

Is hissing behaviour of incubating great tits related to reproductive investment in the wild?

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Abstract Anti-predator behaviour of breeding animals is a complex trait that depends on current reproductive investment as well as individual differences in risk-taking propensities. In response to nest predation, many bird species produce specific sounds, such as the hissing calls in incubating great tits (*Parus major*), that may provoke an acoustic startle response in the predator. However, it is still unclear whether the propensity of incubating females to produce hissing calls towards nest predators depends on the reproductive investment. With our 3-year study, we show that response type (females that do not hiss versus females giving hissing calls) to a potential nest predator, the woodpecker, is a repeatable trait. We found no differences in the studied reproductive traits between hissing and non-hissing birds. Interestingly, among hissing birds, fast-responding females started egg-laying earlier than slow-responding ones. Among non-hissing birds, heavier birds initiated clutches earlier. We also revealed that hissing birds breed in areas with decreased nest-box occupancy, suggesting either that they potentially select different areas to breed or that territory size is larger as a result of hissing birds being more aggressive. These findings demonstrate that response type is not related to the early reproductive value of the brood across distinct behavioural groups. However, our results do suggest that non-hissing and hissing females differ in terms of individual quality or dominance or personality related aspects.

Keywords Anti-predator behaviour · Lay-date · Nest defence · Nesting density · *Parus major* · Repeatability

Introduction

From an evolutionary perspective, the main challenge for behavioural ecologists is to explain the causes of behavioural variation in different animal species in the context of life history. Predation is one of the major selection pressures that affects the behaviour and fitness of animal populations (Lima 2009). Hence, understanding the adaptive value of anti-predator behaviours seems to be especially interesting given that this trait is known to vary between individuals (e.g. López et al. 2005) and between sexes (e.g. Bize et al. 2012) and can be easily measured during the breeding time.

However, the interpretation of anti-predator behaviour in free-living animals during breeding time is complicated owing to several confounding factors. Firstly, although individuals differ in their risk-taking behaviour, partners are likely to influence each other because of compensatory parental behaviours (Mahr et al. 2012; Mänd et al. 2013). Secondly, parental investment theory suggests that anti-predator behaviour is strongly related to the reproductive value of offspring (e.g. clutch size, brood size—Carlisle 1985, Amat 1996, Tilgar and Kikas 2009) because the fitness benefits of deterring a predator will increase with brood size. In theory, the larger the brood, the greater the proportion of genes that contribute to the lifetime reproductive output of parents. Larger clutches and broods should thus be more valuable for their parents. Moreover, it is likely that (older) nestlings and larger broods produce more distress calls, which might trigger a stronger response from the parent (Rytönen 2002). Thirdly, anti-predator responses may partly depend on the overall level of predation risk of a particular environment (Lima 2009). For

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example, Krams et al. (2010) showed that breeding pied flycatchers (*Ficedula hypoleuca*) attended mobs more often and approached a stuffed dummy predator significantly more closely and with higher intensity in areas where the perceived predation risk was experimentally increased. In most bird species, the anti-predator behaviour of a female individual in the early breeding stage (e.g. during incubation) should be relatively independent of its male partner and not influenced by offspring solicitation behaviour. Hence, by measuring avian responses to predators at this stage, it can be more easily associated with initial reproductive investment in terms of clutch size or with individual differences in their personality aspects.

Many small passerine birds, like the great tit, nest in cavities and females incubate the eggs alone (Perrins 1979); males are often not present to warn against predators or to defend the female. If a predator appears at the nest-hole, brooding female great tits produce specific sounds associated with nest defence—hissing sounds similar to a snake—and bang their wings inside the cavity (Perrins 1979). These sounds may effectively confuse or even frighten the predator (Perrins 1979; Krams et al. 2014). A previous study on great tits has shown that within a breeding season, hissing is a repeatable behavioural trait and hissing females were less likely to be killed when attacked by nest predators (Krams et al. 2014), probably due to the deterrent effect of hissing sounds towards the approaching predator. However, there is little evidence as to whether hissing calls as a form of nest defence can be adjusted adaptively in relation to the expected fitness value of the current brood, as predicted by the parental investment theory (Rytönen 2002).

In this study, we wanted to investigate if hissing behaviour indicated any aspect of (1) female reproductive investment, (2) female quality, (3) population density and (4) perceived predation risk. First, we examined correlations between hissing behaviour (non-hissing versus hissing types among all birds and the latency to give hissing calls (hereafter called ‘hissing delay’) among hissing individuals, with both responses measured within 5 s following exposure to the nest predator) and early breeding characteristics, such as lay-date (day first egg is laid) and clutch size, that are related to brood value. It has been demonstrated that lay-date, through its effect on offspring survival, is negatively and clutch size positively related to the future value of the current brood (Perrins 1965). Hence, we predicted that lay-date was negatively and increased egg production positively related to the propensity of hissing birds as well as the propensity of a rapid hissing response among responding individuals. Second, it has been shown that females laying larger eggs are heavier in the nestling stage (Hörak et al. 1995). Hence, we expected female body mass to be a reliable indicator of individual quality and positively related to hissing behaviour. Moreover, we predicted that the relationship of lay-date with clutch size and

parental body mass may differ between non-hissing and hissing birds. In early birds, there is selection for larger clutches, while in later birds, there is selection for smaller clutches and high fledging mass (Naef-Daenzer et al. 2000). If hissing females are high-quality individuals, then their reproductive investment, as well as individual condition, should be less affected by seasonal constraints in breeding conditions when compared to non-hissing (low-quality) birds. Hence, hissing birds might produce more eggs in the late season when compared to non-hissing females. Third, hissing behaviour may be related to breeding density, which could reflect female dominance or personality via territory selection. It has been suggested that more dominant (and presumably aggressive) individuals have larger territories than shy individuals (Slagsvold 1993; Mougeot et al. 2003). Hence, we predicted that females that rapidly produce hissing sounds towards a predator are more aggressive and also drive neighbours farther away leading to larger territories and lower breeding densities when compared to those females that delay hissing or give no response at all. As a proxy of population density, we used two complementary indices: the nest-box occupation rate per transect (Mänd et al. 2005) and the distance of an occupied nest-box from the nearest breeding neighbour. Fourth, we assumed that hissing behaviour may be positively related to the perceived predation risk. This prediction is based on previous studies showing that anti-predator behaviours may be enhanced in risky environments (Lima 2009; Krams et al. 2010; Tilgar and Moks 2015). In addition, hissing response may vary in relation to seasonal changes in perceived predation risk. For example, it has been shown that nest predation is high early in the breeding season, before decreasing sharply, and then remaining relatively constant thereafter (Shustack and Rodewald 2011; Borgmann et al. 2013). Hence, individuals with an earlier lay-date might have increased alertness towards predators, including a higher propensity to give hissing calls than those that start egg-laying later in the season. Given that seasonal changes in the perceived predation risk can be non-linear, we explored both linear and quadratic relationships between hissing delay and lay-date.

Material and methods

Study site and subjects

Data were collected in the forests surrounding Kilingi-Nõmme in southwest Estonia (58° 7' N, 25° 5' E) in 2011–2013. Our study area of about 50 km² is largely covered by a mosaic of deciduous and coniferous forest. The conifer woodlands consist mostly of managed pine (*Pinus sylvestris*) forests on nutrient-poor sandy or peaty soils. Deciduous woodlands occur mainly as isolated patches between cultivated fields or as belts along stream valleys. Growing on fertile soils and

having a rich deciduous understory, the dominating tree species are grey alder (*Alnus incana*) and silver birch (*Betula pendula*).

The great tit (*Parus major*) is a small (ca 19 g), short-lived, cavity-breeding passerine bird widespread throughout the Palearctic region (Perrins 1979). The female builds the nest alone and in our study area lays, on average, 9–12 eggs per clutch (Mänd et al. 2005). Incubation starts as soon as the clutch is completed and lasts up to 14 days. In our study area, the natural predators of great tits include sparrowhawks (*Accipiter nisus*), great spotted woodpeckers (*Dendrocopos major*), pine martens (*Martes martes*) and red squirrels (*Sciurus vulgaris*). The three latter predators threaten eggs and nestlings in particular but also incubating females. Great tits in our study population bred in nest-boxes mounted on tree trunks at a height of 1.5–2.0 m. Nest-boxes were arranged in 17 distinct transects, with each transect consisting of 20–160 boxes (two exceptional transects with 8 and 17 nest-boxes), and altogether over 1000 nest-boxes. The internal dimensions of nest-boxes were approximately 10 × 10 × 30 cm, and the diameter of the entrance was 3.5–4.0 cm. The distance between adjacent nest-boxes on the same transect was 50–60 m. Old nest material was removed each year before the beginning of the breeding season.

As great tits may breed twice per season, we carried out our study during the first breeding attempt (during April and May in our study area). Nests were checked weekly throughout the nesting period to obtain data on lay-date, clutch size and start of incubation. Females were caught using nest-box traps during the second half of the nestling period (between days 7 and 15). The body mass was weighed using a Pesola spring balance to a precision of 0.1 g, and tarsus length was measured to the nearest 0.1 mm with a digital calliper. All captured females were also ringed so we could recognise recaptured individuals over the study period.

In order to evaluate the perceived predation risk in each transect, we recorded the occurrence of nest predation events during the nesting period. We considered each nest that had been deserted (probably due to one or both parents being killed) or depredated by woodpeckers, martens or other predators as an indicator of predation. Every depredated or abandoned nest was counted as a single event. Predation risk was calculated in each transect separately as the ratio of failed nests (depredated and deserted nests combined) to occupied nest-boxes (hereafter called as ‘nest-box occupancy’).

Experimental protocol

We tested anti-predator behaviour of females in the first half of the incubation period. We considered the day when a female laid her last egg as day 0 of incubation. To standardize female stress level, an initial trial was conducted around 5–7 days after females started incubating (with a few exceptions, never

less than 2 days or more than 9 days after incubation started). In order to simulate a predator intrusion in the nest-box, we presented a stuffed great spotted woodpecker to incubating females through the nest-hole for up to 5 s and observed whether birds gave hissing calls in reply. If the bird did not react in any way during the trial, we removed the lid of the nest-box to confirm the female was present. (See Krams et al. 2014 for further details how the trial was conducted.)

Our aim was to measure hissing behaviour during a relatively short time period as females usually reply quickly to disturbance and the startle effect against a predator may work best in the first few seconds. Initially, we measured the response up to 30 s. As most of the responding females hissed during first 5 s (72 % of responding birds in 2011), we continued to only measure the response for up to 5 s. Additionally, we used the hissing delay within this 5 s period as a continuous variable by excluding those birds that did not respond to the presentation of the woodpecker (responding birds only).

Based on each female’s reaction towards the woodpecker, we divided birds into hissing (responded during 5 s) and non-hissing (did not respond during 5 s) groups (hereafter called ‘response type’). To assess trait repeatability, in 2011 and 2012, a number of birds ($N=69$) were given a repeat trial 3–5 days later. In addition, in 2011 and 2013, we measured hissing delay as a continuous parameter (latency to start hissing after the woodpecker had been presented, 1–5 s). The minimum delay value was always considered to be 1 s, and the maximum delay was 5 s. Note that in 2012, we only recorded whether birds responded during the initial 5 s or not. Hence, repeatability of response type (yes/no) was studied in 2011 and 2012, and repeatability of hissing delay (1–5 s) was studied only in 2011. Otherwise, all the procedures were the same. None of the nests where we conducted the woodpecker trial were deserted except due to natural causes (i.e. predation by woodpeckers or martens).

Statistical analyses

A total of 190 females were tested during the study period, with 49 in 2011, 93 in 2012 and 43 in 2013. For the analyses, we used the response type of the first trial if the bird was tested for repeatability. Given that a few birds bred in different seasons, we also included only one replicate per each recaptured individual in our analyses. This was done by flipping a coin and randomly removing data for the first year or second year for a given bird. We excluded two nests from the analyses related to an extraordinary high population density on one small transect in 2012 (density estimation incomparable to other transects).

First, in order to test our hypothesis that hissing behaviour was related to reproductive investment, we used general linear mixed models (GLM, R version 3.2.0, package ‘lme4’, Bates et al. 2014) for lay-date (square-root transformed prior to

analysis to meet the model assumptions of normal distribution of residuals) and clutch size as dependent variables with response type (responding versus non-responding birds) or hissing delay (1–5 s) among hissing individuals, habitat (deciduous versus coniferous), two indicators of population density (neighbour distance, nest-box occupancy) and nest predation as predictors in the full models. Yearly, nest-box occupancy was defined as the proportion of nest-boxes occupied by breeding birds for each transect (see Mänd et al. 2005 for details) and the distance (m) was calculated to the closest breeding neighbour. Given that lay-date may reflect seasonal non-linear changes in the perceived predation risk (see Introduction), we included both linear and quadratic term of hissing delay in the full model. Second, in order to test our hypothesis that hissing behaviour was related to female quality, we used GLM model with female body mass as a dependent variable and the same set of other predictors as in the first model. According to our specific predictions (see “Introduction”), we used the interaction between response type and lay-date as an additional predictor in the above models. Third, we used general linearized mixed models with binomial link (GLZ) for response type as a categorical dependent variable to test the associations with two indices of population density (neighbour distance, nest-box occupancy) and nest predation. Note that lay-date and clutch size were also

included the latter model as predictors. All analyses were corrected for year and transect as random factors. The repeatability of the categorical response trait (hissing response: yes/no) was calculated using Cohen’s Kappa (R version 3.2.0, package ‘irr’, Gamer 2012); the repeatability of hissing delay (1–5 s) among responding birds was calculated using the formula of Lessels and Boag (1987). In order to assess main effects and interactions from the same models, a Type 2 Wald Chi-square test (package ‘car’ in R, Fox and Weisberg 2011) was used and continuous predictors were standardized to obtain a standardized regression coefficient (beta). All models included R^2 (see Tables 1 and 2).

Results

Over the 3-year study period, 115 out of 190 females gave hissing calls during the 5 s trial period (61 % of all birds), while 75 did not respond to the woodpecker during the same exposure time (39 % of all birds). Out of 69 females, 57 (83 %) did not change their response type (responding/non-responding) when measured 3–5 days later (Cohen’s Kappa for 2 Raters; Kappa = 0.63, $Z = 5.23$, $P < 0.0001$, $N = 69$ individuals; using the formula by Landis and Koch 1977). Among responding birds, the repeatability for hissing delay (measured

Table 1 Mixed effects full models on lay-date ($N = 188$), clutch size ($N = 188$) and female body mass ($N = 140$)

	Lay-date (hypothesis 1 and 4)			Clutch size (hypothesis 1)			Female body mass (hypothesis 2)		
	Beta	SE	$\chi^2 (p)$	Beta	SE	$\chi^2 (p)$	Beta	SE	$\chi^2 (p)$
Fixed effects									
Intercept	0.07	0.60		0.003	0.42		-0.03	0.16	
Response type (level 1 = no)	-0.06	0.08	0.53 (0.47)	0.03	0.14	0.18 (0.67)	-0.07	0.18	1.10 (0.29)
Habitat (level 1 = deciduous)	0.16	0.12	2.07 (0.15)	-0.24	0.20	2.11 (0.15)	0.06	0.08	0.11 (0.74)
Lay-date				-0.18	0.15	5.85 (0.016)	-0.32	0.15	1.05 (0.31)
Clutch size							0.08	0.08	0.84 (0.36)
Neighbour distance	0.04	0.04	0.79 (0.37)	-0.01	0.09	<0.01 (0.98)	-0.13	0.11	1.39 (0.24)
Nest-box occupancy	-0.05	0.06	0.72 (0.40)	-0.09	0.11	0.72 (0.40)	0.08	0.12	0.46 (0.50)
Nest predation (level 1 = no)	0.06	0.09	0.45 (0.50)	-0.11	0.16	0.52 (0.47)	-0.34	0.19	3.34 (0.07)
Response type* Lay-date				-0.19	0.14	1.98 (0.17)	0.40	0.19	4.17 (0.041)
Random effects	VC			VC			VC		
Transect	<0.01			0.02			<0.01		
Year	1.09			0.46			<0.01		
R^2 GLMM	79.1 %			41.1 %			11.0 %		

Hissing response is a categorical factor (non-responding versus responding birds); R^2 is variance explained by fixed and random effects (Nakagawa and Schielzeth 2013), $N_{\text{years}} = 3$ and $N_{\text{transects}} = 18$

SE standard errors, VC variance components

Table 2 Mixed effects full models of lay-date ($N_{\text{individuals}} = 59$, $N_{\text{years}} = 2$ and $N_{\text{transects}} = 17$), clutch size ($N_{\text{individuals}} = 59$, $N_{\text{years}} = 2$ and $N_{\text{transects}} = 17$), female body mass ($N_{\text{individuals}} = 34$, $N_{\text{years}} = 2$ and $N_{\text{transects}} = 14$) among responding birds (hissing delay varies from 1 to

5 s) and a binary mixed model (logit link) on the hissing response (non-responding versus responding birds, $N_{\text{individuals}} = 188$, $N_{\text{years}} = 3$ and $N_{\text{transects}} = 18$)

	Lay-date (hypotheses 1 and 4)			Clutch size (hypothesis 1)			Female body mass (hypothesis 2)			Response type (hypotheses 3 and 4)		
	Beta	SE	χ^2 (p)	Beta	SE	χ^2 (p)	Beta	SE	χ^2 (p)	Beta	SE	χ^2 (p)
Fixed effects												
Intercept	-0.19	1.00		-0.65	0.54		-0.35	0.34		0.48	0.21	
Hissing delay	0.56	0.20	7.61 (0.006)	0.10	0.10	1.06 (0.30)	0.17	0.12	1.82 (0.17)			
Hissing delay ²	-0.08	0.03	5.31 (0.021)									
Habitat	-0.05	0.14	0.14 (0.71)	0.25	0.27	0.83 (0.36)	0.06	0.36	0.03 (0.87)	0.03	0.51	0.01 (0.95)
Lay-date				-0.21	0.23	0.81 (0.37)	-0.05	0.18	0.08 (0.78)	0.05	0.17	0.09 (0.76)
Clutch size							0.29	0.19	2.38 (0.12)	0.01	0.16	0.01 (0.93)
Neighbour distance	0.02	0.05	0.18 (0.67)	0.01	0.10	0.01 (0.93)	-0.01	0.15	0.01 (0.94)	-0.37	0.19	3.86 (0.05)
Nest-box occupancy	-0.17	0.09	3.82 (0.05)	0.07	0.17	0.17 (0.68)	<0.01	0.22	<0.01 (0.94)	-0.46	0.21	4.79 (0.028)
Nest predation										0.05	0.36	0.02 (0.89)
Random effects	VC			VC			VC			VC		
Transect	<0.01			<0.01			0.02			0.26		
Year	1.90			0.45			<0.01			<0.01		
R ² GLMM	92.4 %			42.8 %			14.6 %			49.3 %		

R² is variance explained by fixed and random effects (Nakagawa and Schielzeth 2013)

SE standard errors, VC variance components

over 5 s) was moderate ($r = 0.45$, $F_{32, 33} = 2.32$, $P = 0.010$; using the formula by Lessels and Boag 1987).

Our results do not confirm an association between hissing behaviour and early reproductive investment. Lay-date was not related to response type (Table 1). Among hissing females, a quadratic relationship was found between lay-date and hissing delay (Fig. 1, Table 2). Clutch size was not related to response type, while this parameter was negatively related to

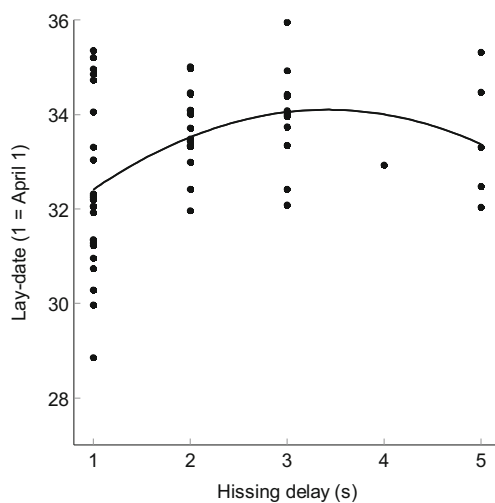


Fig. 1 Among hissing females, delay was non-linearly related to lay-date (curve represents quadratic relationship). Latency to hiss was measured as the time taken from the start of the trial (presentation of the woodpecker) until the first hissing sound was produced. The trial lasted 5 s

lay-date (Table 1). Note that the relationship between clutch size and lay-date was not influenced by response type (Table 1). Among hissing birds, clutch size was not associated with hissing delay (Table 2).

Hissing behaviour did not directly relate to female quality. Female body mass was not related to response type (Table 1), while a significant interaction term was observed between response type and lay-date (Table 1). Heavier females lay earlier in the season among non-responding females (Fig. 2, $\chi^2 = 5.57$, $\text{beta} = -0.32$, $P = 0.018$, $N = 57$), whereas no such pattern emerged among responding birds ($\chi^2 = 0.40$, $\text{beta} = 0.08$, $P = 0.53$, $N = 83$; both models adjusted for other predictors). Among hissing birds, female body mass was not associated with hissing delay (Table 2).

We found a link between hissing behaviour and population density: responding females bred in locations with decreased nest-box occupancy when compared to non-responding birds (Fig. 3, Table 2).

Contrary to our prediction, response type of females was not related to nest predation risk (Table 2).

Discussion

Nest predation is one of the most important mortality factors of wild animals (Lima 2009). Cavity nesting birds can escape from a nest predator using acoustic signals by making the

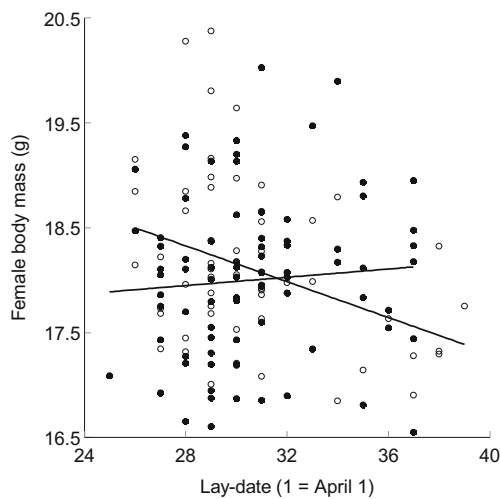


Fig. 2 The relationship between lay-date and female body mass by female response type (*empty circles*—non-hissing, *filled circles*—hissing females). The regression line is corrected for other factors in the model

approaching predator retreat. However, given that this anti-predator behaviour varies between individuals, it seems that direct benefits and costs of such behaviour depend on environmental as well as individual characteristics.

In this study, we found that when female great tits are exposed to a potential nest predator, the woodpecker model, about 61 %, gives hissing calls within 5 s, while 39 % of individuals do not respond at all. We revealed that such distinct behaviour was highly consistent over time, given that about 83 % of individuals did not change their response type when the model was presented 3–5 days later. Further, we showed that among responding birds, the magnitude of hissing delay was also moderately repeatable, suggesting there was no habituation to the predator model.

Our reported repeatability values (response type, $Kappa = 0.63$; hissing delay, $R = 0.45$) are well within the

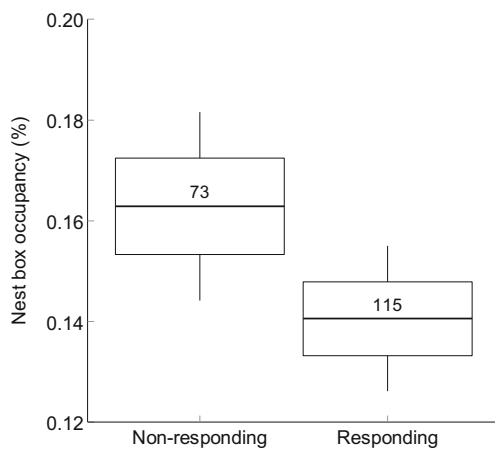


Fig. 3 Responding type of females (non-responding versus responding) was related to nest-box occupancy (% of occupied nest-boxes per transect). Boxes and whiskers denote standard errors and confidence limits, respectively. Numbers are sample sizes

range of those of anti-predator- and aggression-related behavioural traits reported in other animal species, including birds (according to a meta-analysis by Bell et al. 2009, repeatability values (R) typically range from 0.3 to 0.5). Hence, our data supports Krams et al. (2014) that the propensity to hiss during the incubation stage is a consistent behavioural trait in great tits that may entail some information on aspects of personality.

Hissing behaviour and reproduction

Our results show that response type was not directly connected to early reproductive traits when explored across all individuals belonging to two distinct behavioural types. However, within the responsive group, we observed a quadratic relationship between lay-date and hissing delay. The latter result can be interpreted as early breeders rapidly responding towards the nest predator, perhaps due to heightened predation risk (Shustack and Rodewald 2011; Borgmann et al. 2013), while this association between lay-date and hissing delay diminishes quickly as the season progresses. Moreover, it is possible that early breeders responded stronger because offspring from early broods tend to survive better (Perrins 1965) and produce larger clutches (Tilgar et al. 2011), thus being more valuable to their parents. Hence, this finding indirectly supports the parental investment theory stating that nest defence can be adjusted to the level of current reproductive investment (Rytkönen 2002). However, it is important to emphasize that the current study is correlative and it is difficult to disentangle the factors that potentially influence clutch size and the timing of breeding among responsive birds.

According to the brood value hypothesis, those parents that delayed their response over the 5 s period should have the smallest investment into the current brood. However, we revealed no differences in lay-date, clutch size and female body condition between hissing and non-hissing groups. It suggests that the brood value hypothesis does not explain behavioural differences between hissing types. Furthermore, it is more likely that the passive anti-predator response of non-hissing birds can be better explained as an alternative strategy of nest defence. On the other hand, we did find that parental body mass was negatively affected by lay-date among non-hissing birds only. Possibly, non-hissing females were low-quality birds that were more affected by seasonal constraints of the late breeding conditions than non-hissing individuals. Alternatively, considering that female body mass was measured during the nestling stage, we cannot exclude that non-hissing birds that bred in the late season lost more body mass when compared to hissing birds because they provided higher level of parental care under poor environmental conditions. Unfortunately, we did not measure breeding success in the current study to prove this assumption.

Overall, in the face of such alternative strategies, determining the fitness consequences of hissing behaviour is indeed a

difficult task. Nevertheless, it seems that non-hissing behaviour is definitely not predictive of reduced reproductive success. Also, we cannot exclude the possibility that non-hissing birds represent different type of personality (Krams et al. 2014). However, this remains to be addressed in future studies.

Predation risk and population density

While acknowledging individual variation is becoming commonplace, the link between anti-predator behaviour and territory quality (e.g. perceived predation risk or food supply and social interactions) has been poorly studied. In our study area, hissing birds were more likely to breed in areas with decreased nest-box occupancy compared to non-responding great tits.

We cannot rule out the idea that response type is connected to individual quality or personality. It is known that female great tits do not only defend the immediate surroundings of the nest but will attack a caged female intruder positioned 30 m away, suggesting that female–female aggression is of importance for the maintenance of monogamy or may be connected to the defence of a feeding area or the nest site (Slagsvold 1993). Hence, it is possible that hissing females behave more dominantly or aggressively towards conspecifics than non-hissing individuals, e.g. driving neighbours farther away, leading to larger territories and lower densities. In agreement with this assumption, a study with the red grouse (*Lagopus lagopus scoticus*) revealed that by experimentally increasing aggressiveness for a short period in the autumn, the subsequent breeding density was reduced by 50 %, suggesting that aggressiveness limits density through changes in territory size (Mougeot et al. 2003). Moreover, it may be that more actively hissing females form a breeding pair with the same behavioural type—that is with an aggressive male. Previous studies on different vertebrate taxa have shown that aggressive males have larger territories (fishes—van den Assem 1967; birds—Harris 1979; Moss et al. 1994; Krebs 2007). The great tit is a territorial species, and short-lasting fights are very common and often determined by male–male aggression, while females may join in the mock fights but usually to the rear of the males (Kluyver 1951). Hence, we may argue that aggressive males are able to acquire and maintain larger than average territories resulting in a low population density.

We failed to find evidence that response type is related to the risk of nest predation. Previous studies have shown that the probability of nest predation is positively associated with predator abundance (Angelstam 1986, Andren 1992). Hence, we propose that variation in the perceived predation risk in different breeding areas (transects) did not alter the propensity to hiss. This result is inconsistent to previous studies showing that anti-predator behaviours may be enhanced in risky environments (e.g. Lima 2009, Krams et al. 2010). One reason can be that differences in predation risk between territories and habitats were rather small and cannot contribute

significantly to variation in hissing responses. Moreover, given that we showed moderate repeatability of the hissing types, the other possibility is that intra-specific variation in hissing behaviour is an inherited trait that changes little in different environments. In line with this assumption, we found no support to our prediction that response type can vary in relation to seasonal changes in the perceived predation risk. However, we remind in this context that among responding birds, hissing delay was non-linearly related to lay-date, possibly following seasonal changes in the probability of nest predation (see the section on hissing behaviour and reproduction). Given this, it seems that the hissing response type is a less flexible behavioural trait than hissing delay and these traits potentially reflect different aspects of anti-predator behaviour.

Conclusions

There was correlative evidence that hissing latency was adjusted to the earlier lay-date among responsive birds, partly supporting the parental investment theory. However, non-responding birds did not invest less into clutch size than responding females, suggesting that these distinct behavioural responses can be regarded as alternative decision-making strategies. We also found that responding birds tended to breed in areas with decreased nest-box occupancy when compared to silent conspecifics, suggesting that distinct response types can be connected to consistent differences in dominance or personality.

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Conflict of interest The authors declare that they have no conflict of interest.

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