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Nest survival of Great Tit *Parus major* in spatial and temporal gradient

Preživetje gnezd velike sinice *Parus major* v prostorskem in časovnem gradientu

Dejan Bordjan and Davorin Tome*

National Institute of Biology, Večna pot 111, 1000, Ljubjana, Slovenia.
*correspondence: davorin.tome@nib.si

Abstract: The aim of the study was to compare nest survival of Great Tit between different regions, altitudes and years to discern which has the highest influence. Temperature is known to be prominent for breeding parameters and it changes consistently with altitude. Our hypothesis was that altitude has greater influence on nest survival than the region and year. Breeding parameters were monitored with the use of nest-boxes over a three year period at three altitude belts in two regions. The main factor influencing nesting success was modelled using daily survival rate in the program MARK. We gathered data from 104 first nesting attempts of which 26 failed. Although nest failure increased with altitude this was significant only for one region. There was significant difference in nest failure between the regions but not between the years. Modelling showed higher support in data for regions than for altitudes and years thus rejecting the hypothesis. Some possible reasons for such results are discussed.

Keywords: Great Tit, nest survival, altitude, Slovenia

Izvleček: Namen raziskave je bil primerjati preživetje gnezd velike sinice med različnimi regijami, nadmorskimi višinami in leti ter tako ugotoviti, kateri dejavnik ima največji vpliv. Temperatura ima velik vpliv na gnezditvene parametre in se spreminja konsistentno z nadmorsko višino, zato je postavljena hipoteza, da ima nadmorska višina večji vpliv kot leto in lokacija. Gnezditveni parametri so bili z uporabo gnezdilnic spremljani v treh letih, na treh nadmorskih višinah in dveh lokacijah. Poglavitni dejavnik, ki vpliva na preživetje gnezd, je bil zmodeliran s pomočjo programa MARK. Skupaj je bilo spremljanih 104 prvih gnezd velikih sinic med katerimi jih je 26 propadlo. Čeprav je število propadlih gnezd naraščalo z nadmorsko višino, je bilo to statistično značilno samo na eni lokaciji. Je pa bila statistično značilna razlika v številu propadlih gnezd med obema regijama, ne pa tudi med posameznimi leti. Modeliranje je izkazalo večjo podporo podatkov regijam kot letom in nadmorski višini in tako zavrnilo postavljeno hipotezo. V diskusiji je omenjenih nekaj možnih razlogov za dobljene rezultate .

Ključne besede: Velika sinica, preživetje gnezd, nadmorska višina, Slovenija

Introduction

Nest survival is influenced by many factors such as breeding density (Verhulst 1995 Newton 1998), habitat (Riddington and Gosler 2008), food availability (Newton 1979), predation (Wesołowski 2002), parasites (Eeva et al. 1994), weather (Bionda and Brambilla 2012) and competition for resources (Högstedt 1980, Prokop 2004). It may also depend on nest site (Neal et al. 1993, McCleery et al. 1996, Naef-Daenzer et al. 2001, Strusis-Timmer 2009). Cavity nesting reduces, but does not exclude, threats from predators and weather (Kluijver 1951). In most studies of breeding failure in hole-nesting species, predation was found to be the most important factor (McCleery et al. 1996, Julliard et al. 1997, Naef-Daenzer et al. 2001, Wesołowski 2002), while weather was considered as less important (Kluijver 1951, Wesolowski et al. 2002, Radford and du Plessis 2003).

Great Tit is one of the most studied hole-nesting bird species (Bednekoff et al. 1994, Noordwijk et al. 1995, Cresswell and McCleery 2003, Nussey et al. 2005, Tanner et al. 2008, Eeva et al. 2009). It utilizes variety of habitats, natural or manmade (Gosler and Wilson 1997). It can breed from sea level up to the tree line (Schmid et al. 1998) and from tropics to the edge of tundra (Quader 1995). In Europe Great Tit is one of the birds most associated with studies on the influence of temperature change on breeding (Slagsvold 1976, Sather et al. 2003, Visser et al. 2006, 2009a, 2009b). While there have been some studies considering change of breeding parameters with latitude and across several years (Kluijver 1951, Slagsvold 1976, Sasvári and Orell 1992, Sanz et al. 2000, Sather et al. 2003, Silverin et al. 2008, Visser et al. 2009a) and also considering constraints they are facing at the northern limit of their distribution (Veistola et al. 1995, Rytkönen and Krams 2003), there were only few studies considering change in breeding parameters across elevation. They consider breeding distribution, species richness or altitudinal range of species (Klosius 2008). A few of them consider influence of altitude on breeding parameters (Slagsvold 1976, Krementz and Handford 1984, Belda et al. 1998, Sanz 1998), while none report about the influence on nest survival.

Our aim was to compare nest survival between Great Tits from different altitudes. To put the results into the perspective, we compared them with results of nest survival in different regions and in different years, to found out which of the three variables is more important. Since temperature is known to influence breeding parameters prominently (Neal et al. 1993, Visser et al. 2009b) and since it changes consistently with altitude (Begon et al. 1996) our hypothesis is that the altitude has greater influence on nest survival than does region or year.

Materials and Methods

Data were gathered at two sites in two different regions (Fig. 1) in central and in north-eastern Slovenia from 2010 to 2012. The first site, Mt. Krim (45°55'N, 14°28'E), is an 1107 m high mountain covered with extensive forest dominated by Beech *Fagus sylvatica*, White Fir *Abies alba* and Norway Spruce *Picea abies*. Three separate altitudinal belts 300-400, 600-750 and 900-1150 m a.s.l. were selected at this site. The second site, Mt. Pohorje (46°30'N, 15°34'E), is a 1543 m high mountain dominated by Beech and locally by Norway Spruce and White Fir. Again three altitudinal belts with same altitudinal ranges were selected. Mt. Krim has in general about 30% more rain than Mt. Pohorje and similar temperature (Tab. 1). Bedrock on Mt. Krim is consisted mainly from limestone and on Mt. Pohorje mainly from silicate rocks (Perko and Orožen Adamič 1998).

Great Tit breeding data were collected using 112 nest-boxes with dimensions 23x15x16cm and with an entrance-hole of 32mm. Nest-boxes made from wood-concrete material were placed in a line more than 50 m apart. On Mt. Krim 48 nest-boxes (16 at each altitudinal belt) were installed in 2009 and additional 16 (8 on each of the upper two altitudinal belts) in 2010. In 2010 48 (16 at each altitudinal belt) nest-boxes were installed on Mt. Pohorje. Nest-boxes were checked about once a week from mid-March to the end of June regardless whether they were empty, occupied or deserted in previous inspection. During each visit, occupancy of the nest-boxes was noted and the number of eggs / nestlings counted. To minimize the impact of human inspections nest-boxes were

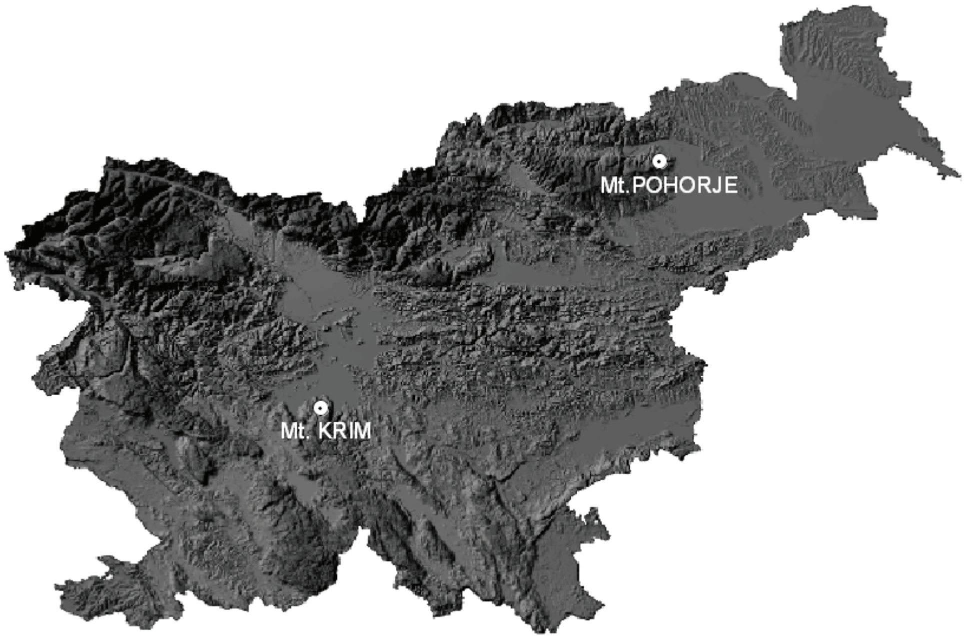

Figure 1: Location of study sites in Slovenia.
Slika 1: Lokaciji obeh raziskovanih območij v Sloveniji

checked quickly on dry, warm days only (Kania 1989, Keller and van Noordwijk 1994). Only the first nesting attempts in any year were used in the analysis of sources of variation in nest survival. We regarded as failed all nests where at least one egg was laid, but breeding did not end with any successfully fledged chicks.

Data on cumulative monthly rainfall for April and May (main breeding period for Great Tits in Slovenia; unpublished data) from 2010 to 2012 was obtained from the nearest meteorological station (within radius of 10 km from the study site) operated by the Environmental Agency of the Republic of Slovenia (for Mt. Krim: Pokojišče and Črna vas; for Mt. Pohorje: Maribor-Tezno). Temperatures were measured using temperature loggers (LogTag Trix-8 Temperature recorder, accuracy ±0.5°C) on both study sites on all altitudinal belts. From four daily measurements (at noon and then every six hours) average temperature was calculated for both regions.

Table 1: The average amount of rain and the average ambient temperatures in April and May 2010–2012 at two study regions.
Tabela 1: Povprečna količina dežja in povprečna temperatura okolja v Aprilu in Maju obdobja 2010–2012 na dveh lokacijah.

	Mt. Pohorje	**Mt. Krim**
Precipitation (mm)	151	233
Temperature (^{o}C)	11.3	11.1

The program MARK was used to model the daily survival rate and to estimate true nest survival (equivalent for nest success) of the Great Tit nests (White and Burnham 1999, Rotella et al. 2004). The program is sensitive to date of nest failure – nests failed at the beginning of the breeding cycle reduce nest survival rate more than nests failed at the end of breeding cycle although none of them produced offspring at the end. Due to weekly nest inspections, nest failure was established with an accuracy of 7 days. Seven models (all possible additive combinations) were carried out from three sources of variance: 1) Region (R), 2) Altitude (A) and 3) Year (Y). Akaike weights (w_i) were used to select the model with the best support in the data, to find out which of the three variables influence nest failure more.

Chi square test was used for comparison of proportion of failed nests among altitudes, regions and years.

Results

Altogether 104 first nesting attempts of Great Tits were monitored, of which 26 failed (25%). Among years, regions and altitudes the percentage of failed nests was highest in 2010, on Mt. Krim and on upper belt (Tab. 2), but the difference was significant only for regions and for altitudes on Mt. Pohorje (Chi square; Region: $\chi^2_1 = 4.04$, $P < 0.05$; Year $_{Mt.Krim}$: $\chi^2_2 = 3.04$, $P = 0.22$; Year $_{Mt.Pohorje}$: $\chi^2_2 = 3.63$, $P = 0.16$; Altitude $_{Mt.Krim}$: $\chi^2_2 = 2.21$, $P = 0.33$; Altitude $_{Mt.Pohorje}$: $\chi^2_2 = 4.04$, $P < 0.05$).

Assuming constant survival for the Great Tit the daily nest survival was 0.989 and an estimated true nest survival rate was 0.706. Model with Region (R) as a source of variance had more support in the data than models with altitude (A) and year (Y) (Table 3). Also when considering all models that included any source of data, region had again more support (75.7%) than altitude (35.4%) and year (32.2%). Thus among the three sources of variance region seems to explain more variance in nest survival than the other two.

Table 2: Percentage of failed nests on different altitudes, years and in regions, with the number of nests in parenthesis.
Tabela 2: Delež propadlih gnezd po različnih nadmorskih višinah, letih in na lokacijah s prikazanim številom gnezd v oklepaju.

	Year	**Upper (%)**	**Middle (%)**	**Lower (%)**	**Total (%)**
	2010	/	20 (5)	55 (11)	44 (16)
Mt. Krim	2011	0 (1)	33 (9)	8 (12)	18 (22)
	2012	75 (4)	22 (9)	31 (16)	34 (29)
	All	60 (5)	26 (23)	31 (39)	31 (67)
	2010	100 (1)	50 (2)	0 (4)	29 (7)
Mt. Pohorje	2011	/	33 (6)	9 (11)	18 (17)
	2012	0 (1)	0 (2)	0 (10)	0 (13)
	All	50 (2)	30 (10)	4 (25)	14 (37)
Total		57 (7)	27 (33)	20 (64)	25 (104)

Table 3: The model selection for Great Tit *Parus major* nest survival. Models in bold with ΔAIC ≤ 2 have the greatest support in data (Burnham and Anderson 2002).
Tabela 3: Izbor modelov uspešnosti gnezd velike sinice *Parus major*. Poudarjeni modeli imajo ΔAIC ≤ 2 in imajo največjo podporo v podatkih (Burnham in Anderson 2002).

Model	**K**	**AICc**	**ΔAIC**	**Model likelihood**	**wi**	**w1/wj**
S(.R)	**2**	**173.6690**	**0.0000**	**1.0000**	**0.35294**	**1.00**
S(.R+A)	**3**	**175.1394**	**1.4704**	**0.4794**	**0.16920**	**2.09**
S(.R+Y)	**4**	**175.3752**	**1.7062**	**0.4261**	**0.15039**	**2.35**
S(.)	1	176.3623	2.6933	0.2601	0.09180	3.84
S(.R+A+Y)	5	176.5387	2.8697	0.2381	0.08405	4.20
S(.A)	2	177.0899	3.4209	0.1808	0.06381	5.53
S(.Y)	3	177.5583	3.8893	0.1430	0.05048	6.99
S(.A+Y)	4	178.1627	4.4937	0.1057	0.03732	9.46

R = region, A =altitude, Y = year, S. = basic model

Discussion

We confirmed significant influence of altitude on nest failure of Great Tit nest only in one of the two studied regions. While in both regions percentage of failed nests, increased with altitude, with greatest percentage just on the upper altitude (Table 2). Both indicate that altitude may influence nest success but this may be true only locally or it may be obscured by some other factors. Later is supported by significantly different proportion of failed nests between regions and our modelling results. These show that the effect of altitude was less important compared to the effect of region (Table 3), thus rejecting proposed hypothesis. Overall habitat on both regions are similar, with similar human presence factor (Perko and Orožen Adamič 1998) and ambient temperature (Table 1), but differs in number and density of some predator / competitor species (Kryštufek 1991, Mihelič et al. 2000, unpublished data), which could influence different predation or abandonment rate, in bedrock (Perko and Orožen Adamič 1998), which could influence reproduction through different calcium availability (Tilgar et al. 2002) and in rainfall (Table 1).

Predation is the most important reason for nest failure in birds (Wesolowski et al. 2002). Although there are no known predators specialised on Great Tits on either locality, some influence of bird and mammal predator generalists could be expected over apparent competition (Holt 1977). Apparent competitors (i.e. small mammals) can fluctuate greatly between years (Kryštufek and Flajšman 2007) and can support high population of predators which can increase predation pressure on alternative prey in years of low dominant prey population (Schmidt et al. 2008, Sotenšek 2012). But if this would be the case, we would expect year models to support the data better. Rather they have the lowest support in data of all three parameters.

We also argue that the storage of calcium in the bedrock is less likely the candidate for different proportion of failed nests between two regions, since other breeding parameters, such as breeding density and clutch size were virtually the same among them. Average percentage of all occupied nest-boxes on Mt. Pohorje was 31.3% and 31.7% on Mt. Krim, with average clutch size in both regions being 8.9.

Rain and temperature fluctuate through the season and both can have high influence on breeding success of open nesters (McDonald et al. 2004, Fairhurst and Bechard 2005, Denac 2006, Bionda and Brambilla 2012). Although it generally has lower effect on hole nesters (Wesolowski et al. 2002), in the absence of predation it is still the most important external cause of nest failure (Kluijver 1951, Wesolowski et al. 2002). The cause of weather related failure is a trade-off in energy allocation between incubation / brooding and feeding in adult birds. Bad weather increases on-bout time (Keller and van Noordwijk 1994, Radford et al. 2001), but also increases energetic expenditure, which can almost double during cold spells (Haftorn and Reinertsen 1985). Prey is also less visible or accessible in bad weather conditions, which also prolongs feeding time (Keller and van Noordwijk 1994, Pasinelli 2001, Avery and Krebs 2008). Assumption that the rainfall, compared to the temperature, is more important cause of nest failure on breeding success of the Great Tits is supported by the fact that region in our study had greater influence than altitude and that there is about 30% more rain on Mt. Krim than on Mt. Pohorje, while at the same time the difference in average temperature between regions is minimal. So although altitude indeed had some influence on survival of Great Tit nests, probably indirectly through the availability of food, region can have even greater when sites lie in regions with markedly different precipitation regimes.

Povzetek

Razmere v okolju so povezane z geografskimi danostmi območij in tako določajo razširjenost in gnezditvene parametre ptic. Pri veliki sinici je bilo narejenih nekaj raziskav o razlikah v gnezditvenih parametrih po geografski širini in med različnimi leti, zelo malo pa je bilo narejenega na področju vpliva nadmorske višine. Namen raziskave je bil primerjati delež preživetja gnezd velike sinice med lokacijami, nadmorskimi višinami in leti ter ugotoviti, kateri od teh dejavnikov ima večji vpliv. Temperatura ima velik vpliv na gnezdenje ptic, zato smo postavili hipotezo, da ima nadmorska višina večji vpliv na preživetje gnezd kot regija ali pa leto. Podatki o gnezdenju so bili s pomočjo 112

gnezdilnic na treh višinskih pasovih zbrani na dveh lokacijah, Krim in Pohorje, med leti 2010 in 2012. S programom MARK je bila izračunana dnevna stopnja preživetja gnezd in izdelanih sedem modelov (vse aditivne kombinacije parametrov lokacija, nadmorska višina in leto). Šest vrst ptic je skupaj zasedlo 49.5% gnezdilnic. Od 104 prvih legel velike sinice jih je 26 propadlo. Največ jih je propadlo v letu 2010, na Krimu in na zgornji višini, vendar je bila razlika statistično značilna samo pri razlikah med lokacijami in med nadmorskimi višinami na Pohorju. Dnevno preživetje gnezd je bilo 0.989, gnezditveni uspeh pa 0.706. Na obeh lokacijah je delež propadlih gnezd naraščal z višino z največjim deležem na zgornji višini, kar kaže, da nadmorska višina verjetno ima vpliv na preživetje gnezd. Predpostavljamo, da vpliv deluje posredno preko razlik v temperaturi, ki se med višinami značilno razlikujejo. Po drugi strani rezultati modela kažejo, da je bil vpliv nadmorske višine manj pomemben od vpliva lokacije, s čimer je bila postavljena hipoteza zavrnjena. Ocenjujemo, da razlika med lokacijama verjetno ni bila posledica možnih razlik v sestavi plenilcev in kompetitiorjev, ki bi lahko vplivali na propad gnezd, niti v razliki količine plena, temveč v količini padavin. Krim je v času raziskave prejel okoli 30% več padavin kakor Pohorje.

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