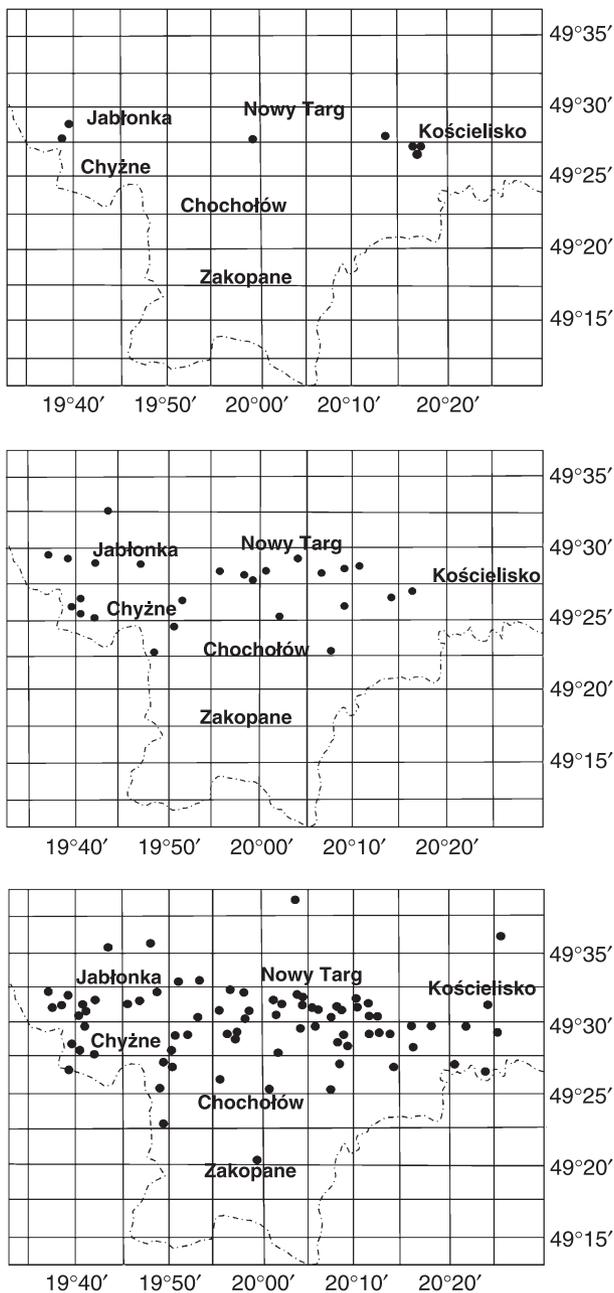


Figure 1 Examples of distribution maps of white stork in the Podhale region, in three different years (upper map 1933, middle map 1975, lower map 2002). Note that mountainous areas adjoin the national border (dotted line) and are located in the southern part of the study area.

($r = -0.104$, $P = 0.60$). The minimum and lower quartile altitudes of nests decreased significantly ($r = -0.690$, $P < 0.001$ and $r = -0.669$, $P < 0.001$, respectively) following earlier occupation of suitable lower altitude sites before uphill expansion (Fig. 2).

A multiple regression model ($F_{3,23} = 4.10$, $R^2 = 35\%$, $P = 0.018$) suggested that March temperature had a positive effect on median nest altitude ($b = 1.09 \pm 0.38$, $P = 0.009$) even after the elimination of pasture extent ($b = -0.87 \pm 0.40$, $P = 0.042$) and

population size (i.e. number of nests $b = 0.21 \pm 0.13$, $P = 0.109$).

Differences in breeding success

White stork nests located in the three altitude bands differed significantly in chick productivity ($F_{2,58} = 18.73$; $P < 0.001$, in an ANOVA based on annual means of each altitude band after removing the year effects as a factor). Storks below 580 m (1.91 ± 0.11 chicks, derived from a total of 390 nesting events over the study period) and those between 580 m and 680 m (1.99 ± 0.09 chicks, 725 nesting events) had significantly better productivity than those above 680 m (1.36 ± 0.14 chicks, 145 nesting events).

Occupancy as a measure of nest quality

ANOVA results of all 1260 fledgling numbers, eliminating year effects, confirms a significant difference in productivity between the 123 nest sites ($F_{122,1108} = 2.90$; $P < 0.001$). Taking each nest site as a basic unit there is a strong correlation between the mean CNOI and the number of years occupied ($r = 0.76$, $P < 0.001$).

Nests that were to be unoccupied in the following year fledged significantly fewer chicks (1.25 ± 0.14 , $n = 114$ nesting events) in comparison to nests which were to be occupied the following year (1.93 ± 0.04 chicks, $n = 1073$ nesting events, t -test; $t_{1185} = 4.85$; $P < 0.001$). ANOVA results after first eliminating year effects were very similar. Similarly, nests unoccupied last year fledged significantly fewer chicks (1.19 ± 0.11 , $n = 167$ nesting events) than those occupied the previous year (2.04 ± 0.03 , $n = 1073$ nesting events, t -test; $t_{1238} = 7.17$; $P < 0.001$).

White stork nests located in the three altitude bands differed significantly in their CNOI ($F_{2,908} = 12.05$; $P < 0.001$). Storks below 580 m (5.53 ± 0.26 years; $n = 309$ nesting events) and those between 580 m and 680 m (6.75 ± 0.27 years, $n = 487$ nesting events) had significantly longer continuous nest occupation than those above 680 m (4.33 ± 0.32 years, $n = 115$ nesting events). The longer occupancy of lower altitude nests was, however, insufficient to explain all of the differences in fledging numbers between altitude bands. An ANOVA examining for altitude band effects, after elimination of CNOI, was still significant ($F_{2,879} = 8.06$; $P < 0.001$).

CNOI was not a surrogate for the identification of the best nest sites. In an ANOVA of fledging number, after elimination of the effects of nest site identifier ($F_{114,767} = 2.42$; $P < 0.001$) and year ($F_{28,767} = 4.89$; $P < 0.001$), there was still a CNOI effect ($F_{1,767} = 5.70$, $b = 0.039 \pm 0.016$; $P = 0.017$) indicating that longer occupancy benefited productivity irrespective of nest site location or year.

DISCUSSION

During the last century the white stork settled in the Podhale region and during the last 30 years increased its elevational range. Why have white storks, traditionally wetland species (Creutz, 1985; Schulz, 1998), increased their altitudinal breeding range by at least 500 m in upland and mountain areas with relatively small water bodies? The drivers are likely to be complex.

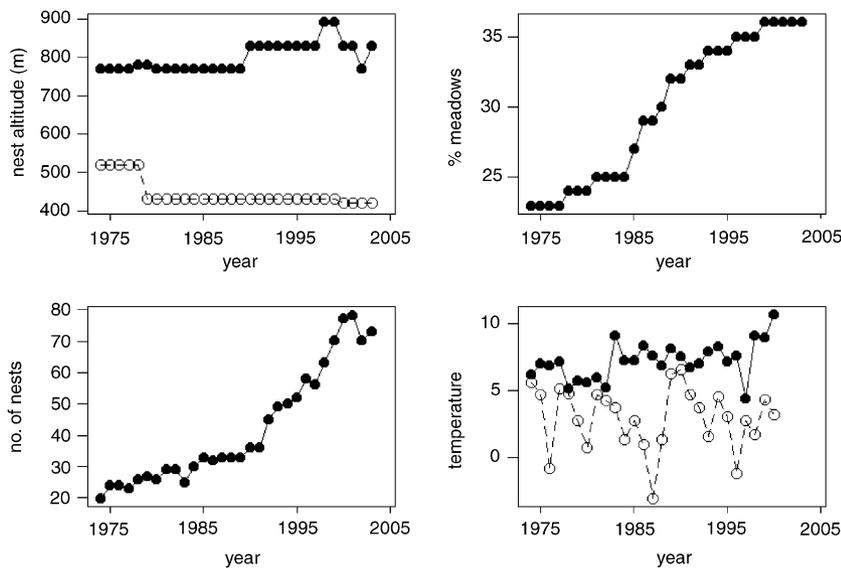


Figure 2 Changes in a, maximum (solid symbol) and minimum (open symbol) nest altitude; b, number of nesting pairs; c, percentage of pasture in the surrounding area; and d, March (open symbol) and April (solid symbol) mean temperature.

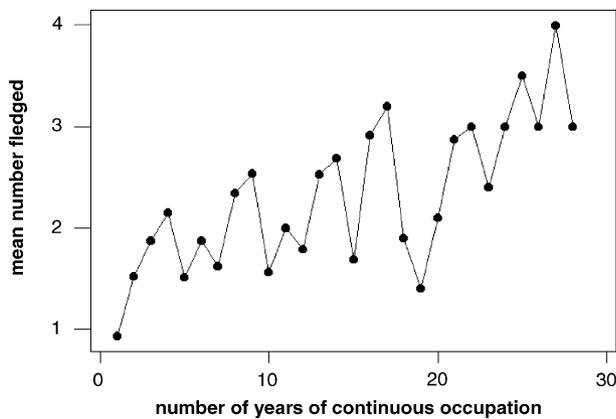


Figure 3 The relationship between the number of years of continuous occupation of the nests and their mean productivity over the study period.

Firstly, because the species has the biological potential to colonize mountain areas, and in other part of their geographical range breeds in environments up to 2500 m in Morocco, to 1350 m in Europe (Sierra de Gredos, Spain) and even c. 1000 m on the Slovakian side of the Tatra Mountains (Creutz, 1985; Schulz, 1998); and secondly, because storks appear to follow habitat and/or climate changes. During the study period in the Podhale region a lot of arable fields were abandoned and/or changed to pasture following the collapse of communism. This, together with climatological factors (changes in temperatures and runoff), created new habitat and offered new foraging opportunities for storks (see also Carrascal *et al.*, 1993). An increase in voles *Microtus arvalis* has been shown to be influenced by habitat and climatological factors which in turn influenced white stork numbers and productivity (Profus & Mielczarek, 1981; Tryjanowski & Kuźniak, 2002). Additionally, it is well known that the spatial distribution of the white stork is dependent on temperature (Carrascal *et al.*, 1993). Hence, when climatological conditions were

good, and after saturation of lower altitude nest sites, white storks expanded to higher ground, and occupied new areas.

In this paper we present a further example of an animal species that is affected by changes in habitat and climate (see also Pounds *et al.*, 1999; Warren *et al.*, 2001; Hill *et al.*, 2002; Konvicka *et al.*, 2004; Peñuelas & Boada, 2003). Previous analysis with the white stork, albeit in lowland areas, showed that they had responded to a warming climate by earlier spring migration (Ptaszyk *et al.*, 2003), as well as by improved breeding success (Ptaszyk *et al.*, 2003; Tryjanowski *et al.*, 2004). We show that a warming climate has been associated with an uphill shift in its nesting behaviour despite such sites being currently suboptimal, i.e. located in higher elevations (see Results).

Previously reported changes have been mainly based on a comparison on two time points, such as those based on atlas data sources at large scale (e.g. Konvicka *et al.*, 2004) or by repeated studies (Peñuelas & Boada, 2003; Archaux, 2004). Such approaches will not be as sensitive to detect changes (see also Davis *et al.*, 1998). In contrast to the majority of previous studies, we used a 30-year annual series based on individual nest locations that gave an improved analysis and the option to directly compare change to climatic data. We propose the following scenario of how the white storks occupied new habitats (and altitudes) in Podhale region. Firstly, storks occupied good habitats located in median altitudes of the study area where long-term occupied and more productive nests were located. After successful breeding events here white stork colonized new areas, both at lower and higher altitudes. However, higher-located sites were colonized only in very favourable climatic conditions.

Moreover, our results confirm the importance of prioritizing conservation of high quality (mainly old) nests. Occupancy may be a reliable method of quality assessment, especially for populations in which not all territories are always occupied, as in white stork populations (cf. Sergio & Newton, 2003).

To conclude, we document evidence of, and a potential mechanism for, the white stork ascending to higher elevations and that

the altitudinal shifts previously found for butterflies, plants and whole biomes (Grabherr *et al.*, 1994; Pounds *et al.*, 1999; Grace *et al.*, 2002; Hill *et al.*, 2002; Konvicka *et al.*, 2004; Peñuelas & Boada, 2003) can be detected in birds as well.

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