BREEDING PERFORMANCE OF THE MIDDLE SPOTTED WOODPECKER *DENDROCOPOS MEDIUS* IN RELATION TO WEATHER AND TERRITORY QUALITY

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Reproductive success in birds is influenced by a variety of factors, many of which can be attributed to human activities such as land use or forest management. Others like weather or age of the birds are not under human control but are influential as well. From 1992-96, I examined breeding phenology and performance of Middle Spotted Woodpeckers *Dendrocopos medius* in northeastern Switzerland in relation to weather, territory quality and age of the birds. Timing of breeding, length of the nestling period as well as nesting and breeding success significantly differed between years. On average, incubation started earlier in years with higher daily temperatures in March-April. Neither territory quality nor the participation of 1-year old individuals in pairs influenced breeding success, whereas low temperatures and high amounts of rainfall during the nestling phase negatively affected breeding performance, which probably reflects the difficulties encountered by the woodpeckers in provisioning their young with sufficient food during periods of bad weather. These findings suggest that weather events can strongly influence reproduction even of primary cavity-nesting species, exceeding presumed differences in habitat quality at a local scale.

Key words: *Dendrocopos medius* - breeding biology - reproductive success - habitat quality – weather - radio-tracking - oak forest - *Picidae*.

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INTRODUCTION

Management decisions in favour of threatened or desired species are often based on density estimates. These are believed to reflect habitat quality, although the assumed positive correlation between population density and habitat quality does not necessarily exist (Van Horne 1983; Kellner *et al.* 1992). Reproductive performance, along with other demographic parameters, has been suggested as a superior estimator of habitat quality. Moreover, information on reproductive success is particularly important, for example to estimate population viability (e.g. Haig *et al.* 1993), or to investigate processes of extinction (e.g. Pettersson 1985). Reproductive success in birds is influenced by a variety of factors, which differ widely among species (Newton 1989). In the context of species conservation, questions pertaining to the relation between reproductive success and territory quality are of particular interest, because quality is often defined by specific habitat structures (e.g. Conway & Martin 1993), which might be affected by management decisions. However, it is also important to identify factors that are not under human control, but that might influence reproductive success such as the age of the breeding birds (Saether 1990) or weather conditions during the breeding period (Wiktander *et al.* 1994). Therefore, reproductive performance along with factors affecting it must be known, both to take appropriate conservation measures and to assess their suitability.

In this paper, I present data on annual and seasonal patterns of the breeding cycle as well as on nesting and breeding success of the Middle Spotted Woodpecker *Dendrocopos medius* in northeastern Switzerland. I also evaluate the effects of weather, age and territory quality as some potentially influential factors of breeding performance. The results suggest that weather events can have a dramatic influence on breeding success, even overriding presumed differences in habitat quality. This is particularly striking, as this study was carried out on a primary cavity nesting species, which would be assumed to be less affected by weather and/or predation than open nesting species due to protection offered by cavities (Martin & Li 1992).

METHODS

The Middle Spotted Woodpecker is a medium-sized (59 g), non-migratory species mainly inhabiting mature oak forests (Winkler *et al.* 1995). The social system is characterized by seasonal social and genetic monogamy (Michalek 1998) and territoriality in spring (Pasinelli 1999). One clutch is normally produced per year, although replacement clutches have been observed in some cases (e.g. Pasinelli 1993). Food consists during the whole year of bark-living arthropods (Glutz von Blotzheim & Bauer 1980), whereas the young are primarily fed with caterpillars gathered from the foliage (Török 1990). A new cavity is excavated each year, with the male taking the larger share (Michalek 1998; own obs.). The species has declined in many parts of its range (Mikusinski & Angelstam 1997) as a consequence of habitat destruction due to intensive timber harvesting.

From 1992-96, breeding biology was studied in the northeastern part of the Swiss lowlands. Twenty-eight nests were monitored in the study area Niderholz (47°37'N, 8°37'E; 120 ha, 380 m a.s.l.), which is part of an 800 ha forest, situated 35 km north of Zürich near the river Rhine. The study area consists of an oak-hornbeam forest managed for centuries as coppice-with-standards ('Mittelwald'), a forestry practice that results in a two-layered forest with large trees forming the canopy and small trees below the canopy. In the Niderholz, the canopy is dominated by oak *Quercus sp.*, with occasional Scots Pine *Pinus sylvestris*, Norway Spruce *Picea abies* and Norway Maple *Acer platanoides*, whereas the dominant tree species below the canopy are Hornbeam *Carpinus betulus* and lime *Tilia sp.* Additional data were gathered in forests close to Bülach (four nests) and Kreuzlingen (three nests) in 1995 and 1996, respectively. These study areas essentially consist of mature deciduous forest fragments within large mixed forests (> 500 ha). In the Bülach study area (47°32'N, 8°32'E; 440 m a.s.l.), the fragments are remnants of the formerly widespread oak high forests which have declined since the early 19th century (Bürgi 1997). The dominant tree species are oak, Beech *Fagus sylvatica*, and Hornbeam, whereas Larch *Larix decidua*, Scots Pine, Norway Spruce, birch *Betula sp.* and poplar *Populus sp.* occur less frequently. Fragments in the Kreuzlingen study area (47°36'N, 9°12'E; 510 m a.s.l.) still show the characteristic structure of past coppice-with-standards management practice. Main tree species are oak, Ash *Fraxinus excelsior* and Great Maple *Acer pseudoplatanus*, intermixed with some Larch, Scots Pine, Norway Spruce and Black Alder *Alnus glutinosa*. As the reproductive parameters examined differed neither between the study areas Niderholz and Bülach in 1995 nor between Niderholz and Kreuzlingen in 1996 (Mann-Whitney *U*- and Fisher's exact tests, $P > 0.05$ in each case), I pooled the data of 1995 and 1996, respectively, across study areas for subsequent analyses.

As a part of a larger study on the Middle Spotted Woodpecker's ecology (Pasinelli 1999), individuals were caught with mist nets either at feeders (one per 12 ha, not refilled after trapping), by attracting them with a playback tape and a stuffed woodpecker, or at their roosting cavities. Each bird was classified as 1-year old when it possessed unmoulted brownish-black greater wing coverts or as adult (≥ 2-year old) when it had only black coverts (Glutz von Blotzheim & Bauer 1980). All individuals were marked with colour rings and then fitted with a small radio transmitter (1.5 - 2.0 g, c. 3.5% of the bird's body mass), which was glued onto the base of the two central tail feathers using a cyanoacrylate glue.

Of 35 nests found by following the radio-equipped birds, twelve could be reached with a 12 m ladder, whereas the others were either higher up or in rotten stems, making inspection too dangerous for observers and carrying the risk of destroying the cavity tree. I counted the numbers of eggs and nestlings at an age of 4 - 6 d, respectively, in seven of the twelve accessible nests, and the number of nestlings at an age of 16 - 19 d in all twelve nests using a dentist mirror and a lamp. The young present in the cavity during the latter inspection were assumed to survive to fledging, and their number was therefore taken as breeding success. At the 23 inaccessible nests, breeding progress was deduced from daily observations with a telescope. Incubation start was defined as the day, when the pair-partners took turns in performing nest duties and remained invisible in the cavity until the next turn. I defined hatching date as the day when the first feeding was observed (cf. Pettersson 1984) and nestling period as the time between hatching and the day the last young had left the cavity. When the fledging day approached - easily told from the changes in the begging calls of the young - nests were observed daily for several hours to determine the number of young leaving the cavity, which then was considered as breeding success. If neither begging calls of nestlings nor feeding by parents were observed for three more hours after a nestling's leaving the cavity, all young were assumed to have fledged, which usually occurred within a day (own obs.). There was no significant difference in breeding success between nests inspected with the ladder and those where the young were counted when leaving the cavity (unpaired t-test $t_{33} = 0.99$, $P > 0.32$). Therefore, the two data sets were pooled for further analysis.

Territory quality was defined on the basis of two variables, which have been shown to influence home range size of the Middle Spotted Woodpecker (Pasinelli 2000). The first one is the density of large oaks (≥ 36 cm diameter at breast height, *dbh*) and relates to food supply within a home range; the second variable is the density of potential cavity trees (having either old cavities, limb holes or polyporous fungi), describing the availability of suitable nest sites within the home range. Some large oaks were also potential cavity trees (see Pasinelli 2000), but other tree species such as Ash or birch can account for up to 68% of all the potential cavity trees in an area (own unpubl. data). These habitat data had been sampled on circular plots of 0.03 ha, located at the intersections of an 150 x 80 m grid. Based on the plots within a home range (= 95% convex polygon), I calculated an average value for each variable with RANGES V (Kenward & Hodder 1996).

Data on weather conditions during the study period were obtained from the SMI-MeteoSwiss of lowland stations located at approximately the same altitude in the immediate vicinity of my study forests. I examined the influence of weather on breeding performance using the means of both the daily temperature means and the amount of rain during March/April and the nestling period, respectively. For between-year comparisons, the latter was defined as the time between the median hatching and fledging date of a year. For 1993, median incubation start and hatching date were determined by calculating back from the median of three fledging dates using the grand medians of incubation and nestling period length of the other years, respectively. Because incubation and nestling period length calculated in this way for 1993 do not represent real values, 1993 was excluded from all analyses dealing with the lengths of incubation and nestling periods of individual broods.

RESULTS

Timing of breeding

Over all years, the beginning of incubation ranged from 27 April to 11 May. The median

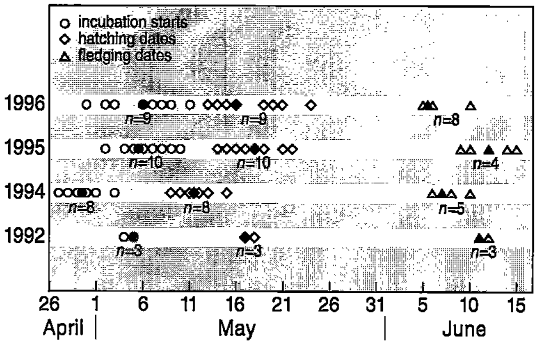

Fig.1. Breeding phenology of the Middle Spotted Woodpecker. Medians are shown as filled symbols, n = number of pairs.

dates of the incubation start differed significantly between years (Kruskal-Wallis test, H_3 = 14.0, P < 0.003; Fig.1). These differences were linked to the temperatures in early spring, which is suggested by a strong negative correlation between the mean temperature in March/April and the median incubation start (Spearman rank correlation, r_s = -0.98, n = 5, P < 0.005; Table 1).

The number of days within which the observed pairs had initiated incubation in a year varied between 7 (1994) and 12 (1996). Incubation length did not differ between years (Kruskal-Wallis test, H_3 = 4.2, P > 0.24): the medians were thirteen days in 1992 and twelve days in the other years (range: 10 - 13).

The durations of the nestling period varied considerably (Fig. 1) and the annual medians were significantly different (Kruskal-Wallis test, H_3 = 15.8, P < 0.002). The shortest nestling period was recorded in 1996 with a median of 22 d (n = 8), whereas the corresponding values were 24 d in 1995 (n = 4), 25 d in 1992 (n = 3) and 26 d in 1994 (n = 5). Average length of the nestling period in a year was neither related to the mean temperature nor to the mean amount of rain in that period.

Nesting and breeding success

Clutch size of seven nests averaged 6.4 eggs (range: 5 - 8); mean hatching success (= number of hatchlings per laid egg) was 71% (range 63 - 83%) and mean fledging success (= number of fledglings per laid egg) 40% (0 - 83%).

74.3% of the 35 nests were successful (i.e. fledged at least 1 young). In 1995, nest success was only 40% and significantly lower than in the other years combined (Fisher's exact test, P < 0.008; Fig. 2). This might have been due to the low temperatures during the nestling phase, which is suggested by a positive relation between the average temperature during that phase and nesting success (r_s = 0.95, n = 5, P < 0.015, Table 1). Overall, 82 young fledged from the 35 nests, resulting in a breeding success of 2.3 young per pair. Excluding the unsuccessful nests, mean breeding success of 26 pairs was 3.2.

There were significant differences in breeding

Table 1. Weather conditions, incubation start and nesting success from 1992-96. n = number of nests. Nestling period: time between the median hatching and fledging date of a year.

Year	Ø temperature (°C)		Ø rain (mm)	median date	nesting	n
	March/April	nestling period	nestling period	incubation start	success (%)	
1992	7.1	16.0	2.02	5 May	100.0	3
1993	7.8	17.1	3.55	4 May*	100.0	4
1994	8.5	14.5	7.53	29 April	87.5	8
1995	6.3	12.9	5.32	5 May	40.0	10
1996	6.0	14.5	3.13	6 May	80.0	10

*calculated back from fledging dates (see Methods)

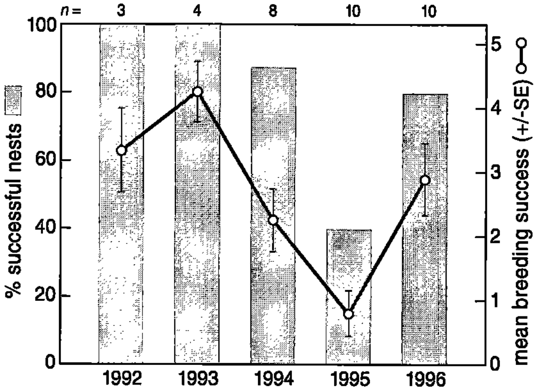

Fig.2. Nesting and breeding success of the Middle Spotted Woodpecker from 1992-96 (n = number of nests).

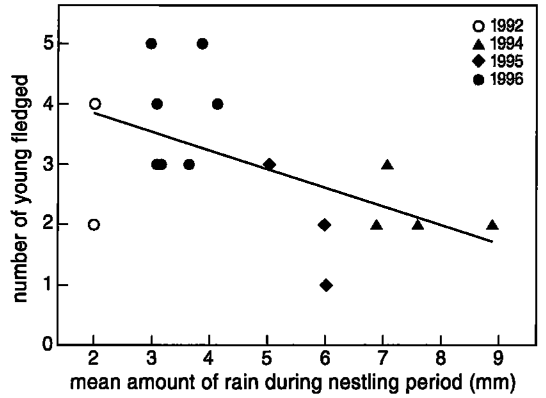

Fig.3. Relation between breeding success and mean rainfall (mm) during the nestling period (n = 16).

success between years both on the basis of all nests (1-way-*ANOVA*, $F_{4,30}$ = 5.61, P < 0.002; Fig.2) and when considering only successful nests ($F_{4,21}$ = 3.28, P < 0.04). Post-hoc pairwise comparisons between all years revealed that for all nests breeding success was lower in 1995 than both in 1993 (Tukey's *HSD*, P < 0.003) and in 1996 (P < 0.02); after excluding the unsuccessful nests, only the 1995/1993 difference remained significant (Tukey's *HSD*, P < 0.05).

Ecological reasons for differences in breeding success between individuals were examined with a backward stepwise multiple regression analysis (Table 2). In the resulting model just one of the four independent variables (mean amount of rain during the nestling period) had a significant effect ($F_{1,14}$ = 6.36, P < 0.024), but it explained only 31% of the variation in breeding success. Mean amount of rain during the nestling period correlated negatively with breeding success (Fig. 3), whereas none of the two variables used to describe territory quality, i.e. the density of large oaks and the density of potential cavity trees, turned out to be useful predictors.

Breeding performance in relation to age

Age effects were investigated by comparing pairs with at least one individual being 1-year old with pairs consisting only of 2-year old or older birds. To account for differences between years, I standardized incubation start, length of incubation and nestling period as well as breeding success by using the deviations from the annual averages (medians or means). I found no significant differ-

Table 2. Results of a backward stepwise multiple regression analysis with breeding success as the dependent variable and Ø temperature (°C) and Ø amount of rain (mm) during the nestling period as well as the densities of large oaks and potential cavity trees as independent variables.

Variable	Regr. Coeff.	SE	Std. Coeff.	T	P<
Ø rain	-0.305	0.121	-0.559	-2.522	0.024
Constant	4.442	0.623	-	7.129	0.001

Model: $F_{1,14}$ = 6.359, P < 0.024, SE = 0.991, R^2 = 0.31, R^2_{adj} = 0.26, n = 16[1].

[1]Each individual used only once.

ences between pairs with and without 1-year old birds, neither regarding date of incubation start (Mann-Whitney *U*-test, $U = 7.5$, $P > 0.49$, $n_1 = 7$, $n_2 = 3$), duration of incubation ($U = 6.0$, $P > 0.3$, $n_1 = 7$, $n_2 = 3$), length of the nestling period ($U = 4.0$, $P > 0.5$, $n_1 = 6$, $n_2 = 2$), successful nesting attempts (Fisher's exact test, 1-tailed, $P > 0.68$, $n = 12$) nor breeding success (unpaired *t*-test $t_{10} = -0.61$, $P > 0.55$). Thus, a 1-year old bird does not seem to be disadvantageous to a pair's breeding performance.

Nest failures

At least eight of the nine nests that failed to produce fledglings must have contained nestlings because feedings were observed. The young of two nests perished within the first ten nestling days, and those of two other nests during the week prior to fledging. Three of the nine unsuccessful nests were raided by predators: in two cases, the entrance hole was enlarged, casting suspicion on larger woodpecker species, whereas in the third, feathers with characteristic bite signs of a mammalian predator were found at the base of the cavity tree. Interestingly, these three losses happened in the week before fledging in 1995, which was a year with low temperatures during the nestling stage (Table 1). Finally, one nest was destroyed during a storm that caused the limb with the nest to break at the position of the cavity. In two pairs, replacement broods were observed, of which one was successful (Pasinelli 1993).

DISCUSSION

Timing of breeding

The breeding season of the Middle Spotted Woodpecker in northeastern Switzerland is highly synchronized both within and between years. All woodpeckers initiated incubation within 15 d, with 80% of the pairs starting in the last four days of April and the first week of May. In birds of highly seasonal environments, the general timing of the reproductive period is under photoperiodic control (Immelmann 1971). On a smaller time scale, numerous studies have been conducted to identify those factors that fine-tune the onset of breeding both within and between seasons (e.g. Blondel *et al.* 1990). In the present study, incubation started on average earlier in years with warmer early spring weather. Similar relations between weather conditions in early spring, measured either as temperature-sum or average, and the beginning of egg-laying have been reported for different inhabitants of temperate zone forests such as tits *Parus* spp. (Schmidt 1984; Nager & Van Noordwijk 1995; Wesolowski 1998), Eurasian Nuthatches *Sitta europaea* (Matthysen 1989; Enoksson 1993), or woodpeckers *Dendrocopos* spp. (Wiktander *et al.* 1994; Hogstad & Stenberg 1997). Since spring temperatures regulate vegetation development in temperate latitudes (Schmidt 1969; Nizinski & Saugier 1988; Buse *et al.* 1999), the relation between weather conditions and the annual onset of breeding is probably only of indirect nature, reflecting the birds' use of some environmental features as proximate cues to initiate laying. Middle Spotted Woodpeckers primarily feed their young caterpillars gathered from the foliage (Török 1990), and since the emergence of caterpillars depends on the leaf bud burst (Van Balen 1973; Buse *et al.* 1999), it is very likely that vegetational cues govern egg-laying in this species. Alternatively, food availability in spring might be a causal factor determining the timing of breeding (Daan *et al.* 1988), either by serving as a (further) proximate cue or by influencing female body condition in a time of high energetic needs due to egg production. Presumably, there are several interacting factors accounting for the variation in the onset of reproduction between years, and the importance of each factor might differ among species. Ultimatively, the Middle Spotted Woodpecker's timing of breeding is probably adapted to synchronize the period of highest food demand of the nestlings to the peak of caterpillar abundance, as suggested by studies on tits (Van Balen 1973; Zhandt *et al.* 1990; Perrins 1991; Nager & Van Noordwijk 1995; Naef-Daenzer & Keller 1999).

Factors affecting breeding performance

Breeding performance of the Middle Spotted Woodpecker seems to be primarily affected by weather conditions during the nestling phase. Particularly, mean temperature and mean amount of rain during that period were significantly related to nesting and to breeding success, respectively, with warm and dry weather being advantageous. Most likely, these correlations reflect the varying food supply during breeding time, because activity and growth of caterpillars is positively influenced by temperature (Liebhold & Elkinton 1988; Stamp & Bowers 1994; Fischbacher *et al.* 1998). Therefore, parents might not find enough food in periods of cold and humid weather, so that the young either starve to death or are more susceptible to parasites because of poor body condition or to predators.

Pairs with 1-year old birds were not less successful than pairs with only 2-year or older individuals. Wiktander (1998) showed that old pairs of the Lesser Spotted Woodpecker, i.e. consisting of birds breeding together for consecutive years, had a higher breeding performance than newly established pairs, mainly by starting egg-laying earlier and by rearing more fledglings. Since I did not have enough data to determine the reproductive success of such old, experienced pairs, an effect of age on breeding performance cannot completely be ruled out.

Territory quality has been shown to be one of the influencing factors of reproductive success in birds (e.g. Stacey & Ligon 1987; Catchpole & Phillips 1992). Yet, it is not always clear how to quantify territory quality. For woodpeckers, measures such as the availability of cavity trees (Walters 1990) or the densities of dead stems and deciduous trees have been considered (Carlson 1998). The Middle Spotted Woodpecker shows high population densities in mature oak forests with many old oaks (e.g. Müller 1982; Schmitz 1993), which are by far the most preferred foraging trees (Pettersson 1983; Pasinelli & Hegelbach 1997) and hence, the density of such oaks has been proposed as a measure of habitat quality. Furthermore, Pasinelli (2000) has found an inverse relationship between home range size of this woodpecker and the densities of large oaks (≥ 36 cm *dbh*) and of potential cavity trees. However, there was no relation between these two measures and breeding success of the Middle Spotted Woodpecker in the present study. This somewhat unexpected result suggests that either the considered variables do not adequately represent territory quality or that differences in territory quality do not translate into breeding success. Since the birds obviously adjust their home range size to the available resources (Pasinelli 2000), differences in habitat quality may already be compensated. Nevertheless, breeding pairs of the Middle Spotted Woodpecker are, with few exceptions (see: Günther & Hellmann 1997), only found in mature deciduous forests rich in oaks (Winkler *et al.* 1995), and therefore, habitat quality does govern the breeding performance of the species, be it not on a small scale, but rather on the landscape level.

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SAMENVATTING

Broedsucces is een belangrijke component voor de *fitness*, en dieren zijn voortdurend doende dit te optimaliseren. Omdat broedsucces zo belangrijk is, zijn ook terreinbeheerders hierin geïnteresseerd: de kwaliteit van een (broed)terrein wordt vaak afgemeten aan het broedsucces van zijn bewoners. Toch hebben vogels, in welk terrein dan ook, niet alles in de hand. Uiteraard is de eerste keuze die een vogel die wil gaan broeden moet maken de terreinkeus. Kiest de vogel een voor de soort totaal ongeschikt terrein, dan zal het broedsucces nul zijn: dergelijke terreinen worden dan ook zelden gekozen. Echter, ook binnen 'optimale' broedgebieden hoeft het broedsucces niet altijd optimaal te zijn. Dit wordt namelijk ook beïnvloed door factoren die niet door de terreinbeheerder of de vogel zelf kunnen worden bepaald. Deze studie toont aan, dat zelfs vogels die in boomholtes broeden, dus vrij van directe weersinvloeden, nog wel degelijk te leiden kunnen hebben van slecht weer, met als gevolg een verlaagd broedsucces. De relatie met het weer is natuurlijk overduidelijk aanwezig bij soorten van zeer open terreinen zoals sterns, maar een groot weerseffect op een soort als de Middelste Bonte Specht *Dendrocopus medius* ligt misschien minder voor de hand. De auteurs volgden van 1992 tot 1996 35 paren broedvogels in oude Zwitserse bossen. De vogels hakken ieder jaar een nieuw hol uit, zijn elkaar in de regel ten minste gedurende het broedseizoen trouw en produceren één legsel. Het broedsucces bleek tussen jaren te verschillen, maar dit hing niet samen met de kwaliteit van het territorium, gemeten aan het aantal grote eiken en het aantal potentiële nestbomen (veel meer soorten komen in aanmerking) binnen dit territorium. Ook hing het broedsucces niet duidelijk samen met de leeftijd van de vogels, dat wil zeggen de aanwezigheid van een eenjarige vogel binnen een paar had geen invloed. Wel was er een duidelijke invloed van het weer. Een warm voorjaar leidde tot vroege legsels; lage temperaturen en veel regen in de jongenfase leidde tot een verminderd succes, vermoedelijk als gevolg van problemen voor de ouders bij het voedsel zoeken. Deze resultaten laten zien dat zelfs voor een zeer beschut broedende vogelsoort, een optimaal territorium in een optimaal habitat, geen garantie biedt op succes. (MFL)

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