The Effect of Male Incubation Feeding, Food and Temperature on the Incubation Behaviour of New Zealand Robins

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Abstract

Because of finite resources, organisms face conflict between their own self-care and reproduction. This conflict is especially apparent in avian species with female-only incubation, where females face a trade-off between time allocated to their own self-maintenance and the thermal requirements of developing embryos. We recorded incubation behaviour of the New Zealand robin (*Petroica longipes*), a species with female-only incubation, male incubation feeding and high nest predation rates. We examined how male incubation feeding, ambient temperature and food availability (invertebrate biomass) affected the different components of females' incubation behaviour and whether incubation behaviour explained variation in nest survival. Our results suggest that male incubation feeding rates of 2.8 per hour affect the female's incubation rhythm by reducing both on- and off-bout duration, resulting in no effect on female nest attentiveness, thus no support for the female-nutritional hypothesis. The incubation behaviours that we measured did not explain nest survival, despite high nest predation rates. Increased ambient temperature caused an increase in off-bout duration, whereas increased food availability increased on-bout duration. While males play a vital role in influencing incubation behaviour, female robins attempt to resolve the trade-off between their own foraging needs and the thermal requirements of their developing embryos via alternating their incubation rhythm in relation to both food and temperature.

Introduction

Organisms have finite resources, and therefore must make decisions on how to allocate these limited resources between self-care and reproduction. Studying resource allocation trade-offs and reproductive cost is prominent in avian systems because these activities are not mutually exclusive in species which exhibit contact incubation. In the Passeriformes, where over 60% of families exhibit female-only incubation (Deeming 2002), the female faces a trade-off between time allocated to foraging for maintaining her own energy requirements, and the thermal needs of her developing embryos. Females divide the day

into periods of foraging (off-bouts), when the unattended clutch begins to equilibrate with the ambient temperature, and incubation periods (on-bouts), when females use energy re-warming their eggs after feeding bouts. This incubation rhythm affects egg temperature and overall nest attentiveness, defined as the proportion of daylight hours spent on the nest.

Avian eggs, to hatch successfully, must maintain temperatures that facilitate embryonic development (between 34 and 38°C, Webb 1987; Williams 1996). Therefore, by understanding what factors influence incubation rhythm, we may better explain the enormous variation documented in avian incubation strategies (Conway & Martin 2000a), and how

females deal with the life-history trade-off between self-care and parental care.

Although a number of factors may influence a female's optimal incubation rhythm, the most common constraints hypothesised in the literature are ambient temperature, food availability and nest predation (Skutch 1962; Davis 1984; Conway & Martin 2000a,b; Deeming 2002; Londono et al. 2008). Inconsistent results investigating the relationships between these factors and incubation behaviour likely reflect opposing selective pressures on a female's optimal incubation strategy in certain environments. For example, species that suffer high nest predation have evolved incubation behaviour to reduce nest activity (longer on- and off-bouts) (Conway & Martin 2000b), but longer periods away from the nest can restrict embryo development and extend predator exposure. In a cold environment, a female will take shorter off-bouts to minimise the time her eggs fall below optimal temperatures. With less time to forage the female must make more frequent trips away from the nest (Conway & Martin 2000b), consequently shortening her on-bouts and increasing nest activity. The same authors (2000a) illustrated a non-linear relationship between ambient temperature and bout duration across a wide range of temperatures to help explain some of the discrepancies in studies investigating these two traits. Similarly, inconsistent results exist concerning how food availability influences incubation behaviour (Rauter & Reyer 1997; Conway & Martin 2000b; Eikenaar et al. 2003; Pearse et al. 2004). However, a recent experimental study manipulating both food and temperature revealed the two factors offset each other (Londono et al. 2008), highlighting the different trade-offs females face in varying environments.

In many species where females incubate alone, the male can supplement the female's energy costs by supplying her with food (Ricklefs 1974). There is extensive variation in the frequency and manner of incubation feeding between avian families (e.g. Silver et al. 1985), and several hypotheses have been proposed to explain the evolution of incubation feeding. Early researchers thought incubation feeding served to maintain pair-bonds (Lack 1940), but it is now generally seen as providing essential nutritional value for the female and improving reproductive success, that is, the female-nutrition hypothesis (Royama 1966). Several studies have supported this hypothesis by demonstrating male incubation feeding increases a female's nest attentiveness and reduces the incubation period (Lyon & Montgomerie 1985; Lifjeld & Slagsvold 1986; Halupka 1994).

However, if the increased number of male nest visits attracts nest predators the benefits of increased incubation feeding may be reduced (Skutch 1949; Martin & Ghalambor 1999; Tewksbury et al. 2002).

South temperate species in general exhibit reduced nest attentiveness and longer incubation periods compared with northern counterparts (Martin 2002; Chalfoun & Martin 2007), despite similar or higher nest predation rates. Here we studied the New Zealand robin (*Petroica longipes*), an endemic passerine that exhibits female-only incubation and male incubation feeding. Across robin territories, nest survival in our study system is positively correlated with invertebrate biomass (Boulton et al. 2008), and like many of New Zealand's endemic fauna, they suffer high adult and nest mortality due to introduced mammalian predators (Powlesland et al. 1999; Boulton et al. 2008). Despite evolving with a restricted suite of arboreal predatory birds, robins in this region have likely co-existed with these exotic mammalian predators for at least 700 yr. Here we examine whether incubation behaviour explains variation in nest predation for a species that historically evolved with predators more likely to cue onto nest activity than their present predators. Additionally, we examine the influence of male incubation feeding on female's incubation behaviour.

We examined the following questions: (1) Increased nest activity (male and female nest visitation) is unlikely to increase the risk of predator detection for robin nests due to the depletion of native predatory birds and dominance of olfactory searching predators. (2) Male incubation feeding will influence a female's nest attentiveness by decreasing her off-bout and/or increasing her on-bout duration, supporting the female-nutrition hypothesis. In addition to male incubation feeding, we predict that both food availability and ambient temperature will influence females overall nest attentiveness. (3) Females on territories with high food availability will decrease foraging time (off-bout), increasing overall nest attentiveness via longer on-bout periods. (4) Females during cooler conditions will decrease their foraging time (off-bout), and take more foraging trips per time, causing a change in incubation rhythm with shorter on- and off-bouts as predicted by Conway & Martin (2000a).

Methods

Study Site and Species

The New Zealand robin is a small (26–32 g) insectivorous bird belonging to the endemic Australo-

Papuan family Petroicidae distributed throughout New Zealand, Australia, New Guinea and the western Pacific. We located and monitored robin incubation behaviour in 15 mixed podocarp-broadleaf forest fragments near the township of Benneydale, central North Island, New Zealand (38º 32′S, 175º 22′E) from August to February 2002–2005. See Boulton et al. (2008) for further description of the study site.

Females build a bulky open-cup nest and begin laying clutches of 2–3 eggs in late August. Females continue nesting attempts through to early February, with individual pairs attempting up to five nests in a single season (Boulton et al. 2008). The male regularly feeds the female during the nest-building period but reduces his feeding rate during egg laying (Powlesland 1983). Females incubate for about 19 d and although the male brings her food, she intermittently leaves the nest to forage, with both adults helping feed the nestlings for about 21 d (Powlesland 1983). New Zealand robins exhibit social and genetic monogamy (Ardern et al. 1997; Taylor et al. 2008), with pair bonds usually retained throughout the breeding season and frequently through subsequent years until the death of the partner.

Between 2002 and 2005, we captured and individually banded nearly every male and female robin in the study area using a claptrap (manually operated, spring-loaded drop net) baited with mealworm (*Tenebrio molitor*) larvae. This allowed us to follow individually identifiable robins for at least 30 min on separate occasions to determine their nesting status and subsequently allowed us to account for individual variation among birds during our analyses. We determined nest status (incubation, brooding, or failure) by observing parental feeding behaviour near nest sites, as the majority of nests were too high (>10 m) to observe their contents without considerable disturbance. We checked each nest within 1–4 d of the estimated day of fledging to determine nest outcome.

Incubation Behaviour

We estimated female nest attentiveness by observing nests from a distance of 25–30 m using binoculars between the hours of 09:00 and 17:30 during fine weather (absence of rain or high winds). During the 2002–2003 and 2003–2004 breeding seasons, we attempted to watch each nest twice during the incubation period to test for differences in early and late-stage incubation behaviour, but could only do this for 18 out of 96 nests due to high nest predation

rates experienced at our sites. Therefore, during the 2004–2005 breeding season we only observed each nest once. Because of their inquisitive nature, robins usually visited the observer (R.L.B) on arrival near the nest site, so we commenced 1-h-long nest watch only when females returned to the nest and males resumed normal behaviour. If the female was off the nest at the end of the hour nest watch, the observer waited until she returned to record her last off-bout duration, resulting in some nest watches greater than 1-h long.

Over the three breeding seasons, we undertook nest watches for 51 different robin pairs, with a number of pairs monitored throughout 2 or 3 yr; 11 pairs in 2002–2003 (17 nest watches at 13 nests), 32 pairs in 2003–2004 (66 nest watches at 52 nests) and 25 pairs in 2004–2005 (31 nest watches at 31 nests). We recorded the following variables during each nest watch (per hour): nest attentiveness (proportion of total time female spent on the nest); mean on-bout duration (mean time female spent on nest per bout); mean off-bout duration (mean time female spent off nest per bout); nest activity (number of times female left the nest) and incubation feeding (number of times the male fed the female). Unlike many species where the male feeds the female on the nest, robin males rarely bring food directly to the nest (2/317 incubation feedings). Female robins tend to only leave nests when males call to feed them (76% of female recesses from nest), generally feeding her within sight of the observer. This meant we could have slightly underestimated incubation feeding as males may have fed females multiple times, if the female left the nest area, although females generally foraged close to their nest sites and additional feedings were still within view of the observer and included in the analysis. We recorded ambient temperature (°C) under the nest tree (in shade) during each nest watch. We also recorded clutch age, with nests considered 'early' for the first 10 d of incubation and 'late' thereafter. Because of birds being individually marked and checked frequently, we could determined clutch age from nest building behaviour, known hatching, fledgling or previous failure dates.

Food Availability

New Zealand robins spend 90% of their foraging time on or within 2 m of the ground, searching for ground invertebrates in leaf litter either visually or by flushing prey using foot-trembling and wing-tail-flicking motions (Powlesland 1981). We measured

each robin pair's food availability using a set of six continuous-kill pitfall traps (in 3 × 2 grid at 10-m spacing) placed in the centre of each territory (Boulton et al. 2008). We emptied pitfalls every 6 wk, and dried (at 60°C for 36 h) and weighed (g) all invertebrates except for the larger (>2 cm) carabid beetles as robins generally ignored these (Powlesland 1981, personal observation). We assigned each nest watch an invertebrate biomass measurement that coincided closest to our 6-wk invertebrate collection period.

Statistical Analyses

Prior to analysis, we transformed the three incubation behaviour response variables (attentiveness, mean on-bout duration and mean off-bout duration) to normalise their distributions following the transformations suggested by Quinn & Keough (2002). These variables were analysed using the SAS GLIMMIX macro (Version 9.1, SAS Institute Inc., Cary, NC, USA; Littell et al. 1996), fitting a generalised linear mixed model with pair and nest watch number included as random effects (Version 9.1, SAS Institute 1999). We included random effects because of multiple nests per pair and two nest watches conducted at 18 of the nests. The error distribution and link function were specified as normal and identity for nest attentiveness (arcsine transformed), on-bout (cube root transformed) and off-bout (log transformed) duration. We incorporated ambient temperature (°C), food availability (g, invertebrate biomass), time of day (hour past midnight), clutch age (early or late), year and the number of male incubation feedings as individual covariates in models. Because ambient temperatures did not range widely among our nest watches (8–21°C), in contrast to Conway & Martin's (2000a) study, we used linear models to explain the relationship between temperature and incubation behaviour. During model selection, we obtained the most parsimonious minimum adequate models by sequentially adding the significant terms, p < 0.05.

We estimated daily nest survival during the incubation period (19 d) for the 96 nests for which nest watches were undertaken (first nest watch only), and tested the cause of variation in survival using the generalised linear modelling approach used by Shaffer (2004). Logistic-exposure models were fitted using PROC NLMIXED (SAS Institute Inc., Cary, NC, USA) with a binomial distribution and logit-link function. Predictor variables in the nest survival analysis included invertebrate biomass, nest attentiveness (arcsine transformed), on- and off-bout duration (mean) and nest activity (number of times female left the nest) during each nest watch. With such a strong relationship between female nest trips and male incubation feeding rates, we included the frequency at which females left the nest per hour to reflect nest activity in this analysis. We also present overall nest survival for the whole nesting period (40 d) for comparison.

Results

We conducted 114 nest watches over the 3-yr observation period, with females exhibiting mean nest attentiveness of 72.5% (SE = 0.99, range 43.5–93.5%). Females left the nest on average 3.2 times per hour (SE = 0.15, range 1–12), with off-bouts averaging 6.5 min (SE = 0.38, range 1.9–22.1 min) and on-bouts averaging 18.6 min (SE = 1.15, range 2.6–56.9 min). Males fed their females on average 2.8 times per hour (SE = 0.16, range 0–8).

Overall none of our variables explained a significant amount of variation in female nest attentiveness, although attentiveness tended to be lower at higher temperatures (temperature intercept: = 0.952, estimate: = −0.008, SE = 0.005, p = 0.086), and when male incubation feeding rates were high (male feeding intercept: = 0.886, estimate: = −0.015, SE = 0.008, p = 0.073). Obviously, nest attentiveness was significantly correlated with the duration of on-bouts (Pearson's correlation n = 114: r = 0.491) and off-bouts (r = −0.519), and the effect of male incubation feeding on nest attentiveness was associated with changes in these durations. As male incubation feeding rates increased, females left the nest more times per hour causing the duration of both on- and off-bouts to decrease (Table 1 and Fig. 1). Surprisingly, the effect of male incubation feeding was larger for on-bout duration, which caused females to spend less time on the nest when the feeding rate was high, opposite to the predictions of the female-nutrition hypothesis.

While male incubation feeding rates explained much of the variation in on-bout and off-bout duration, ambient temperature and food availability helped explain the remaining variation (Table 1). However, each variable was only able to explain one component of robin incubation rhythm. Ambient temperature influenced off-bout duration, with females leaving the nests for longer periods as temperatures increased. Food availability influenced on-bout duration, with females on higher biomass territories having longer on-bouts.

During the incubation period, the 96 robin nests for which we undertook nest watches had 61% (CI

49–70%) nest survival. Across the complete nesting period, they had 37% (CI 27–46%) nest survival. We monitored the fate of a further 107 robin nests in our study area, with 49% (CI 41–57%) surviving incubation and 32% (CI 25–38%) surviving the 40-day period from incubation to fledging (n = 203, Boulton et al. 2008). Higher survival for nests where we conducted nest watches reflects the additional time available to conduct a nest watch for successful nests, slightly biasing our sample towards successful nests. None of the incubation behaviours or invertebrate biomass affected the rate of nest predation (Table 2).

Discussion

Two decisions, when to leave, and when to return to the nest largely determine a female's incubation rhythm. Our results show that while both food and temperature influence this rhythm, the male plays an important role in influencing when a female leaves the nest. High male incubation feeding rates changed the incubation rhythm by shortening both the on- and off-bout duration, resulting in no increase in overall nest attentiveness. Similarly, the influence of food and temperature on nest attentiveness was obscured because both factors changed bout duration in different ways, a result analogous to Londono et al. (2008). The length of the female's off-bout duration was positively correlated with ambient temperature, likely reducing the risk of clutch cooling and optimising embryo development. Whereas
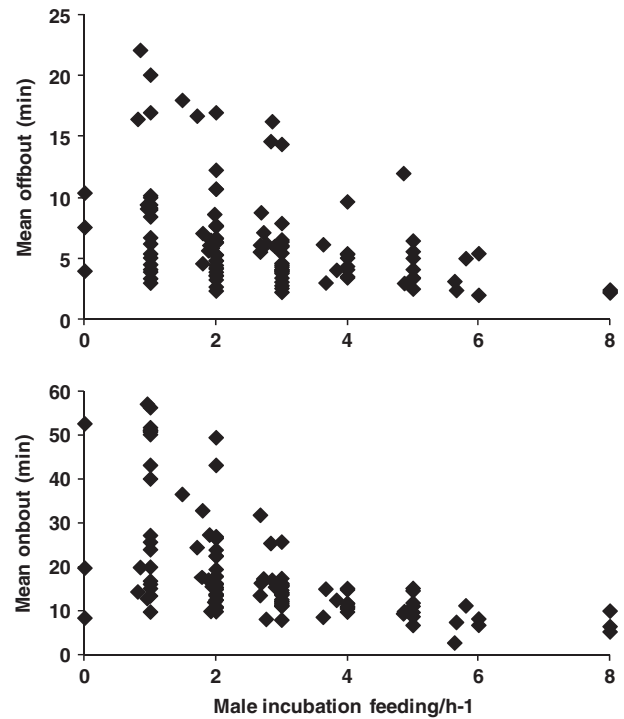

Fig. 1: Scatter plot of mean on-bout and off-bout duration vs. male incubation feeding per hour for nest watches conducted at New Zealand robin nests (n = 114), Benneydale, New Zealand, 2002–2005. We present untransformed bout duration (min) for ease of interpretation.

the female's own energy levels appeared to dictate when she left the nest to forage, with shorter on-bouts taken by females from low biomass territories.

Table 1: Mean female on-bout (cube root transformed) and off-bout (log transformed) duration (min) in relation to ambient temperature, territory food availability (invertebrate biomass), male incubation feeding rate, time of day, clutch age (early or late) and year (2002–2005) in the New Zealand robin, Benneydale, New Zealand

		Univariate models[a]				Reduced model			
		Intercept	Estimate	SE	t	Intercept	Estimate	SE	t
On-bout duration	Temperature (°C)	1.836	0.015	0.009	1.69*				
	Food availability (g)	1.870	0.112	0.050	2.22**	2.197	0.083	0.041	2.05**
	Male feeding (per h)	2.316	−0.104	0.013	−8.10***		−0.106	0.014	−7.62***
	Time (h)		0.004	0.015	0.27				
	Clutch age (late)	2.044	−0.066	0.049	−1.34				
	Year 2004–2005 (2002–2003)	2.038	−0.020	0.095	−0.22				
	(2003–2004)		−0.004	0.062	−0.06				
Off-bout duration	Temperature (°C)	0.448	0.023	0.007	3.17***	0.660	0.020	0.006	3.13***
	Food availability (g)	0.695	0.043	0.039	1.09				
	Male feeding (per hour)	0.934	−0.068	0.012	−5.70***		−0.065	0.012	−5.60***
	Time (h)		0.001	0.012	0.04				
	Clutch age (late)	0.746	0.006	0.043	0.14				
	Year 2004–2005 (2002–2003)	0.747	0.046	0.074	0.63				
	(2003–2004)		−0.010	0.052	−0.20				

[a]Generalised linear mixed model and forwards stepwise selection. Robin pair and nest watch number included as random factors are not shown here. Univariate model results represent each univariate term singly in the model. *p < 0.10; **p < 0.05; ***p < 0.01.

Table 2: Nest survival during incubation (n = 96) in respect to incubation behaviour and food availability of the New Zealand robin, Benneydale, New Zealand, 2002–2005

	Intercept	Estimate	SE	*t*
Nest survival (incubation)[a]				
Nest attentiveness	2.800	1.038	1.193	0.87
Nest activity	3.896	−0.081	0.101	−0.80
On-bout duration	3.430	0.012	0.019	0.62
Off-bout duration	3.748	−0.017	0.041	−0.42
Invertebrate biomass (g)	3.956	−0.239	0.321	−0.74

[a]Generalised linear mixed model fit using a binomial distribution and logit-link function specified by Shaffer (2004). Univariate model results represent each univariate term singly in the model, with no reduced model due to lack of significant terms.

The female-nutrition hypothesis predicts that male feeding allows the female to spend longer bouts on the nest (Lyon & Montgomerie 1985; Lifjeld & Slagsvold 1986; Halupka 1994). Contrary to this prediction, we found male incubation feeding tended to reduce female on-bouts, seemingly rejecting the hypothesis for this species. Perhaps this result is not surprising due to the robin's behaviour, whereby the male normally calls the female away from the nest. However, support for increased nest attentiveness with male incubation feeding comes from species that feed females away from the nest site (cavity nesting species, Martin & Ghalambor 1999; Klatt et al. 2008). In fact, 67% of incubation feeding events in Scarlet Tanagers (*Piranga olivacea*) occur away from the nest (Klatt et al. 2008). We may not have detected benefits in robin reproductive output directly because we were unable to obtain precise data on incubation length or hatching success due to extremely high (i.e. obscured) nests. Alternatively, females with high provisioning rates may spend additional time in other self-maintenance activities such as preening during foraging bouts (e.g. Londono et al. 2008), and this reduction in energy expenditure benefits future female survival and fecundity rates (Visser & Lessells 2001; Hanssen et al. 2005).

There are a number of alternative hypotheses for the role of male incubation feeding; mate assessment, pair-bonding and increased mating opportunities (Lack 1940; Nisbet 1973; Jawor & Breitwisch 2006; Klatt et al. 2008). The high social and genetic monogamy displayed by this species likely eliminates the possibility of females assessing future male effort or quality, and males likely gain no extra mating opportunities. Females have ample opportunity to swap mates in our study system (large numbers of single males), particularly after nest failure, but pair bonds were generally maintained throughout the breeding season and through subsequent years unless their partner died (<8% divorce rate). Male incubation feeding may therefore serve some function in maintaining pair bonds. Unfortunately, with such low rates of divorce, we could not directly test whether males with high feeding rates were favoured mates. Male removal experiments in this system may reveal whether incubation feeding is of essential nutritional value to the female or a retained historic trait evolved in favour of a mammal-free environment. Massaro et al. (2008) demonstrate naive island species can shift some behavioural traits in response to predation risk in ways that appear adaptive, but others remain fixed.

Nest predation can influence the evolution of passerine life-history traits by constraining the amount of parental activity around the nest, leading to the evolution of longer on- and off-bouts to reduce the frequency of nest visits (Martin 1995; Conway & Martin 2000b). We found little evidence to suggest that incubation behaviour greatly influenced nest predation, despite robins suffering high nest predation rates. Unfortunately, because of high nest predation rates our sample size for nests that failed very early in incubation was low. This may have reduced our power of detecting a relationship between nest activity and survival if nest failure for these individuals was due to frequent nest visits. Nevertheless, robin incubation behaviour does appear to attempt reduced nest activity. Male robins call females from the nest during feeding bouts, resulting in low male visitation to the nest and females generally only leave the nest when called by the male. Once the male feeds the female, she commences foraging before returning to the nest. This helps reduce nest activity and may have evolved as a response to the suite of arboreal predatory birds to which robins were historically exposed (Holdaway 1989; Holdaway & Worthy 1996). This type of incubation behaviour may be less effective given that extant robin predators are also nocturnal, olfactory and auditory searching (*Rattus rattus*, Mustelidae species, Morepork *Ninox novaeseelandiae*).

Although nest attentiveness was not associated with invertebrate biomass, the positive relationship with on-bout duration indicates a proximate response to food limitation. This result, coupled with increased robin nest survival with invertebrate biomass (Boulton et al. 2008), suggests robins in this fragmented habitat may be food limited. Further support comes from a study of the closely related *P. australis* where supplementary feeding experiments demonstrated female nest attentiveness was

not constrained by food availability (Mackintosh & Briskie 2005). Both control (79%) and fed (80%) females exhibited higher nest attentiveness than recorded in the present study, unfortunately they do not present data on male incubating feeding rates. Food-supplementation experiments to test if we could increase nest attentiveness and decrease male feeding rates would help answer the degree to which robins in this study area are food limited.

We found a positive relationship between off-bout duration and temperature, suggesting females avoided taking long off-bouts at low temperatures because of potentially harmful effects on the developing embryos. The lack of on-bout duration and temperature dependence was the result of female robins generally only leaving nests when males appeared with food, supporting the suggestion of Conway & Martin (2000a) that their model would be weaker for species that exhibit male incubation feeding.

In summary, females appeared to behave in response to their own energy levels with respect to on-bout duration, while they appeared to avoid the risk of egg chilling during off-bout periods, demonstrating plasticity in incubation behaviour. This variation in avian incubation behaviour demonstrates different strategies utilised by species to deal with their own energetic needs and the thermal requirements of the developing embryos. Although ambient temperature and food availability explained some of the variation observed in incubation behaviour, future work on this species under different conditions (i.e., food supplementation, mammalian predator control, male removal experiments) may reveal further insight into the incubation strategies employed by a species in an altered environment.

Acknowledgements

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