Rain may have more Influence than Temperature on Nest Abandonment in the Great Tit Parus major

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Rain may have more influence than temperature on nest abandonment in the Great Tit *Parus major*

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The main aim of this study was to investigate which weather parameter has greater influence on nest abandonment in the Great Tit Parus major, temperature or rain, and to determine during which breeding period nests are the most susceptible to abandonment. Breeding parameters of a nest-box population in Slovenia were monitored over a three year period at two locations in three altitude belts. Weather parameters were measured daily. From 160 first nesting attempts, 35 nests were abandoned. The majority of abandoned nests were found during the incubation period, followed by the first half of the nestling period. The amount of rainfall was more important than temperature in explaining variation in nest abandonment.

Key words: Great Tit, nest survival, rain, temperature, Slovenia

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Weather is a key factor influencing breeding success in birds (Sasvári & Orell 1992, Pasinelli 2001, Jian-Bin *et al.* 2006, Visser *et al.* 2009b). In most cases, low temperatures and high rainfall cause breeding conditions to deteriorate, having an adverse effect on breeding performance of both open-nesting (Rodríguez & Bustamante 2003, McDonald *et al.* 2004, Fairhurst & Bechard 2005, Bionda & Brambilla 2012) and hole-nesting species (Neal *et al.* 1993, Pasinelli 2001, Wesołowski *et al.* 2002, Radford & du Plessis 2003, Andreu & Barba 2006). Under such unfavourable conditions, birds breed later and in lower numbers, lay smaller clutches, increase incubation bout length and have lower breeding success (Kluijver 1951, Kostrzewa 1989, Conway & Martin 2000, Pasinelli 2001, Gladalski *et al.* 2014).

In cavity-nesting birds, threats from predators and effects of adverse weather may be reduced, but are not eliminated. Most studies on hole-nesting species found that predation was the most important cause of breeding failure (Kluijver 1951, McCleery *et al.* 1996, Julliard *et al.* 1997, Naef-Daenzer *et al.* 2001, Wesołowski 2002, Yamaguchi & Higuchi 2005), while low temperatures and strong rain were less important (Kluijver 1951, Wesołowski *et al.* 2002, Radford & du Plessis 2003). Perhaps as a consequence, although bad weather has been suggested to influence the breeding performance of cavity nesters (Neal *et al.* 1993, Nilsson 1994, Pasinelli 2001, Andreu & Barba 2006), it has rarely been quantified or studied in much detail (Radford & du Plessis 2003).

The Great Tit is one of the most common bird species in Europe, using a variety of habitats (Hagemeier & Blair 1997). It nests in cavities and readily occupies nest-boxes (Perrins 1965), making it ideal for ecological studies (Nussey *et al.* 2005, Tanner *et al.* 2008, Eeva *et al.* 2009), as well as for studies on the impact of climate change (Saether *et al.* 2003, Both *et al.* 2004, Visser *et al.* 2006, 2009a). Temperature is an important factor in determining the breeding performance of Great Tits (Greño *et al.* 2008, van Noordwijk *et al.* 1995, Visser *et al.* 1998, 2006). Low temperatures increase energetic demands (Haftorn & Reinertsen 1985, Mertens 1987, Bryan & Bryant 1999), reduce the availability of invertebrate prey (Tinbergen & Dietz 1994, Avery & Krebs 2008), and – as a consequence – birds delay the start of egg-laying and lay eggs of smaller size (Haftorn & Reinertsen 1985, Pendlebury & Bryant 2005, Ahola 2008, Gladalski *et al.* 2014). The influence of temperature on nest abandonment has not been studied so far. The amount of rainfall is less often considered as a factor that impacts the breeding performance of Great Tits (Keller & van Noordwijk 1994, Radford *et al.* 2001), perhaps also because its effect is difficult to separate from the effect of low temperature – they tend to covary.

The aims of our study were (1) to explore the influence of temperature and rain on the probability of nest abandonment in Great Tits, and (2) to investigate when during the breeding period active nests are most susceptible to desertion by the parents.

METHODS

To separate the influence of temperature from the influence of precipitation, data were collected at two study sites that differ in the amount of rainfall but not in temperature, and at different altitudes within each site that differ in temperature but not rainfall.

The first site, Mt. Krim (45°55'N, 14°28'E), is a 1107 m high mountain in central Slovenia covered with extensive forest dominated by Beech *Fagus sylvatica*, White spruce *Abies alba* and Norway spruce *Picea abies*. The second site, Mt. Pohorje (46°30'N, 15°34'E), is a 1543 m high mountain in north-eastern Slovenia located more than 100 km from Mt. Krim and dominated by Beech and locally by Norway and White spruce. Long-term data show that Mt. Krim, with its surrounding area, has about 30% more rain than Mt. Pohorje but similar temperatures. The necessary temperature gradient for the study was achieved by selecting localities on three different altitudes within both sites. The lowest altitude belt was between 300–400 m, the middle one between 600–720 m and the upper one between 940 and 1140 m a.s.l.

Great Tit breeding data were collected during 2010 to 2012 using 149 nest boxes with dimensions 23 × 15 × 16 cm and with an entrance-hole of 32 mm in diameter. In each locality nest boxes, made from wood-concrete material to increase protection from predators, were placed about 50 m apart. On Mt. Krim 16 nest boxes per altitude belt were placed in November 2008. An additional 53 boxes were put up in early February 2010 (8 at upper, 16 at middle, 29 at lower altitude). On Mt. Pohorje 16 nest boxes per altitude belt were put up in early February 2010. Altogether, there were 40 nest boxes in the upper, 48 in the middle and 61 in the lower altitude belt.

To minimize the influence of human disturbance, all nest boxes were checked once a week, from mid-March to the end of June, before 15:00, on dry, warm days (Kania 1989, Keller & van Noordwijk 1994). During each visit, nest status (box empty, nesting material present, nest finished but no eggs, number of eggs/nestlings), and bird species were noted. Just before fledging, young birds were marked with standard aluminium rings. Nest material from deserted nests was not removed from boxes until September. Based on the number of eggs and the size of the chicks, the start of incubation was estimated for most of the nests, with an accuracy of ±1 day (Bordjan 2013).

For each active nest, we defined four periods: the egg-laying period, the incubation period, the early nestling period (nestlings ≤7 days old) and the late nestling period (nestlings >7 days old). During the early nestling period, offspring are kept warm by the brooding female, while during the late nestling period their ability to thermoregulate has improved and they can survive longer periods without brooding (Kluijver 1951).

Deserted nests were assigned to the period of failure as follows: if less than 6 cold eggs were in the clutch and the number had not increased at the next visit, we assigned the failure to the egg-laying period. If a clutch of cold eggs was found in a previously incubated nest, failure was assigned to the incubation period. If all chicks were dead and intact, failure was assigned to the first or second half of the nestling period, depending on the size of the nestlings. Depredated nests were excluded from analyses, although we cannot exclude the possibility that they were abandoned earlier. Only first nesting attempts in each year were used in the analysis of sources of variation in nest survival.

We monitored temperature at both sites and at all altitude belts by installing one temperature logger per eight nest boxes (LogTag Trix–8 Temperature Recorder, accuracy ±0.5°C). Loggers were placed about 3 m above the ground on a tree and secured from the air humidity, rain and direct sun. They were programmed to measure air temperature in six-hour intervals starting at six in the morning. The mean daily temperature used in analyses was the average of all four measurements. For analysis, nests were assigned temperature data from the nearest logger.

Data on daily rainfall were obtained from weather stations operated by the Environmental Agency of the Republic of Slovenia (ARSO). We used data from three stations near Mt. Krim (Zelimlje 309 m a.s.l., 8 km to the E; Pokojisce 715 m a.s.l., 4 km to the W; Hrusica pri Colu 872 m a.s.l., 23 km to the SW) and from three stations near Mt. Pohorje (Tezno 275 m a.s.l., 3 km to the E; Ribnica na Pohorju 600 m a.s.l., 20 km to the W; Sv Duh na Ostrem Vrhu 870 m a.s.l., 12 km to the NW). The program MARK was used to model daily survival rate of Great Tit nests and to test the influence of different variables on nest desertion (White & Burnham 1999, Rotella *et al.* 2004). Daily nest survival was calculated according to Mayfield (1961, 1975).

To explore which variables predict the occurrence of nest desertion best, thirty-one models (all possible combinations) were run based on five sources of variance: (1) location (L), (2) altitude (A), (3) year (Y), (4) amount of rain (R) and (5) average temperature (T). The first three variables were used because, besides temperature and precipitation, they include other factors that are site, altitude and/or year specific (e.g. predation, food availability, period of snow cover). Including them allowed us to check whether some other unmeasured variables influence nest abandonment more than weather variables. Because only one nest failed in the late nestling period it was omitted from modelling. Because each nest experienced unique environmental conditions during each period, we treated periods as independent replicates. Thus, each successful nest contributes three replicates to the model, while an unsuccessful nest contributes zero to two successful events and one unsuccessful event, depending on the period when it failed. Because nest survival varies through the breeding period (Kluijver 1951), we used a model with a variable daily survival rate (S_{NA}) as our basic model. AICc was used to select the model with the best support given the data.

RESULTS

Weather conditions

Temperature and rain during April and May varied between years, between sites and between altitudes (Table 1). Mt. Krim received about 25% more rain than Mt. Pohorje, while differences in ambient temperature between both locations were minimal. At both locations, 2011 was the warmest year, and 2012 the rainiest. However, if only the incubation and early brood periods are considered, 2010 was the rainiest year (2010: 67.2 mm, 2011: 28.2 mm, 2012: 49.6 mm, combined data for both locations). Temperature decreased steadily with increasing altitude on both sites, from about 13°C down to 9°C. So, as predicted, study sites differed in the amount of precipitation, while the altitude belts differed in temperature.

Nest survival

Altogether 160 first nesting attempts of Great Tits were monitored, of which 40 failed. Of those, 35 showed clear signs of abandonment. The number of abandoned nests varied significantly with the nesting period ($\chi^2 = 16.6$, $df = 3$ $P < 0.01$). Three nests failed during egg-laying, 24 during incubation, seven during the early nestling period and only one during the late nestling period. From those that failed during incubation, eleven failed during the second half of incubation (for the others we could not determine the timing of failure more precisely). This pattern was reflected in daily nest survival calculations: it was highest in the late nestling period (0.9998), followed by the early nestling period (0.9977) and egg-laying periods (0.9952). The lowest daily nest survival was calculated for the incubation period (0.9904). Estimated nest survival rate over the entire breeding period was 0.82.

The percentage of abandoned nests on Mt. Krim was almost double compared to that on Mt. Pohorje (Table 1), but the ratio between sites differed from period to period. The difference was significant when

Table 1. The average, minimum and maximum temperatures, and the amount of rain during the breeding period (April and May), and the percentage of abandoned nests of Great Tits at two study sites in Slovenia. Data are shown separately for each year and for each altitude belt (see Methods). *n* refers to the total number of active nests.

	Mt. Pohorje					Mt. Krim				
	Temperature (°C)			Amount of Rain	Abandoned nests	Temperature (°C)			Amount of Rain	Abandoned nests
	Average	Min	Max	(mm)	% (*n*)	Average	Min	Max	(mm)	% (*n*)
2010	10.7	–0.4	19.7	156.7	28.5 (7)	10.1	–0.5	20.5	283.6	36.4 (33)
2011	12.1	2.0	19.9	156.3	17.6 (17)	12.1	2.2	20.0	158.8	17.5 (40)
2012	11.3	–1.8	22.5	196.3	0.0 (13)	10.8	–2.1	20.0	312.4	22.0 (50)
Low	13.2	3.5	22.5	142.8	4.0 (25)	12.4	2.3	20.5	227.2	25.0 (84)
Middle	11.8	1.0	21.4	204.2	30.0 (10)	11.2	0.8	19.3	209.4	17.6 (34)
Upper	9.2	–1.8	19.4	195.1	50.0 (2)	9.4	–2.1	18.9	287.1	60.0 (5)
All	11.4	–1.8	22.5	180.7	13.5 (37)	11.0	–2.1	20.5	241.2	24.4 (123)

comparing results from the incubation period (χ^2 = 5.9, *df* = 1 *P* = 0.01), when there was also significantly more rain on Mt. Krim than on Mt. Pohorje (Kruskal–Wallis: *H* = 28.7, *P* < 0.001). During the early nestling period the proportion of abandoned nests or amount of rain between sites were similar (abandoned nests: χ^2 = 3.38, *df* = 1, *P* > 0.05; amount of rain: Kruskal–Wallis: *H* = 2.52, *P* < 0.05).

Of all models the one that only included rain had the highest support, but was only slightly better than the model which also included temperature (Table 2). Six models had a ΔAICc < 2 and can be considered equally competitive (Burnham & Anderson 2002). However, the sum of Akaike Weights for models including rain was 0.97, compared to 0.42 for models including temperature, resulting in an evidence ratio of 2.3 in favour of rain as the most important variable. Comparable sums of Akaike Weights for models that included location (0.33), altitude (0.38) or year (0.23) were small, indicating low support.

DISCUSSION

The results of our nest survival model suggests that rain has a greater influence on nest abandonment in Great Tits than temperature. A strong influence of rain on nest survival has already been established for open-nesters (Rodríguez & Bustamante 2003, Fairhurst & Bechard 2005, Bionda & Brambilla 2012), while for hole-nesters it has been suggested, but not studied in detail (Kluijver 1951, Nilsson 1994, Wesołowski *et al.* 2002, Radford & du Plessis 2003).

In spite of lower support for temperature as a possible trigger for nest abandonment, anecdotal evidence suggests that unusual low temperatures can also cause desertion; three out of seven nests (two from upper and one from middle belt) that failed during the early nestling period did so during a sudden cold spell in 2012 when the temperature at higher altitudes fell below 2°C and at middle altitudes to 5°C with only little rain. A possible influence of temperature can also be suspected from the data in Table 1: the proportion of abandoned nests increased with altitude, although this was not significant. The other variables in the exploratory model (location, altitude and year) did not explain much of the variation in nest survival, suggesting that there were no other important unmeasured factors besides rain and temperature.

With respect to rain, one can ask whether extreme events (short heavy showers) are more likely to cause nest abandonment compared to longer periods of moderate rain. Because we monitored nest abandonment only at weekly intervals, we cannot directly relate

Table 2. Model selection for Great Tit nest survival in relation to location, altitude, year, rain and temperature during the respective nesting period. Models in bold with ΔAIC ≤ 2 have the greatest support (Burnham & Anderson 2002). Only models with Akaike Weights (w_i) higher than 0.01 are shown.

Model[1]	*K*	AICc	ΔAIC	Model Likelihood	w_i	w_i/w_j
$S_{NA.R}$	**3**	**232.688**	**0.000**	**1.000**	**0.1858**	**1.00**
$S_{NA.R+T}$	**4**	**233.261**	**0.574**	**0.751**	**0.1395**	**1.33**
$S_{NA.A+R}$	**4**	**233.587**	**0.899**	**0.638**	**0.1185**	**1.57**
$S_{NA.L+R}$	**4**	**234.219**	**1.532**	**0.465**	**0.0864**	**2.15**
$S_{NA.L+R+T}$	**5**	**234.612**	**1.924**	**0.382**	**0.0710**	**2.62**
$S_{NA.A+R+T}$	**5**	**234.679**	**1.991**	**0.370**	**0.0687**	**2.71**
$S_{NA.L+A+R}$	5	235.098	2.410	0.300	0.0557	3.34
$S_{NA.Y+R}$	5	235.450	2.763	0.251	0.0467	3.98
$S_{NA.Y+R+T}$	6	235.803	3.115	0.211	0.0392	4.75
$S_{NA.A+Y+R}$	6	235.808	3.120	0.210	0.0391	4.76
$S_{NA.L+A+R+T}$	6	236.041	3.354	0.187	0.0347	5.35
$S_{NA.A+Y+R+T}$	7	236.989	4.301	0.116	0.0216	8.59
$S_{NA.L+Y+R}$	6	237.027	4.340	0.114	0.0212	8.76
$S_{NA.L+Y+R+T}$	7	237.128	4.440	0.109	0.0202	9.21
$S_{NA.L+A+Y+R}$	7	237.295	4.608	0.100	0.0186	10.01
$S_{NA.L+A+Y+R+T}$	8	238.300	5.612	0.060	0.0112	16.55

[1]L = location, A =altitude, Y = year, R = rain, T = temperature, NA = nest age

the weather just preceding nest abandonment to the event. However, the only nest abandonment during the late nestling period occurred immediately after a severe rain event (>40 mm of rain in one day; the rainiest day during the whole study) and two other nests in earlier stages were also abandoned during the same nest check. Nevertheless, there is indirect evidence that long periods of moderate rain could be more influential than short, intense showers, as explained below.

Why does rain lead to nest abandonment? In hole-nesters, nest soaking is known to cause nest losses (Wesołowski *et al.* 2002). However, our nest boxes were placed in ways that minimised this effect, and in the few nest boxes where we detected nest soaking the broods were successfully raised until fledging. It seems more likely that the cause of weather-related failure is related to the trade-off in females between incubation or brooding and feeding themselves. To prevent cooling of the eggs or chicks during periods of bad weather, birds increase the time they spend on the nest (Keller & van Noordwijk 1994, Radford *et al.* 2001). At the same time, bad weather increases demands for food (Haftorn & Reinertsen 1985, Mertens 1987, Bryan & Bryant 1999), which in rainy periods is less available because it is less visible or accessible (Tinbergen & Dietz 1994). This may force birds to spend more time off-nest feeding (Keller & van Noordwijk 1994, Pasinelli 2001, Avery & Krebs 2008), to the point where, in case of prolonged periods of rain, the female might be forced to abandon reproduction to increase her chances of survival. For that reason, periods of short, intense rain can probably be more easily overcome without leaving the nest, assuming the cavity is protected from soaking.

From the limited available data there is no indication that younger females were more likely to abandon their nest than older ones, or that unsuccessful birds avoided nesting in the same area in successive attempts. The percentage of young females that survived to breed again was similar between abandoned (61% of 18 cases) and successful nests (70% of 33 cases) and the percentage of marked females found re-nesting in the same or subsequent breeding seasons was similar between abandoned (28% of 18 cases) and successful nests (31% of 74 cases). The latter data also suggest that nest failure was probably not caused by the female parent being predated.

Overall, about 20% of the Great Tit pairs in our study abandoned their first nesting attempt in a given season (range: between 0–36% depending on year and location). Most abandonment (69% of 35 cases) occurred during incubation. For all 11 cases where we have the information, the nest was deserted in the second half of the incubation period, suggesting that this might be the most critical period of breeding with respect to nest abandonment. The next most critical period (20% of cases) was when the young were less than 8 days old, confirming Kluijver's (1951) observation that nest abandonment becomes less likely as the offspring get older.

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SAMENVATTING

In dit onderzoek werd bekeken (1) wat het effect van temperatuur en regenval was op het in de steek laten van het nest door Koolmezen *Parus major* en (2) in welke fase de nesten het grootste risico liepen om te worden verlaten. Gedurende drie jaar werden op twee locaties en drie verschillende hoogtes in Slovenië verschillend broedparameters van nestkastpopulaties gemeten. Weersvariabelen werden dagelijks gemeten. Van 160 eerste broedpogingen werden er 35 nesten verlaten. Het merendeel van deze nesten werd in de broedfase en, zij het in mindere mate, in de eerste helft van de jongenfase verlaten. De hoeveelheid neerslag was een belangrijkere factor voor het verklaren van nestverlating dan lage temperaturen. (PW)

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