

## Context-dependent effects of radio transmitter attachment on a small passerine

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Biotelemetry devices provide unprecedented insights into the spatial behaviour and ecology of many animals. Quantifying the potential effects of attaching such devices to animals is essential, but certain effects may appear only in specific or particularly stressful contexts. Here we analyse the effects of radio transmitter attachment on great tits *Parus major* tagged over three environmentally dissimilar years, as part of a project studying social- and communication networks. When we radio-tagged birds before breeding, only those tagged in the coldest spring tended to be less likely to breed than control birds. Breeding probability was independent of relative transmitter weight (between 5 and 8% bodyweight). When we radio-tagged both parents during nestling provisioning (transmitter weight between 6 and 8%), tagged parents were more likely than control parents to desert their brood in two out of three years, while in the other year no tagged parents deserted. Tagged parents provisioning larger broods were most likely to desert, especially during lower average temperatures. Video analyses did not reveal any transmitter effects on provisioning behaviour of parents in the year with no desertion. We conclude that radio tagging before breeding did not lead to negative effects, regardless of transmitter weight, but that decisions about radio-tagging both parents during nestling provisioning need to be made with exceptional care, taking both environmental context and transmitter weight into account. Reporting results from long-term radio-tracking studies comprising several environmentally variable years is crucial to understand and predict potential transmitter effects and maximise the tremendous potential of biotelemetry.

Biotelemetry and biologging studies can provide evidence-based insights into animal behaviour and physiology that are particularly important for understanding wildlife spatial behaviour and planning conservation measures (Sutherland et al. 2004, Wilson and McMahon 2006, Cooke 2008). Recent innovations in biotelemetry and biologging provide us with increasingly accurate methods to remotely assess the behaviour and spatial ecology of many animal species (Rutz and Hays 2009, Hays 2015, Kays et al. 2015, Wilson et al. 2015a), generating valuable information on local movements, social proximity and large-scale animal dispersal and migration (Bensch and Hasselquist 1992, Naef-Daenzer 1994, Neudorf and Pitcher 1997, Amrhein et al. 2004, Rhodes et al. 2006, Roth et al. 2009, van Overveld and Matthysen 2010, Taylor et al. 2011, Jachowski et al. 2013, Dechmann et al. 2014, Pendoley et al. 2014, Snijders et al. 2014). Furthermore, knowledge of proximity networks within populations, assessed with biotelemetry devices, can provide insights into the risks of disease transmission (Bull et al. 2012, Weber et al. 2013), and the use of heart rate sensors (Laske et al. 2011) and accelerometers (Payne et al. 2015) can track changes in stress and

energy expenditure of wild animals experienced as a result of (human) disturbances (Wilson et al. 2015a).

However, transmitter attachment itself can also influence energy investment, behaviour, reproduction, and/or survival (Barron et al. 2010), potentially leading to imprecise conclusions about natural behaviour (Wilson and McMahon 2006, McMahon et al. 2007, Cooke 2008, Jewell 2013). An animal's ability to compensate for potentially negative effects of tagging is likely to be physiologically constrained (Ricklefs and Wikelski 2002), but these constraints may only become apparent when individuals are pushed to their limits by environmental circumstances (Saraux et al. 2011, Wilson et al. 2015b). For example, negative transmitter-induced effects on the foraging behavior in Magellanic penguins *Spheniscus magellanicus* were only clearly apparent in years of low food abundance (Wilson et al. 2015b). The reproductive stage an animal is in during the tagging procedure can also be a critical factor (Pietz et al. 1993, Barron et al. 2010). Transmitter attachment during reproduction regularly goes together with an already present increased level of energy expenditure, which could push individuals over their limits, making a potential transmitter-induced increase in

energy-expenditure more clearly identifiable. This context-dependence provides an extra challenge for the identification and understanding of transmitter effects.

To minimise potential transmitter effects, a common approach is to limit transmitter weights to a certain percentage of the subject's body weight (Naef-Daenzer et al. 2001). A limit of 5% has become a rule-of-thumb for radio-tracking (Kenward 2001), although thresholds of 3% (Gustafson et al. 1997) and 10% (Amelon et al. 2009) have also been suggested. However, how relative transmitter weight relates to the effects of transmitter attachment remains unclear. Several studies have reported negative effects when using devices below 5% body weight (Ackerman et al. 2004, Barron et al. 2010, Barron et al. 2013), while others have reported no negative effects when using devices above 5% body weight (Pennycuik et al. 1989, Neudorf and Pitcher 1997, Cvikel et al. 2015).

Approximately 50% of bat telemetry studies (O'Mara et al. 2014) and 10% of avian telemetry studies (Barron et al. 2010) have used transmitters of 5–10% body weight, and although some studies found effects of increasing transmitter weight on flight performance (Aldridge and Brigham 1988, Zenzal Jr et al. 2014), a large-scale meta-analysis of avian telemetry studies revealed that negative effects did not increase with proportionally heavier devices (up to 10% of body-weight), although in 90% of the reviewed studies the devices were below 5% body weight (Barron et al. 2010). Unfortunately, less than 11% of studies using radio-transmitters report tests of potential transmitter effects (Godfrey and Bryant 2003), presumably because no data about tag effects were available. Yet, such data, where they exist, are highly valuable for refining guidelines for acceptable practice in biotelemetry studies (Dougill et al. 2000, Plous and Herzog 2001, Godfrey and Bryant 2003, Wilson and McMahon 2006, Barron et al. 2010, Hill and Elphick 2011).

Small passerines are especially sensitive to sudden changes in energy expenditure, with both body mass and the environment being important predictors of how much additional energy a bird can spend (McNab 2015). In this study, we investigated the effects of transmitter attachment on a small passerine, the great tit *Parus major*, both before breeding and during breeding in three environmentally distinct years. The data we present herein were gathered incidentally to two behavioural studies using biotelemetry: one investigating the proximity networks of great tits before breeding (Snijders et al. 2014, 2017), and the other investigating their social foraging behaviour during nestling provisioning (unpubl.). Great tits are an ideal species for quantifying such transmitter effects since the reproduction and provisioning behaviour of comparable untagged birds can also be accurately monitored, facilitating identification of transmitter induced effects. For example, a recent study showed no negative long-term effects for male great tits fitted with ca 5% backpacks during nestling provisioning (Atema et al. 2016).

Using procedural controls, we analysed the effects of transmitter attachment on the likelihood of breeding, the likelihood of brood desertion, and on nestling provisioning behaviour. We expected any possible effects to be context-dependent, thus to vary between the years of transmitter deployment, and to be related to factors influencing the energy expenditure of the birds (Obrecht et al. 1988, Gessaman et al. 1991, Godfrey et al. 2003, Barron et al.

2010). Before breeding, such factors are likely to include specific environmental conditions (McNab 2015) such as average temperature, rainfall, or hours of sunshine. General body condition, the transmitter weight relative to body size, and a bird's experience with being tagged could also influence how much energy these birds have available to spend on energy intensive activities such as breeding. Energy expenditure in great tits has been shown to increase with increasing body mass and decreasing temperatures (Tinbergen and Dietz 1994). During breeding, additional factors such as the brood size (Boyce and Perrins 1987) and the age of the chicks might influence the ability of birds to adjust to having a transmitter attached.

## Methods

### Study population

This study was conducted in 2012, 2013, and 2014 in Westerheide, a long-term fully monitored nest box population of great tits near Arnhem, the Netherlands (52°01'00"N, 5°50'20"E). Westerheide is a mixed wood forest of about 120 ha containing approximately 200 nest boxes. As part of a standardized procedure, we conducted nocturnal roost checks in autumn and winter. Un-ringed individuals were fitted with a uniquely numbered aluminium leg ring and taken to the nearby Netherlands Inst. of Ecology (NIOO-KNAW, < 20 km) for a maximum of 24 h. Here they were subjected to a novel environment test to quantify exploration behaviour, an established personality trait in great tits (see Dingemanse et al. 2002 for details). During the breeding season, we checked nest boxes twice a week and recorded laying date, clutch size, start of incubation, number of hatchlings, and number of fledglings (see van Oers et al. 2008 for details). To identify and tag breeding birds, we caught the parents inside their nest boxes with spring traps on approximately the 8th (2012) or 10th day (2013–2014) post-hatching. Nestlings were ringed and measured (body mass and tarsus length) on day 14 post-hatching.

### Radio transmitters and tagging procedure

Our radio transmitter devices were digital EncounterNet devices (Mennill et al. 2012, Snijders et al. 2014, 2017), which were manufactured as light as possible while still providing automatic simultaneous tracking of multiple individuals (Supplementary material Appendix 1, Fig. A1). In total, we conducted six tracking sessions over three years. In each year, we tracked birds 1) before breeding, in March or April (social network study), and 2) during nestling provisioning, in May or June (social foraging study). For birds tracked before breeding, we analysed the likelihood of breeding, while for the birds tracked during nestling provisioning, we analysed the likelihood of desertion and potential transmitter effects on provisioning behaviour. Table 1 provides an overview of the technical details for each of the six transmitter-deployments.

Over the course of the study, due to battery life problems associated with the lighter devices, transmitters with two different batteries were used: one type powered by a zinc-air

Table 1. Overview of transmitter characteristics for each deployment.

		Tagged before breeding	Tagged during nestling provisioning
2012	Absolute transmitter weight	1.03 g	1.29 g
	Relative transmitter weight mean (range)	5.6% (5.0–6.2)	7.3% (6.8–7.8)
	Date of transmitter attachment	7 March	11–14 May
	Average duration of transmitter on bird	2 to 5 months	2 to 4 d
	Number of tagged birds	34	22 (11 pairs)
2013	Absolute transmitter weight	0.99 g	1.29 g
	Relative transmitter weight mean (range)	5.5% (4.8–6.5)	7.3% (6.6–7.7)
	Date of transmitter attachment	2 April	1–10 June
	Average duration of transmitter on bird	2 to 5 months	2 to 4 d
	Number of tagged birds	36	14 (7 pairs)
2014	Absolute transmitter weight	1.30 g	1.29 g
	Relative transmitter weight mean (range)	7.2% (6.3–8.4)	7.4% (7.1–7.9)
	Date of transmitter attachment	10 March	9–13 May
	Average duration of transmitter on bird	2 to 5 months	2 to 4 d
	Number of tagged birds	44	8 (4 pairs)

battery (total transmitter weight: 1.0 g), and a second type powered by a more robust lithium battery (total transmitter weight: 1.3 g). All our transmitter weights were within the natural range of a great tit's daily change in body weight ( $1.47 \pm 0.25$  g, 7.6% body weight on average) (van Balen 1967). Transmitters were fitted to birds with a leg-looped backpack harness, a procedure which took less than two minutes. Harnesses were made of a stretchable, porous material, obtained from common bike baggage straps. These harnesses allow birds to lose transmitters naturally within 5 months if not recaptured sooner. For birds tagged in March or April, we removed any remaining transmitters during standard breeding season capture sessions (2–3 months later). In contrast, birds tagged during breeding in May and June were recaptured sooner (within 2–4 d) since they could be captured at their nest-box when feeding the nestlings. During each of the six deployments, we concurrently handled additional birds following the same procedures, excluding transmitter attachment. These birds served as procedural controls in the analyses of breeding, desertion and provisioning behaviour. See (Snijders et al. 2014) for additional information on the handling, trapping, and tagging procedures.

### Radio-tagging before breeding

We tagged 114 great tits before breeding in three subsequent years (2012, 2013, and 2014). On 7 March 2012, during a routine nest box roost check, great tits were brought to the laboratory if they were inside the designated tracking area or had not previously been personality-tested. The following morning, untested birds underwent the novel environment test for a maximum of ten minutes. A subset of captured birds were fitted with radio transmitters (mean = 5.6% body weight, range = 5.0–6.2%,  $n = 34$ ). We released all birds in the afternoon near the nest boxes in which they were caught. On 2 April 2013, we performed a procedure similar to 2012, with the exception that we tagged birds at night in the field, and returned them to their nest boxes on the same night. The tagging procedure took place later than in 2012 as a consequence of unusually cold temperatures in March that year (Royal Dutch Meteorological Inst. (KNMI) weather station in Deelen: average temperature

March 2013 =  $1.6^{\circ}\text{C}$  compared to March 2012 =  $7.9^{\circ}\text{C}$  and March 2014 =  $8.1^{\circ}\text{C}$ ). These great tits were fitted with similar radio transmitters as in 2012 (mean = 5.5% body weight, range = 4.8–6.5%,  $n = 36$ ). On 10 March 2014, the tagging procedure was similar to 2013. However, due to problems with battery life in the previous years, we decided to use transmitters with more robust, but slightly heavier, lithium batteries (mean = 7.2% body weight, range = 6.3–8.4%,  $n = 44$ ). Some individual birds were tagged in two subsequent years: nine of the birds tagged in 2013 had also been tagged in 2012, and in 2014 twelve of the tagged birds had also been tagged in 2013.

### Radio-tagging during nestling provisioning

To study the social foraging behavior of parents, we radio-tagged 22 great tit pairs with chicks (first broods) during the same three years. We fitted pairs with transmitters 7–10 d after their chicks had hatched (mean 2012 = 8 d, 2013–2014 = 10 d). Tagging took place between 10:50 and 14:00 h, and transmitters were removed again 2–4 d later. On 11 May and 14 May 2012, we fitted a total of eleven pairs (22 birds) with transmitters. Because of the previously mentioned problems with the battery life of the transmitters used earlier in the season, we used the devices with more robust lithium batteries (mean = 7.3% body weight, range = 6.8–7.8%,  $n = 22$ ). Between 2 and 9 June 2013, we radio-tagged seven great tit pairs (14 birds) following a similar procedure to 2012 (mean = 7.3% body weight, range = 6.6–7.7%,  $n = 14$ ). Unlike in 2012, we did not tag any birds before day 10 post-hatching, as we expected to cause less disturbance when catching parents with older nestlings. Based on the positive experience in 2013 (no brood desertion, see Results), we repeated this procedure between 9 and 13 May 2014, using the same transmitter type as in 2013 (mean = 7.4% body weight, range = 7.1–7.9%). Yet, due to several nest desertions, we then halted the study after having tagged four great tit pairs (8 birds). We classified a nest as deserted when all chicks died within two days of the tagging procedure. In total, we tagged seven parents twice: three birds in 2012 were also tagged during pre-breeding, and four birds in 2014 were also tagged in 2013.

## Provisioning behaviour

In 2013, we video-recorded nests on day 11 post-hatching to examine potential effects of tagging on nestling provisioning behaviour. Cameras were inserted in nest box lids that replaced the original lids at least five days before tagging. The camera was connected to a battery and a video-recorder (Archos 405) between 07:00 and 08:00 the morning following the tagging procedure. All the recording equipment was placed in a concealed black plastic box (20 × 30 × 20 cm). Of the seven pairs tagged in 2013, five had seven nestlings at the time of recording, one had six nestlings, and one was excluded from the analysis because the female lost her tag prior to recording. We also recorded six control nests following the same procedure, including catching parents on day 10 post-hatching, but without attaching a radio transmitter. All recordings were made between 1 and 10 June 2013. We used The Observer XT10.5 (Noldus, Wageningen, the Netherlands) software to analyse the video footage. One person quantified feeding rate (feeds min<sup>-1</sup>) and mean visit duration (s) for both parents, based on one hour of footage recorded between 09:30 and 10:30 (except for one 45 min-recording resulting from a technical problem). To test for potential differences in quality of nest box location between tagged and control parents, we inferred nest location quality using the mean number of fledged chicks per nest box over the previous ten years (2005–2014). There were no significant differences between nest boxes of tagged and control birds (independent t-test;  $t_{10} = 0.44$ ,  $p = 0.67$ ).

## Statistical analysis

We started our analysis by evaluating if environmental conditions (temperature, sun and rain) differed between the years of tag deployment. Environmental variables were retrieved from the nearby (< 10 km) KNMI weather station in Deelen. To investigate potential transmitter effects on reproductive behaviour (likelihood of breeding and likelihood of brood desertion), we compared tagged birds to procedural control birds using generalized linear models (GLM) with a logit link function and binomial error distribution. If there were differences between years in environmental conditions, we incorporated interactions between treatment and the specific year of the procedure. Models with and without the relevant variables were compared using likelihood ratio tests (Chi-square).

### Conditions before breeding

The population density fluctuated between the years and was lowest in 2013, reflected by the small number of breeding pairs raising their offspring to at least 7 d of age (2012: 135, 2013: 65, 2014: 85). Moreover, despite the tagging procedure being postponed for a month in 2013, the first seven days following tag attachment were significantly colder compared to the other two years (one-way ANOVA; average daily temperature between years: mean 2012 = 6.9°C, mean 2013 = 3.3°C, mean 2014 = 8.7°C; one-way ANOVA:  $F_{2,18} = 23.58$ ,  $p < 0.001$ ; Tukey HSD; 2012–2013:  $p = 0.001$ , 2013–2014:  $p < 0.001$ ). There were no significant differences in daily hours of sunshine (one-way ANOVA:  $F_{2,18} = 1.82$ ,  $p = 0.191$ ) or daily amount of

rain (2012, two days of rain < 1.5 mm; 2013, no rain; 2014, one day of rain < 0.3 mm).

Birds tagged before breeding did not differ in weight between the years (one-way ANOVA; mean 2012 = 18.30 g, mean 2013 = 18.22 g, mean 2014 = 18.13 g,  $F_{2,111} = 0.31$ ,  $p = 0.73$ ), but the proportion of tagged birds younger than one year varied significantly between the years and was substantially lower in 2013 compared to 2012 (Supplementary material Appendix 1, Table A1). This was a reflection of the overall significant drop in the proportion of captured first-year birds from 2012 to 2013 (64 to 37%).

### Likelihood of breeding

We calculated the likelihood of breeding as the proportion of treatment birds that were provisioning chicks during the following breeding season (May–June of the same year). Using recatching records from standardized nest box breeding checks (Supplementary material Appendix 1, Table A2), we analysed whether individuals tagged in March or April were less likely to be recaptured during the subsequent breeding season, at least 2 months after initial capture, compared to two controls: 1) birds handled in the field on the same night but left in the nest box and 2) birds brought to the laboratory on the same night and released the next day close to their nest box. The latter is the more appropriate control in 2012, when we also took the tagged birds to the lab, while the former is more appropriate in 2013 and 2014, when birds were tagged in the field. We used generalized linear models with a Logit link, including the interaction between treatment (transmitter: yes/no) and year (2012, 2013, 2014). Because in great tits, older birds are generally more successful breeders than first-year birds (Perrins 1965, Perrins and McCleery 1985), age (second calendar year or older) was also included as a control variable.

To test if differences in breeding probability between tagged and control birds could be explained by differences in long-term recapture probability (and thus potentially mortality), we analysed recapture records for all tagged and control individuals. This analysis included recapture data from after the relevant breeding season up to 10 March 2015, retrieved from standardized nest box roost checks (December and March each year) and nest box breeding checks (April to June each year) (Supplementary material Appendix 1, Table A3).

To examine if relative transmitter weight had an additional effect on the proportion of tagged birds later found breeding, we used a GLM with a Logit link, including transmitter weight (relative to body weight), standardized transmitter weight (relative to standardized tarsus length as measure of body size), age, and year. For birds older than two calendar years, we also analysed the potential effect of retagging (yes/no) as in 2013 and 2014 nine and twelve birds (respectively) were tagged that had been tagged in a previous year.

### Conditions during breeding

During nestling provisioning, there was likewise a difference between years in the average temperature (Kruskal–Wallis;  $H = 8.12$ ,  $p = 0.02$ ) and a trend towards a difference in hours of sunshine (Kruskal–Wallis;  $H = 5.55$ ,  $p = 0.06$ ). However, in contrast to early spring, temperatures (Mann–Whitney  $U = 2.00$ ,  $p = 0.02$ ) and hours of sunshine (Mann–Whitney



$U = 2.00$ ,  $p = 0.02$ ) were significantly higher during nestling provisioning in 2013 compared to 2014. Additionally, in 2014 it rained on some of the transmitter attachment days (daily mean = 7.68 mm, SD = 10.99), while it did not rain on attachment days in 2012 and 2013 (Supplementary material Appendix 1, Table A4). It never rained during the transmitter attachment procedure itself. Finally, pairs tagged during nestling provisioning did not differ in average brood size between the years (Kruskal–Wallis;  $H = 2.32$ ,  $p = 0.314$ ), although the range of brood sizes did vary (brood size range 2012 = 3 to 9, 2013 = 6 to 7, 2014 = 6 to 10).

### Brood desertion

We calculated the likelihood of desertion as the proportion of treatment birds that deserted their brood after the procedure. We analysed whether or not the likelihood of desertion increased due to the tagging procedure by comparing parents tagged during the nestling provisioning phase to parents that were caught but not tagged, and also investigated whether these potential effects differed between years (Supplementary material Appendix 1, Table A5). To investigate the potential influence of small sample sizes on our significant findings (see Results), we additionally conducted bootstrap analyses (without replacement). These analyses suggest that our findings were unlikely to be primarily attributable to small sample sizes (Supplementary material Appendix 1, Methods A1).

We analysed which factors best explained whether or not tagged parents deserted their nest using a logistic regression, pooling the data for all three years. We examined environmental variables that varied between years, as well as brood- and parental characteristics that were likely to influence the energy expenditure of the tagged birds. Specifically, we investigated the role of average temperature (°C), sun hours and rainfall on the day of tagging, along with effects of the chick age, brood size and the body condition of the male and the female (the residual of weight over tarsus). Age of the male and female and whether the male or female had been tagged before were added as control variables. Because absolute transmitter weights were the same in all years during nestling provisioning (Table 1) and because we already included body condition, we did not additionally test for relative tag weight in this model. To explicitly uncover which yearly varying factors (temperature, rain etc.) could potentially explain the observed differences in tag effects between the years (see Results), we did not add 'year' as an independent variable to the model.

Due to the relatively low sample size and the low variation in the explanatory variables, we could only fit a maximum of two variables into the model. Therefore, we conducted a forward stepwise model selection, starting with a model containing a single predictor variable. Subsequently, we performed model comparisons with likelihood ratio tests (Chi-square) to test if the best starting model significantly improved when adding a potential second explanatory variable. Finally, we likewise tested whether the final model was significantly better than a null-model.

### Provisioning behaviour

Potential effects of tagging on nestling provisioning behaviour were analysed by conducting two linear mixed model (LMM) analyses with either feeding rate or mean visit duration as the

dependent variable. We used treatment (tagged or control), sex, and brood size (six or seven) as explanatory variables and nest box identity as a random factor. We tested differences in average chick body weight and chick tarsus length between tagged and untagged nest with independent t-tests.

We tested for normality of the data and model residuals with the Shapiro–Wilk test. We used parametric tests when distributions were not significantly different from a normal distribution ( $p > 0.05$ ). The degrees of freedom between similar models might differ slightly due to a small number of individuals missing accurate biometric measurements or age estimates. Incorporating individuals as random factors in mixed models did not significantly change the results. Statistical tests were performed in R ver. 3.2.1 (R Core Team) or SPSS ver. 22 (IBM, Armonk NY, USA). We used the R-package 'lsmeans' to calculate contrasts and effect sizes from estimates of factors and interactions.

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.j4v4b>> (Snijders et al. 2016).

## Results

### Likelihood of breeding

Birds tagged before breeding were not less likely than procedural control birds to be recaptured during nestling provisioning, although there was a trend towards a negative effect in 2013 (logistic regression with Transmitter  $\times$  Year interaction: DF = 206,  $p = 0.06$ ; 2012: Z-ratio =  $-0.94$ ,  $p = 0.35$ ; 2013: effect size = 2.54, SE = 1.68, Z-ratio = 1.80,  $p = 0.07$ ; 2014: Z-ratio =  $-1.24$ ,  $p = 0.21$ ). This trend is unlikely to be caused by mortality, since these birds did not have an overall lower long-term recapture probability, compared to procedural control birds (logistic regression 2013: DF = 56, Z-ratio = 0.95,  $p = 0.34$ ). Older birds were overall more likely to breed, independent of being tagged (logistic regression: DF = 206, effect size = 2.30, SE = 1.37, Z-ratio = 2.66,  $p = 0.008$ ).

Within tagged birds, the likelihood of breeding also positively associated with age (logistic regression: DF = 107, effect size = 2.48, SE = 1.57, Z-ratio = 2.04,  $p = 0.04$ ) and varied between years (logistic regression:  $p = 0.001$ , DF = 107; 2012–2013: effect size = 7.77, SE = 1.79, Z-ratio = 3.52,  $p = 0.001$ , 2014–2013: effect size = 3.86, SE = 1.68, Z-ratio = 2.66,  $p = 0.02$ ; 2012–2014: Z-ratio = 1.36,  $p = 0.36$ ). The weight of the radio transmitter as a percentage of bodyweight (4.8–8.4%) did not significantly affect the likelihood of breeding (logistic regression: DF = 106,  $z = -0.29$ ,  $p = 0.77$ ), nor did the weight of the transmitter relative to tarsus length (logistic regression: DF = 106,  $z = -0.14$ ,  $p = 0.89$ ). Tagged birds older than their second calendar year were not significantly more likely to breed if they had experience with being tagged (logistic regression: DF = 47, Z-ratio =  $-1.13$ ,  $p = 0.25$ ).

### Brood desertion

The percentage of control pairs deserting their nests tended to vary between the years (14% in 2012 ( $n = 124$ ), 5% in 2013 ( $n = 58$ ) and 17% in 2014 ( $n = 81$ ); logistic

regression;  $DF = 260$ ,  $p = 0.07$ ). The number of pairs that deserted their nest following a tagging procedure during the nestling provisioning phase also varied significantly between the years (2012 ( $n = 11$ ), 55%; 2013 ( $n = 7$ ), 0% and 2014 ( $n = 4$ ), 75%; logistic regression;  $DF = 19$ ,  $p = 0.006$ ). In 2012 and 2014 more tagged pairs deserted their nest than control pairs (Transmitter  $\times$  Year interaction:  $DF = 279$ ,  $p = 0.0001$ ; 2012: effect size = 7.54,  $SE = 1.93$ ,  $Z$ -ratio = 3.07,  $p = 0.002$ ; 2014: effect size = 14.30,  $SE = 3.29$ ,  $Z$ -ratio = 2.24,  $p = 0.03$ ), while in 2013 there was no effect of tagging during nestling provisioning on nest desertion (no brood desertion by any tagged birds in 2013; 2013:  $Z$ -ratio = 0.015,  $p = 0.99$ ). Individual tagged parents were equally likely to be recaptured after the breeding season in 2012 and 2014 compared to control birds (logistic regression with Transmitter  $\times$  Year interaction:  $DF = 516$ ,  $p = 0.78$ ; 2012:  $Z$ -ratio = 0.33,  $p = 0.74$ ; 2014:  $Z$ -ratio = 0.59,  $p = 0.55$ ; Supplementary material Appendix 1, Table A6).

Overall, tagged parents with more nestlings were more likely to desert their nests (logistic regression;  $DF = 20$ , effect size = 6.05,  $SE = 2.20$ ,  $z = 2.26$ ,  $p = 0.0005$ ) and the likelihood of brood desertion tended to increase with lower average temperatures (logistic regression;  $DF = 20$ , effect size = 1.51,  $SE = 1.27$ ,  $z = 1.74$ ,  $p = 0.06$ ). Additionally, tagged females in lower body condition were more likely to desert (logistic regression:  $DF = 20$ , effect size = 5.70,  $SE = 2.39$ ,  $z = 2.01$ ,  $p = 0.02$ ). The combination of brood size and average temperature was the best predictor of brood desertion (model comparison against best starting model (brood size): deviance = 3.99,  $p = 0.046$ ; Fig. 1). Daily rainfall (mm), sun hours, nestling age, male body condition, male and female age, and being tagged before (for both male and female) were not significant predictors of brood desertion (logistic regression; all  $p > 0.1$ ). Average temperature and female body condition did not significantly associate with brood size (Spearman rank test; all  $p > 0.1$ ). Thus over the three years, parents with a large brood and tagged during relatively low

temperatures were most likely to desert their nests (model comparison against null model; residual deviance = 15.93,  $p = 0.0003$ ).

## Provisioning behaviour

Tagged parents with eleven-day old chicks in 2013 (the year with no brood desertions) had similar feeding rates (linear mixed model;  $F_{1,10} = 0.83$ ,  $p = 0.38$ , mean feeding rate =  $0.46 \text{ min}^{-1}$ ;  $SD = 0.15$ ; Fig. 2a) to non-tagged parents (mean feeding rate =  $0.40 \text{ min}^{-1}$ ;  $SD = 0.16$ ). Likewise, tagged parents did not differ in the time spent in the nest box during visits (linear mixed model;  $F_{1,10} = 1.90$ ,  $p = 0.20$ , mean visit duration = 14.98 s;  $SD = 9.30$ ; Fig. 2b) compared to non-tagged parents (mean visit duration = 11.04 s;  $SD = 5.46$ ). There was no effect of brood size (6 or 7 chicks) on either feeding rate ( $F_{1,9} = 0.29$ ,  $p = 0.60$ ) or mean visit duration ( $F_{1,9} = 0.01$ ,  $p = 0.91$ ). Males and females did not differ in feeding rate ( $F_{1,11} = 0.002$ ,  $p = 0.97$ ), but females stayed longer during visits, regardless of whether or not they were tagged ( $F_{1,11} = 6.95$ ,  $p = 0.02$ ; Fig. 2b). There were no significant differences between the average weights of fourteen-day-old chicks of tagged and non-tagged parents (independent T-test;  $t_{10} = 0.32$ ,  $p = 0.76$ ) or in their average tarsus length (independent T-test, equal variances not assumed;  $t_{8,577} = 1.80$ ,  $p = 0.11$ ).

## Discussion

This study reveals that the effects of transmitter attachment on a small passerine species can vary strongly between years. Tagging birds before breeding did not negatively affect their breeding probability in 2012 and 2014, but in 2013 there was a trend towards a negative effect on the likelihood of breeding. The early spring (March) of 2013 was substantially colder than in the other two years, while later in spring (during nestling provisioning) the average temperature was highest in 2013. When tagging both parents during nestling provisioning, we recorded elevated nest desertion rates in 2012 and 2014, but no desertions by tagged parents in 2013. A large brood size in combination with low average temperatures best predicted whether tagged parents would desert. Tagged parents did not differ in their provisioning behaviour from untagged parents, and their chicks were in similar body condition in the single year (2013) these data were collected.

Birds tagged before breeding in 2013 tended to be less likely ( $p = 0.06$ ) to breed compared to control birds caught in the field and released on the same day. The similar recapture probabilities for tagged birds compared to control birds, within our fully-monitored study-site, strongly suggests that the lower breeding probability in 2013 was indeed the result of tagged birds foregoing reproduction, rather than decreased survival chances or increased dispersal. However, the proportion of tagged individuals found breeding did not differ from control birds taken to the institute on the day of tagging (Supplementary material Appendix 1, Table A2), suggesting a general sensitivity to disturbance during spring that year, rather than a transmitter effect per se. The lower temperatures in 2013 and the decrease in the

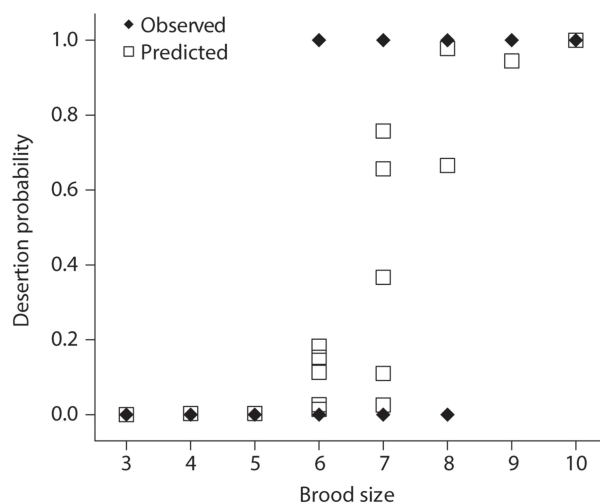


Figure 1. Probability of nest desertion by tagged parents in relation to brood size for observed values (closed diamonds) and predicted values by the final model (open squares).

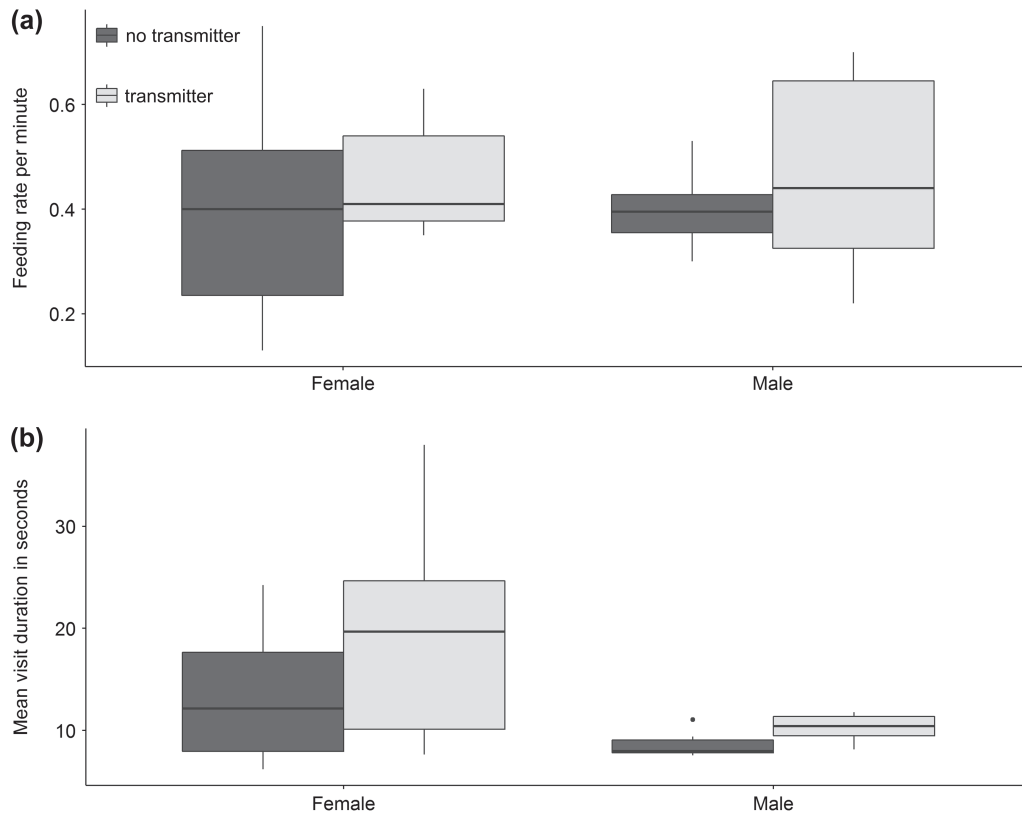


Figure 2. Difference between tagged (light grey) and untagged (dark grey) pairs in (a) feeding rate per minute and (b) mean visit duration in seconds for males and females.

proportion of first-year birds compared to 2012, indicates that the early spring of 2013 was exceptionally tough for the great tits. Birds may have expended more energy on thermoregulation in the early spring of 2013, lowering the energy reserves they had available for reproduction (McNab 2015) and/or decreasing the competitive ability of young birds to acquire or retain a breeding territory (Krebs 1982, Sandell and Smith 1991). Energy expenditure in great tits increases with decreasing temperatures (Tinbergen and Dietz 1994), and our analyses also suggest a tendency for temperature to modulate negative transmitter effects both before and during breeding. Additional studies covering several environmentally variable years would be necessary to confirm whether temperature is indeed a significant general predictor of transmitter effects in great tits and other small passerines.

None of the pairs tagged during nestling provisioning deserted in 2013, but more than half of the tagged pairs deserted their nests in 2012 and 2014. One possible explanation for this difference would be selection towards higher-quality birds at the start of the cold spring of 2013 leading to only high-quality individuals breeding that year, but we did not find strong evidence for this. For example, age did not have a significant effect on desertion and although there was a significant effect of female body condition on the likelihood of desertion, this was not the best explaining factor. Similarly, relative body size did not greatly influence transmitter-related survival in juvenile great tits and coal tits *Parus ater* (Naef-Daenzer et al. 2001), suggesting that body condition or body size is generally not a major factor

influencing negative transmitter effects in tits. Unfortunately, our sample size was too small to examine the effect of adding female body condition to the final model, which included both brood size and average temperature. Thus, selection for high quality females may have played an additional role in likelihood of brood desertion.

The negative effect of brood size on desertion probability agrees with a long-term (23 breeding seasons) study in great tits showing that poor years mostly affect the reproductive success of individuals with larger clutches (Boyce and Perrins 1987). Pairs with many nestlings might experience a larger depletion of their energy reserves, especially in unexpectedly poor years (those with few surviving chicks overall). Adding an additional stressor might hence push them over their limits (Wilson et al. 2015b). The year 2014 was the most extreme breeding season for our study area during the last fifteen years in terms of nest failures, with 17% of caught but untagged parents deserting (Supplementary material Appendix 1, Table A5). 2012 was also a relatively poor year, with 14% desertions by caught but untagged birds (procedural controls), compared to 5% in 2013 (Supplementary material Appendix 1, Table A3). These percentages suggest that both tagged and untagged great tits in the late spring of 2012 and 2014 were overall more likely than normal to abandon their broods (Both and Visser 2000, Both et al. 2005). Thus, the additional disturbance caused by the tagging procedure might have resulted in a disproportionately large increase in brood desertions.

Alternatively, tagged parents might initially have left their broods only temporarily, while habituating to the transmitter.

The time that (larger) broods can hold out without parental care might, however, be shorter in poorer years, increasing negative transmitter effects on reproductive success. A study investigating transmitter effects on faecal glucocorticoid levels in dickcissels *Spiza americana* indeed found that glucocorticoid levels significantly increased within 24 h after transmitter attachment, but had returned to baseline levels within two days (Suedkamp Wells et al. 2003). Moreover, birds in our study that were tagged with the same transmitters before breeding in 2014 were equally likely as procedural controls to raise nestlings, further supporting the possibility that the timing and context of the tagging procedure was crucial in determining whether negative transmitter effects would occur in our study.

Given the rate of nest desertion for parents tagged during nestling provisioning, one might also expect reduced parental care behaviour by those parents that did not desert. However, we did not find a reduction in either the provisioning effort of tagged parents or the condition of their chicks. It is possible that one hour of provisioning does not provide enough information to quantify potential effects of the transmitters on great tit provisioning behaviour, although a study in 2013 revealed that provisioning data collected over one hour serves as a good predictor for overall provisioning rate in great tits (Pagani-Núñez and Senar 2013). Since our provisioning analysis only includes the year in which parents did not desert, the possibility remains that tagging significantly affected provisioning effort of non-deserted nests in other years, but unfortunately we do not have video data available to test this. Similarly, transmitters did not affect provisioning effort in male northern cardinals *Cardinalis cardinalis*, but did affect how vigorously they defended the nest (Barron et al. 2013). It is conceivable that, to maintain this normal feeding rate, tagged parents invested substantially more energy than normal, at the cost of other energy intensive behaviours, but if so we could not identify these neglected behaviours. More work is needed to understand these trade-offs in investment, as they are crucial to estimating the impact of stressors such as transmitter attachment on individual animals (Wikelski and Cooke 2006, Cooke 2008, Cooke et al. 2014).

The transmitters we used before breeding in the final year (2014) and in all years during nestling provisioning were heavier (ca 7.3% body weight) than the commonly suggested guideline of 5%. Yet our findings suggest that it was not transmitter weight per se, but rather the timing and context of tagging that predicted transmitter effects in our study. The only year in which we found a potential negative effect of tagging on the likelihood of breeding was a year in which we used lighter devices (ca 5.5% body weight), and we found no effects of variation in relative transmitter weight on the likelihood to breed or desert in any year. These results concur with the meta-analysis of Barron et al. (2010), who did not find an increase in negative transmitter effects with heavier devices.

Given that tagged parents deserted within two days, it is likely that the overall disturbance of tagging, rather than the transmitter weight itself, led to their decision to desert. Yet, two previous great tit tracking studies did not find such negative effects of tagging during nestling provisioning (chicks between 8 and 17 d of age), using 4–5% transmitters (van

Overveld et al. 2011, Atema et al. 2016), so we cannot rule out that the use of heavier tags in our study made an important difference. However, both these studies only tagged one of the parents, and this reduced disturbance might have been as important as the lower transmitter weights in preventing nest desertion. Relative transmitter weight appears to be a fairly poor predictor of transmitter effects on parental care, as negative consequences have been found in birds tagged with transmitters below 5% of their body weight (Ackerman et al. 2004, Barron et al. 2013), but have also been absent for individuals tagged with transmitters above 7% body weight (Neudorf and Pitcher 1997). Regardless of the precise mechanism, tagging birds during stressful periods, like parental care, should be undertaken with stricter limits on disturbance than at other times of the year.

In addition to our study, there is evidence that light devices (<3% body weight) and even flipper-bands on penguins can have significant effects in some years but not others (Bro et al. 1999, Saraux et al. 2011, Wilson et al. 2015b, van Wijk et al. 2016). We cannot infer from our study the maximum transmitter weight that great tits or other similar songbird parents can carry without an increase in desertion rates, only that it is below 7.3% body weight under poor conditions, but at least 7.3% under good conditions. These estimates are within the natural range of daily body weight changes for great tits (van Balen 1967), and hence daily weight variation is not a reliable guideline for appropriate tagging weights. While researchers should continue to fit devices that are as light as possible, our study shows that factors other than weight can be equally important to consider.

In summary, our study shows that transmitter effects on the ecology and behaviour of a small passerine were absent before breeding, but are context-dependent during more stressful periods like parental care. Hence, considering the context of tagging, such as temperature, breeding stage, and brood size, is crucial to maximising the tremendous potential of biotelemetry and biologging (Cooke et al. 2004, Cooke 2008, Hallworth and Marra 2015, Wilson et al. 2015a), while minimising its potentially negative effects. When unexpected negative transmitter effects are found, reports of these effects can most effectively guide future studies if comprehensive information on both the environmental context and transmitter weight are included (Godfrey and Bryant 2003).

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Supplementary material (Appendix JAV-01148 at <[www.avianbiology.org/appendix/jav-01148](http://www.avianbiology.org/appendix/jav-01148)>). Appendix 1.