Supplemental food alters nest defence and incubation behaviour of an open-nesting wetland songbird.

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ABSTRACT

Climate-driven increases in spring temperatures are expected to result in higher prey availability earlier in the breeding season for insectivorous birds breeding in wetland habitats. Predation during the incubation phase is a major cause of nesting failure in open-nesting altricial birds such as the Eurasian reed warbler. The nest predation rate in this species has recently been shown to be substantially reduced under conditions of experimentally elevated invertebrate prey availability. Food availability near the nest may be an important determinant of adult incubation and nest defence behaviours during the incubation period. We used two experimental studies to compare incubation behaviour and nest defence in food-supplemented and unsupplemented adult Eurasian reed warblers during the incubation phase. In the first study we measured nest defence behavioural responses to a taxidermic mount of a native predator (a Stoat, *Mustela erminea*). In the second study we used temperature loggers installed in nests to measure breaks in incubation as a measure of nest vulnerability. Food-supplemented birds responded aggressively to the presence of a predator more quickly than those in the unsupplemented group, suggesting they are closer to their nest and can more quickly detect a predator in the vicinity. Food-supplemented birds also had shorter breaks in incubation (both in terms of maximum and mean off-bout durations), presumably because they were foraging for shorter periods or over shorter distances from the nest. This study therefore identifies the behavioural mechanisms by which changes in food availability may lead to changes in nest survival and thus breeding productivity, in open-nesting insectivorous birds.

Keywords

Supplemental food, Incubation, Insectivore, nest defence, nest predation

INTRODUCTION

Nest predation is a prime determinant of reproductive success in passerines, particularly open-nesting species, and therefore behavioural strategies that minimise nest predation should be strongly favoured by natural selection (Martin 1993; Halupka et al. 2014). Concealment of nests in dense vegetation does not guarantee protection of the nest against predation so parents may engage in active defence of the nest with behaviors including alarm calling, “bill-snapping”, and physically attacking the predator (Weidinger 2002, Trnka *et al.* 2009; Leisler et al. 2011; Beckmann & Martin 2016). The parents often forage at considerable distances from their nest, leaving the nest exposed to predators (Duckworth 1991; Poulin et al. 2000; Eikenaar et al. 2003). Parent birds must therefore trade-off time spent foraging away from the nest, against time spent at the nest for incubation, guarding and defending the nest against predators (Orians and Pearson 1979; Martin 1992). The availability of abundant food close to the nest is expected to alter this trade-off in favour of more time spent on the nest and more rapid defence against predators.

European populations of Eurasian reed warblers *Acrocephalus scirpaceus* (henceforth “reed warblers”) are increasing (Robinson *et al.* 2015). This may be due to several inter-related factors, including higher breeding productivity due to warmer spring conditions leading to higher food availability during earlier and longer breeding seasons (Halupka *et al.* 2008). Experimental food supplementation (used to simulate more abundant food earlier in the breeding season, as expected under projected climate change scenarios (Bale *et al.* 2002; Dell *et al.* 2005)) has been shown to induce reed warblers to nest earlier, shortening their incubation phase and nestling growth periods (Vafidis *et al.* 2016). These food-driven changes in breeding behavior lead to earlier and more successful fledging, increasing the overall productivity of the first brood and allowing the first brood to be fledged early enough in the breeding season for second breeding attempts to be initiated (Vafidis *et al.* 2016). Food-supplemented pairs of reed warblers also suffered substantially lower rates of nest predation compared with control (unsupplemented) pairs. Reed warbler nests are depredated by a range of predator species including birds such as water rail *Rallus aquaticus*, sparrowhawk *Accipiter nisus*, carrion crow *Corvus corone,* and Eurasian jay *Garrulus glandarius*, and mammals including stoat *Mustela ermine*, Grey Squirrel *Sciurcus carolinensis* and other smaller rodents (Honza *et al*. 1998, Kleindorfer *et al.* 2005; Leisler *et al.* 2011; Halupka *et al.* 2014). European Cuckoos *Cuculus canorus* are a major brood parasite of reed warblers and will depredate whole clutches of eggs if they are too advanced to be parasitized (Davies & Brook 1988). The cuckoo, like many of the other bird species are alerted by visual as well as acoustic cues, and will react to prey and host movement and sound (Batary *et al*. 2004). The mammal predators are more likely to search the area for nests using olfactory cues (Hogstad 2004).

The three primary non-exclusive hypotheses accounting for the reduced nest predation with supplemental feeding are (i) that the incubation and nestling phase is shorter for supplemented nests, reducing the period of vulnerability to nest predation. (ii) Supplemented parent birds may have shorter and/or fewer off-bouts, leaving the nest less exposed (and therefore less cryptic) and providing fewer visual cues for predators. (iii) Supplemented parent birds may be able to spend less time foraging, and forage closer to the nest, enabling them to detect and respond to predators more quickly than unsupplemented parents.

In this paper we test the nest-defence responses of parent reed warblers to a mounted predator ('*Predator presentation*') under experimental increases in food availability ('supplemented'), compared to those under natural foraging conditions ('unsupplemented'). We provide support for the influence of supplementation on general nest attentiveness by measuring the number and duration of breaks in incubation ('*incubation off-bouts*') of supplemented pairs of reed warblers compared with unsupplemented pairs. We hypothesise that supplemented pairs would show a faster nest-defence response to the predator than unsupplemented pairs. We also predict that supplemented pairs would have fewer breaks in incubation spend shorter durations away from the nest than unsupplemented pairs.

METHODS

Animal Welfare

The guidelines promoted by the Association for the Study of Animal Behaviour for the ethical use of animals in research are followed. Reed warblers are common and not registered as an endangered or protected species in any country. All fieldwork was conducted by experienced field personnel who are licenced by the British Trust for Ornithology (BTO) ringing unit (Vafidis licence no; A5475). Reed warbler nests are monitored regularly in the BTO nest record scheme and are not prone to nest desertion by adults in response to predator presentation trials (Duckworth 1991; Davies *et al.* 2003; Kleindorfer *et al*. 2005) or the use of nest temperature probes (Kleindorfer *et al*. 1995).

Study sites

The '*Predator presentation*' study was undertaken in 2015 and replicated in two wetland locations in South Wales, UK; (1) Cardiff Bay Wetland Reserve (CBWR; 51º 27' 32'' N, 3º 10' 11'' W), a four-hectare wetland, and (2) Cosmeston Lakes Country Park (CLCP, 51° 24′ 53″ N 3° 6′ 0″ W), consisting of two adjacent small reedbed sites (with a total area of approximately 1.5 hectares) separated by 200 m of freshwater lake habitat. Both sites are publicly owned and access was arranged through the local authorities. The '*Incubation off-bout*' study was undertaken in 2016 in CBWR only.

Bird ringing

Breeding adult reed warblers were captured at the study sites during regular mist-netting sessions between April 2015 and June 2016. All reed warblers in the study were fitted with a unique combination of three plastic colour rings and a numbered metal ring, to enable individual identification in the field.

Nest monitoring

Active nests were located by systematic searching of suitable nesting habitat (dense, tall stands of *Phragmites* reeds) and by visually tracking adults back to the nest. The status of each nest was checked every two days until the first eggs were laid, then they were checked once a day until the fourth egg was laid. All nests in this study contained a total of four eggs.

Food supplementation

Prey availability for reed warblers was experimentally increased in a subset of territories at both study sites during the early breeding season (Table 1). This was achieved by dividing the available nesting habitat into six subsections of approximately 5,000 m^2 using satellite maps and GIS software, and randomly selecting two subsections at each site for supplementation. Supplementation was achieved by providing live mealworms, *Tenebrio molitor* larvae (Coleoptera), in containers (2 litre capacity) resting on small feeding-tables at 1.5 m height, from early April onwards. Two of these feeding stations were installed in each selected subsection at each site, with each station supplied with at least 200 mealworms and refilled every day throughout the study. Feeding bowls were enclosed in a wire mesh cage (measuring 300 x 200 x 200 mm of 10 mm mesh) to prevent the mealworms being taken by larger bird species and rodents, but permitting access to reed warblers and other small passerines. All adult reed warblers nesting within 50 m of the feeding stations discovered the mealworms within three to five days of nest building activity, and were observed feeding daily from containers. The nests used for the unsupplemented pairs were located at least 150 m away from the nearest feeding stations, to minimise the likelihood of accidental supplementary feeding of control birds visiting feeding stations (no such incidences were observed). This was confirmed by individually identifying the adult reed warblers using the feeding stations, and by remotely monitoring the stations with small video cameras (custom-built raspberry pi camera units https://www.raspberrypi.org/products/camera-module/) and infrared-triggered trail cameras (Bushnell HD http://Bushnell.co.uk). Activity around the feeding stations was recorded between 06:00 and 18:00 BST every two days throughout the onset and duration of incubation in both studies (see also Vafidis *et al*. 2016).

Predator presentation study

In 2015 at CBWR and CLCP, active first-clutch nests of reed warblers at varying stages of incubation (between 1 and 8 days following the laying of the fourth egg), were presented with a taxidermic mount of a stoat, a typical nest predator (Honza et al. 1998, Leisler et al. 2011; Halupka et al. 2014). The choice of predator used in this study was arbitrary on the basis that parent birds are just as likely to react to any potential threat near their nest. A taxidermic mount of a stoat at a proximity of 1m from reed warbler nests was shown to stimulate a significant defence response compared to further distances (Kleindorfer *et al.* 2005). The stoat was mounted on a pole so that it could be positioned at nest height, adjacent to the nest (< 1 m from the nest), so as to simulate a potential threat to the nest, for a period of five minutes. Following the placement of the predator mount, the observer (JOV) quickly retreated well away from the nest (> 20 m). Trials were conducted between 08:00 and 10:00 under similar weather conditions with low wind and no rain.

The response behaviours of adult reed warblers were monitored using two digital video cameras (camera details as in '*Food supplementation*' section above), arranged to capture activity in an approximate 2.5 m radius around the nest and taxidermic mount. This approach has been used to measure defence investment in other passerines during the breeding season (Radford & Blakey 2000; Leech *et al.* 2006). Cameras were installed 15 minutes prior to the trials in both predator and non-predator trials. Each nesting pair (and potentially also their close neighbours) were only subjected to a single presentation of a predator during this study. To control and test for observer effects, the same nests were also subject to the same monitoring procedures using video cameras and approach of the observer, but without a taxidermic mount, on different days, either before or after the predator simulation. The video footage from both control and presentation trials was used to measure the time taken for an adult to appear within 1 m of the nest/predator mount ('Latency to response') from the moment of presentation (or control 'null' presentation). The intensity of response was recorded by measuring the duration of alarm calling and bill snapping, and any instances of birds physically attacking the mount.

Incubation off-bout study

The presence or absence of a parent bird on the nest was determined using measurements of nest temperature across the entire incubation period. Temperature probes and dataloggers (Thermister probe PB-5005; Tinytag Talk 2 TK4014; Gemini Data Loggers Ltd., Chichester, U.K.) were installed on active reed warbler nests prior to egg-laying. This technique has been used to monitor incubation behavior in a number of passerine species (e.g. Joyce *et al*. 2001; Camfield and Martin 2009). The installation of the data loggers involved carefully inserting temperature probes through the nest material so the tip of the probe was flush with the lining of the nest cup. The probe wire was fixed to a stem of common reed *Phragmites australis* just below the nest using clear adhesive tape. The probe jack was then inserted to the datalogger, which was attached to a separate stem of common reed. This activity required a license from Natural Resources Wales (under section 1. (1)(b) of the Wildlife and Countryside Act 1981) and the adherence to a method statement that minimised damage and disturbance to nests (Appendix A1). Data loggers were programmed to begin recording temperature measurements from within the nest every minute from the first day following the laying of the fourth egg and continuing for nine days. The temperature recordings were analysed to identify incubation off-bout behaviour. The start of incubation off-bouts are indicated by large immediate declines in nest temperature (approximately >1.25 °C per minute) and continuing to decline until the parent has returned (See Figure 1 for an example of off-bout assessment). All nests were filmed (camera details as described in '*Food supplementation*') so that temperature signatures could be cross-referenced manually to confirm off-bouts and to identify off-bouts resulting in less-rapid temperature loss (e.g. during warmer ambient temperatures). The mean ambient temperature was recorded using an external temperature datalogger (Tinytag Ultra 2 TGU4017) set within typical nesting habitat in CBWR.

Weather variables

The mean air temperature, mean relative humidity, mean wind speed and total rainfall data were summarised from measurements collected by an automated weather station (Davis Instruments Vantage Pro 2, Hayward, CA) located 0.75 km and 4.5 km from CBWR and CLCP, respectively.

Statistical analysis

The *Predator presentation* study tested the effects of food supplementation on the responses of reed warblers to the presence of a potential nest predator. The dependent variable was latency to response (time taken for an adult to appear within 1 m of the nest/predator mount). As well as food supplementation, we examined whether latency may also be affected by factors such as time of day, date, incubation day (i.e. number of days since the fourth egg was laid), study site, and weather variables.

The *Incubation off-bout* study tested the effects of food supplementation on mean off-bout duration, and maximum off-bout duration. These measures were calculated for each nest on each day of incubation between the hours of 05:00 and 20:00 and are analysed as decimal minutes (to retain the same units that were measured). As well as examining the effect of food supplementation, we tested whether these response parameters may also be affected by factors such as date, incubation day, and weather (mean ambient temperature, relative humidity, and mean wind speed).

Both studies were investigated using the statistical package R, version 3.3.1 (R Development Core Team, 2016) fitting generalised linear mixed-effects models (GLMMs) with a ‘Gaussian’ error distribution and an ‘identity’ link function using the R package ‘lme4’ (Bates *et al.* 2015).

All starting models included all relevant variables and all two-way interactions as independent terms. The identity number for each nest was used as a random factor in mixed-effects models to account for repeated monitoring from the same nest. The final models were selected using stepwise deletion of non-significant ($P > 0.05$) terms. Data exploration and model validation procedures followed Zuur *et al.* (2007) and Thomas *et al.* (2015), specifically testing for collinearity between predictor variables using variance inflation factors (VIF) and visually inspecting the model residuals for normality and homoscedasticity.

RESULTS

Predator presentation study

Of the 62 nest trials (comprising 31 nests, each trialed on two occasions), none had sitting (incubating) parents on the observer's arrival. In both predator presentation trials and control trials (i.e. without the predator), at least one reed warbler returned to each nest within three minutes of the observer's visit. The significant predictors of latency to response included predator presence, supplementation, the day of incubation, and the two-way interactions between supplementation and predator presence, and between predator presence and incubation date (GLMM; marginal $R^2 = 0.449$; Table 2). The response latency was shorter during predator presentations than for control trials in both unsupplemented and supplemented groups, and the response latency for supplemented birds was significantly shorter than for unsupplemented birds (Figure 2). The latency also became shorter for both unsupplemented and supplemented birds as the incubation date progressed (Table 2). All reed warblers returning to the nest during the predator presentations approached the mount within one metre, but none physically attacked the mount. The returning reed warbler made alarm calls in only three of the 31 trials.

Incubation off-bout study

The total daily off-bouts between the hours of 05:00 and 20:00 over the incubation period across 16 nests ranged between 59 and 322, with a mean number of 183.7. The off-bout duration ranged between one and 13 minutes with a mean off-bout duration (for each nest on each day of the incubation period) ranging between 1.21 and 3.60 decimal minutes.. Food supplementation, incubation day, and the two-way interaction between supplementation and date were all significant predictors of mean off-bout duration (GLMM; marginal R^2=0.147; Table 3). The mean off-bout duration was shorter in supplemented nests than unsupplemented nests (Figure 3). There was a weak negative effect of incubation day, with off-bouts becoming shorter as the incubation period progressed. There was a very weak positive effect of the interaction between supplementation and date (the increase in mean off-bout duration in supplemented nests was only 0.008 decimal minutes longer for each additional day of the year, compared to unsupplemented nests).

Maximum off-bout duration

The maximum off-bout duration ranged between 3 and 12 minutes across 16 nests. There was a significant difference between supplemented and unsupplemented nests (GLMM; R^2=0.05), with shorter maximum durations in supplemented nests (-0.89 ± 0.38; $F_{1,13.422}$=5.466; P=0.0355; Figure 4).

DISCUSSION

The predator presentation trials resulted in birds returning to the nest more quickly than during their normal undisturbed incubation routine. This suggests they consider the taxidermic mount of a stoat a threat to their nest, and are reacting more quickly than unsupplemented birds as a result of foraging in the nearby area. This response was observed in similar predator presentation trials (Duckworth 1991; Poulin et al. 2000; Eikenaar et al. 2003) and reflects optimal behaviour as modelled by central place foraging theory (Orians and Pearson 1979; Martin 1992). As a result, the food-supplemented birds may have been able to more regularly observe the nest area and check for threats compared to control birds foraging under conditions of natural food abundance. A stronger nest defence response in supplemented treatments is shown in other breeding passerines (Rytkönen 2002; Rastogi *et al*. 2006; Récapet *et al.* 2016) and is attributed to reduction in the constraint of foraging, enabling greater nest vigilance.

All reed warblers approached the taxidermic predator mount within one metre but none physically attacked the mount. It is possible that the birds avoided attacking because they considered the mount to be a threat to themselves. However, few individuals gave alarm calls and birds typically stayed near the nest for approximately 30 seconds before appearing to lose interest in the mount and left the nest area. These observations together suggest that the birds assessed the threat and concluded that the mount was not a threat after all. Alarm calls can deter predators but can also alert other predators and other brood parasites if the threat is not substantial (Smith *et al.* 1984; Krama and Krams 2005; Welbergen and Davies 2008). Such dynamic risk assessment behaviour reflects similar studies of *Acrocephalus* warblers in response to nest predators and brood parasites (Duckworth 1991; Kleindorfer *et al.* 2005; Trynka and Grim 2014; Li *et al.* 2015). In the Kleindorfer *et* al. study (2005), reed warblers and great reed warblers reacted vigorously with alarm calling and bill snapping in response to a taxidermic mount of a stoat when it was placed within 1m of the nest, but reacted less vigorously when it was placed at 5m. In a similar presentation study, Hogstad (2004) observed that fieldfares *Turdus pilaris*, when presented with a carrion crow, would physically attack the mount, but when presented with a stoat would not attack but instead protect or conceal the eggs. This may be a considered response to a more dangerous threat with the risk of injury or mortality to the parent outweighing the value of protecting the nest.

The longer the time elapsed since the initiation of the clutch (i.e. the closer the time to hatching), the more rapidly reed warblers approached the nest when the predator was present. This effect of clutch age can be interpreted as a result of the increasing value of the clutch to the parents as incubation proceeds. This behavior is consistent with the offspring value hypothesis, in which the more valuable the nest contents are, the more risks a parent could be expected to take in their defence (Sargent & Gross 1985, Onnebrink & Curio 1991; Forbes *et al*.,1994; Halupka 1999). Duckworth (1991) found the same pattern of adult reed warbler defence of nests becoming stronger, closer to fledging, attributing this effect to the defence of an increasingly valuable resource.

Due to fast movement of birds and minimal footage showing perching, it was not always possible to identify individuals in order to assign gender or nest ownership to the birds present. It is possible that the birds nesting in the supplemented treatment area may have higher nesting densities, and as such are more likely to encounter threats to neighbouring nests during foraging. Although this reduces the confidence in the effect of supplementation on nest defence, the neighboring birds are likely to benefit directly from supplementation and possibly indirectly from reduced competition for natural food resources. Nest densities at the study sites were relatively low and typically separated by more than 12 m. On this basis, instances of neighbouring birds being recorded as focal nest parents would be low as they would not have a direct line of sight of the taxidermic mount.

The differences in nest attentiveness observed in the predator study was also reflected in the incubation off-bout study, with shorter mean and maximum off-bouts in supplemented nests. The differences in the mean off-bout duration between the groups was small (approximately 0.1 decimal minutes, which is approximately 6 seconds). Supplemented birds are able to obtain their food supply in each off-bout sooner than the unsupplemented birds by travelling directly to a feeding station, rather than actively searching for their food. The mean difference of 6 seconds is small, however, given that the number of daily off-bouts regularly exceed 200 trips, the effect of food supplementation on nest attendance amounts to approximately 20 additional minutes per day, across the incubation period of 11 days (i.e. over 4.5 additional hours of absence from the nest across the whole incubation period).

Furthermore, egg-cooling rates are non-linear (Turner 1985), so shortening an off-bout by as little as 7 seconds may be beneficial in terms of the energy expenditure required to warm the eggs back up. Higher rates of incubation constancy can reduce the incubation period and result in higher hatchling mass, reducing the overall period of vulnerability to predation (Eikinaar *et al.* 2003; Vafidis *et al.* 2016). This result is supported by the significantly lower maximum off-bout durations recorded in the supplemented nests compared to the unsupplemented nests. The incubation off-bout study did not detect an equivalent reduction in off-bout duration with clutch age, however. Although off-bout duration is also determined by thermal requirements, without a predator presented to the nests, there was, perhaps, less reason to return quickly to the nest.

The incubation off-bout study provides support for the faster reactions observed in supplemented birds in the predator presentation study. We can surmise that supplemented birds are returning more quickly to their nests and are therefore more likely to encounter a threat earlier than unsupplemented birds. It is difficult to make broader generalisations about incubation off-bout behavior given the low sample sizes in each treatment group. Despite the shortfall of this study, the findings nonetheless provide important differences between better-provisioned adults and those foraging under natural conditions that warrant further research across the whole nesting period using larger sample sizes across the northern breeding distribution. Furthermore, it is important to understand the influence of stochastic and disruptive weather conditions, which are predicted to occur more frequently with climate change, on incubation off-bout behavior and the consequences for nest predation.

Conclusions

Given that increasing spring temperatures are expected to drive increases in food availability in wetland habitats during the reed warbler breeding season, the results presented here suggest that warmer spring conditions will lead to reed warblers being more attentive to their nests and respond more quickly to threats at the nest. The lower rates of depredation observed in the supplemental food study in this study population (Vafidis et al. 2016) may also be explained partially by the increased latency to respond to predators and the shorter off-bout durations which reduce the period of nest vulnerability to predation.

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Figure Legends

Figure 1. Example of assessment of incubation off-bout using nest temperature signals. Off-bouts were measured when nest temperature drops by approximately 1.25°C in one minute. In this example, 14 off-bouts were measured between 05:00 and 09:00.

Figure 2. Latency to response (time taken to return to the vicinity of the nest, in seconds) of adult reed warblers in both unsupplemented and supplemented groups to presentation of a mounted predator and a control trial (no mounted predator).

Figure. 3. Mean off-bout duration (in decimal minutes; ± SE) of reed warbler nests in unsupplemented and supplemented groups.

Figure 4. Maximum off-bout duration (in decimal minutes; ± SE) of reed warbler nests in unsupplemented and supplemented groups.

Table 1. Sample sizes of unsupplemented and supplemented reed warbler nests

Study	*Site*	*Unsupplemented*	*Supplemented*
Predator presentation	CBWR	N=8	N=9
	CLCP	N=8	N=6
Incubation off-bout	CBWR	N=9	N=7

Table 2. Analysis of predator presentation study. GLMM model explaining adult reed warbler latency to response (time taken to return to the vicinity of the nest, in seconds).

Parameter	***Estimate ± SE***	**df**	**F**	**P**
Predator Present	-52.96 ± 18.45	1,52.50	16.878	0.0001
Food supplementation	-10.47 ± 10.69	1,28.46	9.581	0.0044
Incubation day	-12.10 ± 2.17	1,33.02	26.990	<0.0001
Food supplementation x Predator	-33.44 ± 12.28	1,28.34	7.420	0.0109
Predator x Incubation day	8.86 ± 3.79	1,45.83	5.475	0.0237

Table 3. Analysis of incubation off-bout. GLMM model parameter estimates, standard errors, explaining mean off-bout duration (in decimal minutes).

Parameter	***Estimate ± SE***	**df**	**F**	**P value**
Supplementation	-1.46 ± 0.60	1,14.96	5.878	0.0285
Incubation day	-0.03 ± 0.007	1,172.53	14.025	0.0002
date	-0.003 ± 0.002	1,13.52	0.200	0.6618
Supplementation x date	0.008 ± 0.003	1,15.13	4.877	0.0430