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The functions of adult female begging during incubation in sub-Arctic breeding yellow warblers

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Begging behaviour in birds is frequently studied in nestlings, but the function of adult female begging behaviour remains unknown. We examined begging behaviours of adult female yellow warblers, *Setophaga petechia*, during incubation at the northern limit of their breeding range. Female yellow warblers beg only when their mate arrives at the nest, and vocalization duration, intensity of wing fluttering and position of the female's body on the nest varies between begging events. We measured changes in these characteristics for 696 begging events from nine incubating females and examined how begging intensity changed with temperature and time since a female's last feeding. Begging intensity increased as the duration between feedings increased especially during colder temperatures. Next, we investigated how male feeding rates changed in response to variation in female begging intensity. Males fed females more quickly in response to intense begging during warm temperatures but not during cold temperatures. Finally, we investigated whether male feeding rates influenced the frequency or duration of the female's bouts away from the nest (i.e. 'off-bouts') during which the female had the opportunity to forage. Females that were fed more frequently reduced the average duration, but not the frequency, of their off-bouts. These results suggest that variation in the intensity of female begging behaviour signals energetic need, and that begging during incubation may be an important adaptation allowing female yellow warblers to maximize incubation time when breeding in sub-Arctic environments.

Begging behaviour is thought to convey information on hunger, such that individuals that beg are more likely to receive food from another individual (Godfray 1991). While begging behaviour is seen in many taxa, including mammals (Jensen et al. 1998) and insects (Kaptein et al. 2005), begging behaviour is most commonly studied in birds, with most studies focusing on dependent nestlings (Hinde et al. 2010; Jacob et al. 2011). In many species of birds, adult females also perform begging displays to their mates that include loud vocalizations and wing fluttering, similar to the displays of older nestlings and fledglings. Begging displays of adult females can span much of the breeding period from courtship to incubation and brooding of young nestlings. However, the causes and consequences of such begging by adult females remain poorly understood.

Ellis et al. (2009) proposed five hypotheses to explain the function of begging behaviour in adult female birds. The 'breeder need' and 'offspring need' hypotheses propose that female begging is a signal of nutritional need of either the female herself or her nestlings, and is used to stimulate feedings from the female's mate or other helpers in cooperatively breeding species. The remaining three hypotheses propose that female begging signals reproductive state and functions to (1) stimulate parental behaviour among helpers in cooperatively breeding species (care potentiation hypothesis), (2) suppress reproductive efforts of subordinate females within cooperatively breeding groups (breeding suppression hypothesis) or (3) advertise fertility to males (fertility advertisement hypothesis). These latter three hypotheses are restricted to specific mating systems or to specific stages of the reproductive cycle and are thus not applicable to all species or begging behaviours during nonfertile periods.

Begging behaviour of adult females probably has different functions throughout the breeding period and this most likely explains why studies examining begging behaviour in adult females have found support for two or more of the hypotheses outlined above. Begging behaviour prior to egg laying is often interpreted as either a signal of the breeding female's nutritional need (Ellis et al. 2009) or as a signal of reproductive state, where females broadcast information about their fertility to attract extrapair partners (Tobias & Seddon 2002; Ellis et al. 2009). An additional hypothesis to explain adult female begging prior to incubation is that females beg to evaluate the quality of their

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potential mate based on the frequency of courtship feedings (Wiggins & Morris 1986; Helfenstein et al. 2003). In contrast, studies examining adult female begging during incubation generally show increases in male provisioning rates as a result of more frequent female begging, suggesting that begging behaviour is a signal of the breeding female's energetic need (Otter et al. 2007; Ellis et al. 2009).

Here, we examine the function of adult female begging in a sub-Arctic breeding population of socially monogamous yellow warblers, *Setophaga petechia*, by examining (1) factors influencing the begging behaviour of incubating females, (2) the male's response to female begging intensity, and (3) how the frequency of male feeding visits influences a female's incubation behaviour. During the incubation period, female yellow warblers do not copulate with males and are presumably not seeking extrapair partners (Lowther et al. 1999). Therefore, by examining begging behaviour during the incubation period, we can exclude hypotheses that invoke copulation solicitations and advertisement of reproductive state as likely functions of adult begging.

In socially monogamous species such as yellow warblers, female begging during incubation occurs only when the male comes to the nest to deliver food (S. D. Moore, personal observation). Incubating females thus receive direct nutritional benefits if their social mate feeds them in response to begging behaviour. This behaviour may also benefit the female's mate by allowing the female to remain on the nest, guarding and incubating the eggs and providing constant warm temperatures for embryo development (Conway & Martin 2000a; Camfield & Martin 2009). This hypothesized function of female begging seems especially plausible in cold environments where eggs cool rapidly when the female leaves the nest, or in environments that experience high predation from predators that could be deterred by the incubating female. However, begging may also incur costs such as attracting predators to the nest, which may lead to the loss of eggs or nestlings, or even the death of one or both parents (Conway & Martin 2000b; Haskell 2002). Begging females often vocalize, flutter their wings and adjust their posture; such activities could require more energy than the female receives from food items brought by her mate (Harper 1986; Godfray 1991; Chappell & Bachman 2002). As such, begging most likely involves costs as well as benefits, particularly if the male does not respond by feeding the female, or if he delivers little or low-quality food.

If female begging during incubation is an honest signal of energetic need, then females should beg more intensely when their energetic need is high and males should respond more quickly to intense female begging. At least two factors may influence the energetic state and need of adult females during incubation: (1) time since a female's last feeding and (2) ambient temperature. During incubation, females must either leave the nest to forage for themselves or be fed by their mate. As the time interval between feedings increases, incubating females should increase the intensity of their begging behaviour to convey heightened energetic need to their mate. Similarly, at colder temperatures, females must maintain their body and egg temperatures far above the ambient temperature; thus, female begging behaviour should increase in intensity to reflect increased energetic need during cold temperatures. Additionally, if female begging benefits both members of the pair by allowing females to spend more time on the nest, then females that beg more intensely should receive more frequent male feeding visits, and thus should spend less time away from their nest.

We first tested the prediction that female begging intensity during incubation increases in response to changes in environmental and energetic conditions. If begging is indeed an honest signal of energetic need, then begging behaviour should be most intense during energetically demanding periods of (1) cold temperatures and (2) long intervals between feedings. Second, we tested the prediction that males respond to an increase in female begging intensity by reducing the interval between feeding visits. Third, we examined the relation between male feeding rates and female incubation behaviour. We tested the prediction that more frequent male feeding visits allow females to spend less time away from their nest by reducing either the frequency or duration of bouts away from the nest (hereafter 'off-bouts').

METHODS

Study Species and Study Site

The yellow warbler is a small migratory passerine with one of the most widespread breeding distributions among the North American wood warblers (family: Parulidae) (Lowther et al. 1999). Yellow warblers are socially monogamous, but extrapair copulations are common (Yezerinac et al. 1999). Our study site is located in northern Manitoba, Canada, about 20 km east of the town of Churchill, at the Churchill Northern Studies Centre (58°40′N, 94°25′W; elevation ~20 m). The habitat is a mixture of stunted boreal forest that transitions into tundra flats with scattered ponds and waterways surrounded by willow (*Salix* spp.) thickets. Yellow warblers that breed in northern Manitoba face many environmental challenges such as cold ambient temperatures, high wind speeds and a shorter breeding season, compared with more southern breeding sites. Females typically construct their nest close to the ground (<2 m high), often in willow bushes, and lay clutches of four to five eggs. Only females incubate, but males feed incubating females on the nest. During these feeding visits, female yellow warblers remain on the nest and often beg in response to the presence of the male. At our study site, yellow warblers typically breed from early June until mid-August (Jehl 2004), after which they begin moulting prior to their southward migration.

Data Collection

We videotaped 10 incubating females during the summer of 2009. Incubating females were videorecorded during early incubation (between day 2 and day 4 of incubation) using a Sony Handycam DCR-SR85 video camera. Cameras were placed on a tripod approximately 6–10 m from the nest. Recording began at about 0400 hours and continued until late morning (~1100 hours). Video data were then transferred to portable hard drive units to allow later viewing and analyses. One female did not beg because her mate made no visits to the nest, so our data for begging intensity is based on nine females and a total of 696 begging events. Female incubation behaviour (off-bout frequency and duration) and male feeding rates were calculated from video data. To reduce possible effects of camera set-up on begging and feeding behaviour, we excluded either (1) the first 10 min of video if we observed no male feeding visits or female off-bouts, or (2) the first male feeding visit or the first female off-bout if there was activity in the first 10 min of video.

Time between feeding events was recorded from video data and calculated based on the time interval between two successive male feeding visits, the time interval between the male's feeding visit and the female's first off-bout or the time interval between the female's return to the nest after an off-bout and the next feeding opportunity (either a male feeding visit or the start of another off-bout). While we could not assess whether females foraged during off-bouts, we considered off-bouts to provide an opportunity for females to forage and thus included these in our calculations of time between feedings.

Temperature data for Churchill, Manitoba were collected from Environment Canada's online database (Environment Canada, http://www.climate.weatheroffice.ec.gc.ca/climate_normals) for all dates and times for which we had video data. Environment Canada's weather station in Churchill is approximately 15 km west of our study site and experiences nearly identical climatic conditions. Environment Canada records hourly temperatures, and thus we assigned the same ambient temperature to all begging events that occurred within a single hour.

Quantifying Begging Behaviour

Begging displays by female yellow warblers during incubation consist of multiple signals. During a begging event, females typically remain on their nests and make a series of short, high-pitched chip calls, flutter their wings and change their posture as the male arrives at the nest (S. D. Moore, personal observation; see Supplementary Video S1). Within-individual variation in the intensity of begging displays is striking. During some begging events, females make chip calls that last up to 15 s upon arrival of their mate to the nest, whereas during other begging events, these same females make no calls upon the arrival of their mate; similar variation exists with wing fluttering and changes in female posture. To quantify female begging intensity, we examined each characteristic (chip call duration, wing fluttering and posture) for all 696 begging events. Both wing fluttering and change in female posture required qualitative assessment; thus, to control for possible interobserver biases, a single observer (S. D. Moore), blind to relevant data such as temperature and time since a female's last feeding, scored these characteristics of begging displays. Below, we describe how each of these three components of begging behaviour was quantified.

Chip call duration

Chip calls of incubating female yellow warblers are made in rapid succession, and bouts of chip calling during a begging event can last 1–15 s. We measured the duration of each chip call event that coincided with a male feeding visit using the sound analysis software Syrinx (J. Burt; www.syrinxpc.com), which creates visual spectrograms of chip calls made during each begging event. Spectrograms of chip calls appear as a series of vertical lines, with each line representing an individual chip. We estimated the duration of chip calls in each calling bout (a collection of three or more chips, with each bout separated by more than 1 s) associated with a begging event by measuring the time interval between the first chip and the last chip. We excluded individual chips separated by 1 s or more from our calculations because these vocalizations may represent contact calls instead of begging calls (Searcy & Nowicki 2005). For begging events with two or more bouts of chip calling, we subtracted the time between bouts from the overall duration of chipping to avoid inflating measures of chip-calling duration. We measured call duration, rather than call loudness, because cameras were located at variable distances from the nests, resulting in inconsistent measures of amplitude. In a sample of 22 begging events, the number of individual chips was closely correlated with chipping duration (Pearson product–moment correlation: $r^2 = 0.85$), so we used only chipping duration in subsequent analyses.

Wing fluttering

Wing fluttering is a rapid movement of the wings with no attempt at flight. Wing fluttering was scored on a qualitative scale of intensity, from least intense (score = 1) to most intense (score = 5): (1) female's wings remain stationary, no wing fluttering; (2) slow, nonconstant wing fluttering; (3) slow, continuous fluttering, wing in low position, no underwing visible; (4) moderate, continuous fluttering, wing in mid-position, partial underwing visible; (5) rapid, continuous fluttering, wing in high position, underwing fully visible, wing shape not visible because of rapid wing flapping. This scale incorporates the female's rate of fluttering (e.g. slow, fast), wing position (e.g. low, high) and flank and underwing exposure. Wing position was assessed relative to the female's body, where a low wing position indicates that the wings were held near the body and a high wing position indicates that the wings were raised above the female's back. The higher a female raised her wings, the more visible the pale underwing and flanks became. Thus, visual measures of the female's underwing and flanks were indicative of high-intensity wing fluttering.

Posture

Change in posture was defined as a change in the female's position on the nest with the arrival of her social mate. There was considerable variation in change of posture within females; during some begging events, the female moved only her head, and during other begging events, the same female left the nest to meet her male, exposing her eggs to ambient temperatures. We scored changes in posture on a scale of 1–5, where 1 represents minimal changes in posture and 5 represents dramatic changes: (1) female does not move upon arrival of male; (2) female lifts head in the direction of the male; (3) female stands in the nest without changing body orientation; (4) female stands in the nest and orients towards the male; (5) female moves off of the nest to meet the male. This scale is similar to the scales used by Tschirren et al. (2005) and Redondo & Castro (1992) to evaluate changes in posture of begging nestlings.

Statistical Methods

Chipping duration, wing fluttering and posture were correlated (Pearson product–moment correlation: chipping duration * wing fluttering: $r_{694} = 0.42$, $P < 0.001$; chipping duration * posture: $r_{694} = 0.32$, $P < 0.001$; posture * wing fluttering: $r_{694} = 0.35$, $P < 0.001$). We incorporated these three variables of begging intensity into a principal component analysis to reduce the number of dependent variables; we kept only a single principal component (PC1) of begging intensity because PC1 was the only component with an eigenvalue larger than one (Kaiser 1960).

To test the hypothesis that female begging intensity varied with environmental conditions, we used general linear mixed effect models (GLMM) in R (R Development Core Team, http://www.r-project.org). The principal component of begging intensity was the dependent variable and time since last feeding, temperature and the interaction between these two variables were the independent variables. Female identity was included as a random effect, which nests repeated measures of begging intensity within females. For this analysis, we had a total of 696 begging events. Both temperature and time since last feeding were log transformed to better fit the assumptions of the GLMM; all other variables were normally distributed.

We tested the hypothesis that males respond to changes in female begging using GLMM in R. Here, the time interval between successive male feeding visits was the dependent variable and the principal component of female begging intensity from the previous feeding visit, temperature and the interaction between these two variables were the independent variables. Male identity was included as a random effect, which nests repeated measures of male feeding visits within males. For this analysis we had 693 usable begging events. This sample size differs slightly from that above because it examines only the time interval between two successive male feeding events, not the time interval between feeding events that include female off-bouts and male feedings. Both temperature and the time interval between successive male feedings were log transformed to normalize the data. For this and the previous statistical analyses we treated temperature as a continuous variable, but present temperature data as a categorical variable in Figs 1 and 2 to illustrate the interaction between temperature and time since last feeding on female begging intensity and male feeding visits. We followed statistical procedures in Zuur et al. (2009), and for each analysis, we created four models of increasing complexity and evaluated each model against the others using ANOVA and Akaike's Information Criterion (AIC).

To examine the relations among begging behaviour, male feeding rate and female incubation behaviour, we compared the average principal component score of begging intensity (i.e. averaged across the entire 7 h observation period), the average off-bout duration and frequency of each female and the feeding rate of each male (calculated across the entire observation period). To test for a relationship between female begging behaviour and male feeding rate, we regressed male feeding rate on average female begging intensity; this analysis included only nine pairs because one female did not beg, and thus, was not fed by her mate. To test for a relationship between male feeding rate and female incubation behaviour, we regressed the average off-bout frequency and duration of each female on the feeding rate of each male for all 10 pairs that we videotaped. Average off-bout duration of females was log transformed to better fit the assumptions of normality.

Ethical Note

Videotaping females during incubation is noninvasive and was approved by the Queen's University Animal Care and Use Committee (protocol number Martin-2009-025-R2) and with permission from the Canadian Wildlife Service (permit number CA 0223). During camera placement or removal, we were careful not to disturb vegetation around the nests, and most females remained on their nest.

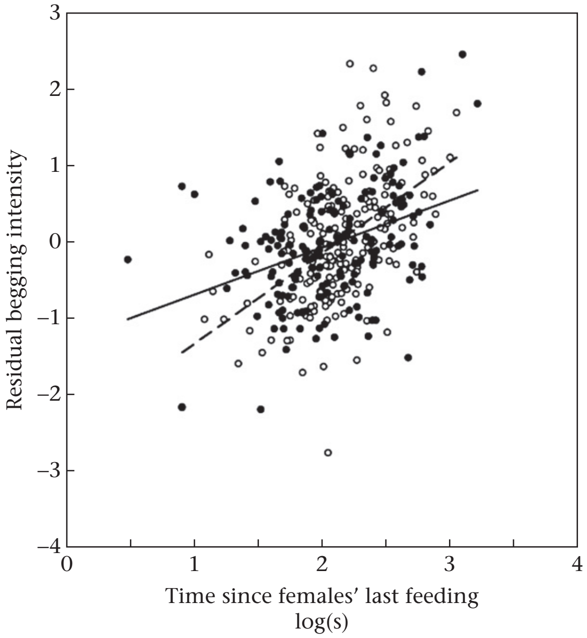

Figure 1. Relation between time since female's last feeding and the principal component of begging intensity for warm (black dots, solid line) and cold (circles, dashed line) temperatures in yellow warblers. Data for warm (8.7–13.5 °C) and cold (2.0–3.1 °C) temperatures represent upper and lower quartiles of all begging events, respectively. Residual begging intensity is plotted to control for the effects of individual female.

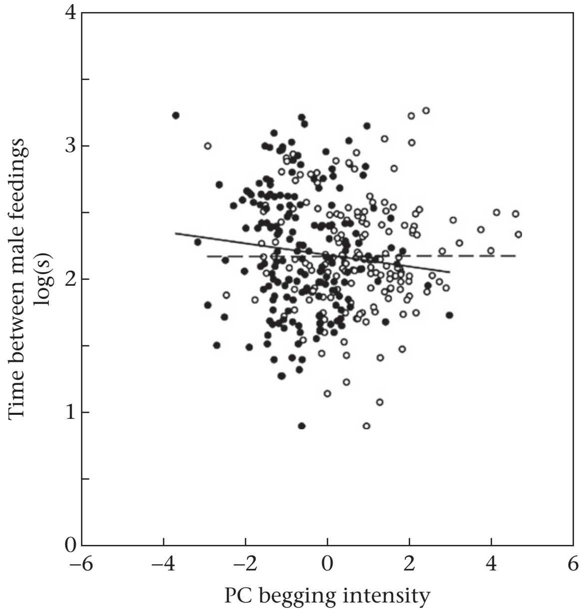

Figure 2. Time between male feedings regressed on the principal component (PC) of female begging intensity for warm (black dots, solid line) and cold (circles, dashed line) temperatures in yellow warblers. Data for warm (8.7–13.5 °C) and cold (2.0–3.1 °C) temperatures represent upper and lower quartiles of all begging events, respectively.

RESULTS

PC1 accounted for 58% of the total variance in all three variables of female begging intensity: chipping duration, posture and wing fluttering. All variables positively loaded on PC1 (chipping duration = 0.771; posture = 0.716; wing fluttering = 0.789). Mean ± SD number of begging events per female was 81 ± 39 (range 3–124, $N = 9$ females), and mean ± SD temperature experienced per female was 6.6 ± 2.8 (mean range per female: 3.8 ± 2.2 °C; range 2.0–13.5 °C).

For our analyses of factors affecting female begging behaviour, our best model included temperature, time since last feeding and the interaction between these two variables; this model had the lowest AIC values compared to all others. Begging intensity increased with time since last feeding ($P < 0.0001$) and warmer temperatures ($P = 0.04$; Table 1). Time since last feeding and temperature also interacted to influence female begging intensity ($P = 0.0003$; Table 1); the effect of time since last feeding on female begging intensity was stronger at colder temperatures (Fig. 1).

For our analyses of male response to female begging intensity, our best model included begging intensity, temperature and the interaction between these two variables. The time between successive male feeding visits was not significantly affected by temperature ($P = 0.70$) or female begging intensity ($P = 0.068$) alone, although the effect of female begging intensity approached statistical significance (Table 2). However, the interaction between temperature and begging intensity influenced male feeding rates ($P = 0.024$; Table 2), with intense begging reducing the time between male feeds at warmer temperatures (Fig. 2).

Average female begging intensity was positively, but not significantly, correlated with average male feeding rate ($r^2 = 0.38$, $t = 2.07$, $N = 9$ females, $P = 0.077$; Fig. 3). Females that were fed more frequently by their mates made significantly shorter off-bouts ($r^2 = 0.59$, $t = -3.38$, $N = 10$ females, $P = 0.0098$; Fig. 4) but did not change the frequency of their off-bouts ($r^2 = 0.0065$, $t = 0.23$, $N = 10$ females, $P = 0.82$; Fig. 4) during incubation.

Table 1
Effects of temperature, time since last feeding and the interaction between these two factors on begging intensity of female yellow warblers

	Slope	SE	*t*	*P*
Temperature	1.854	0.916	2.025	0.043
Time since last feeding	1.580	0.233	6.768	<0.0001
Temp*time since last feeding	−1.069	0.292	−3.657	0.0003

DISCUSSION

Incubating female yellow warblers begged more intensely following longer periods without food especially during colder temperatures (Fig. 1). We interpret female begging behaviour during incubation to communicate energetic need to their mate and that females adjust their begging intensity depending upon environmental conditions and the likelihood of being fed. Intense female begging was characterized by longer vocalizations, faster wing fluttering and posture changes that included the female changing orientations to meet her incoming mate. The male's response to the intensity of female begging appears constrained during cold temperature as males reduced the duration of feeding visits in response to intense female begging only during warmer temperatures (Fig. 2). Additionally, frequent male feeding visits allowed females to spend more time on their nest (Fig. 4), maintaining warm nest temperatures and protecting the nest and eggs from potential predators. Together, our results support the hypothesis that begging during incubation is a signal of the female's energetic need and most likely benefits both male and female by allowing the female to remain on the nest for longer periods, an important benefit especially in sub-Arctic breeding sites.

For begging to be adaptive, signallers (females) must benefit from the behaviour. Females most likely benefit from begging by increasing male feeding rates. Consistent with this, we found that males reduced the interval between successive feeding events following an intense begging event, at least at warm ambient temperatures (Fig. 2). The interaction between temperature and begging intensity on male feeding visits was unexpected, suggesting that multiple factors affect the rate at which males can feed incubating females. At colder ambient temperatures, males showed little response to increased female begging intensity, suggesting that males may have been unable to feed females at faster rates because insects were less active and possibly harder to find (Bergman et al. 1996). Males may also be energetically limited at colder temperatures and thus constrained in their response to female begging.

Contrary to our initial predictions, begging intensity of incubating females increased weakly overall with increasing temperatures (Table 1). We suggest that the decline in begging intensity at colder temperatures is in response to low signal efficacy; during cold temperatures, males do not appear to change their feeding rates in response to intense female begging; thus, females do not benefit by increasing their begging intensity. Our results showing that males reduced intervals between feedings after intense begging at warm but not cold temperatures (Fig. 2) supports this idea. This hypothesis suggests that females may alter their begging intensity to reflect both their energetic state and the costs and benefits of intense begging at different ambient temperatures.

Table 2
Effects of female begging intensity, temperature and the interaction between these two factors on feeding rates by male yellow warblers

	Slope	SE	*t*	*P*
PC begging intensity	0.0763	0.0416	1.830	0.068
Temperature	0.0543	0.139	0.389	0.70
PC begging intensity*temp	−0.127	0.0563	−2.260	0.024

PC: principal component.

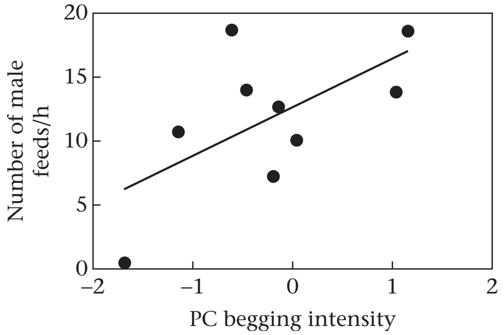

Figure 3. Average frequency of feeding visits/h by male yellow warblers regressed on the average principal component (PC) of female begging intensity ($N = 9$ pairs; one pair was excluded because the female did not beg and was not fed by her mate).

An alternative hypothesis to explain why females beg more intensely during warm temperatures is that females conserve energy during cold temperature by reducing their begging intensity. During intense begging displays, females flutter their wings high above their body and often stand in the nest or move to the nest rim in anticipation of the male's arrival. These behaviours result in females expending energy and exposing eggs to cold ambient temperatures. Cold temperatures demand increased energy from females to maintain their body temperatures and to provide constant warm temperatures to eggs. Haftorn & Reinertsen (1985) showed that at 0 °C, incubating female blue tits, *Cyanistes caeruleus*, increased their metabolic rate 50–90% to maintain the proper egg temperature for development. Thus, energetic costs incurred by females, and possible developmental cost to her eggs,

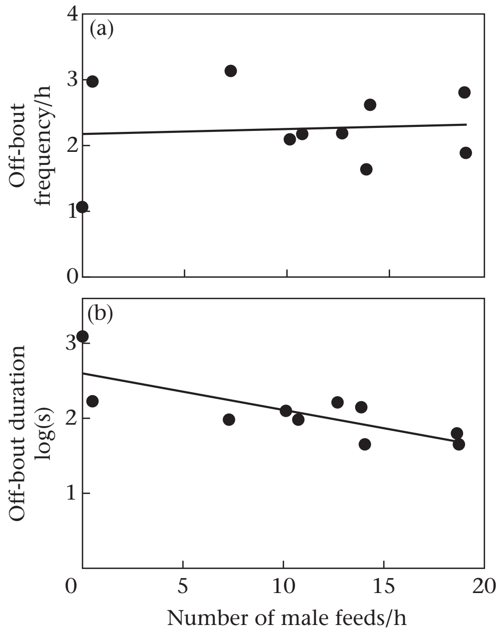

Figure 4. Change in incubation behaviour of female yellow warblers regressed on male feeding rates. Shown are (a) the average off-bout frequency/h of each female and (b) the average off-bout duration (log (s)) of each female regressed on the average number of feeding visits/h of each male for 10 pairs.

may explain why females reduce their begging intensity during cold temperatures.

Factors That May Affect Begging Intensity

At least three factors may influence female begging intensity: (1) risk of predation, (2) rainy weather and (3) anticipation of cold weather events associated with changes in barometric pressure. Females may vary their begging intensity based on the abundance, diversity and proximity of predators (Conway & Martin 2000b; Fontaine & Martin 2006), or if the risk of predation changes with temperature, time of day or season. The extent to which the risk of predation influences begging intensity remains unknown, but it may result in broad latitudinal patterns and/or local, site-specific effects. Rainy weather limits the amount of time females may spend away from the nests because females act as an umbrella, shielding nest, eggs and newly hatched young from rain. As a result, females may take fewer and/or shorter breaks from incubation and may beg more intensely to their social mates during rainy weather. Similarly, females may beg more intensely with reductions in barometric pressure associated with cold weather systems; at least two species of birds, scrub-jays, *Aphelocoma californica*, and black-capped chickadees, *Poecile atricapillus*, adjust their foraging behaviours with approaching inclement weather (Raby et al. 2007; Feeny et al. 2011). In anticipation of colder weather or periods of rain, incubating females may beg more intensely to build energy reserves prior to the arrival of cold weather. This may be especially advantageous if cold weather influences insect abundance and predator activity. None of the females for which we had begging intensity data were exposed to rainy weather or decreases in barometric pressure, so we were unable to test whether females alter their begging intensity in response to incoming weather systems.

Evolution of Begging Behaviour

Communication between incubating females and their mates should be a reliable system, as both sexes have at least partially overlapping reproductive interests (Searcy & Nowicki 2005). We would therefore expect female begging and subsequent male feeding to evolve as an honest signal if it increases fledging success. However, if interests in the young are not shared equally among males and females, we might expect conflicts among the sexes, as males and females have different strategies for maximizing their fitness. Females may beg more than would benefit their mates to maintain their own condition, while males may benefit more by seeking extrapair copulations or by reducing feeding visits when paternity is uncertain. We suggest that the potential conflict between the sexes is high, as male feeding rates in our study were only weakly associated with begging intensity (Fig. 2, Table 2), but this speculation needs further study.

How important are male feeding visits to the success of nests? Studies that have removed males (typically during the nestling period) and measured fledging success suggest that the male's role can be dependent upon seasonal factors (e.g. early or late timing of breeding within a season) (Duckworth 1992; Meek & Robertson 1994), but many studies in temperate regions find that removing the male results in little changes in fledgling success (Wolf et al. 1990; Harrison et al. 2009). Females that compensate for their lost mate by increasing feeding rates, trade off time spent on self-investment with brooding young (Wolf et al. 1990). While this probably translates into reduced survival for females, such compensatory behaviour is probably widespread among passerines that breed at high latitudes (Ghalambor & Martin 2001), like the yellow warblers in our study. The loss of a male mate or pairing with a male that rarely feeds during incubation probably has fitness consequences for females at sub-Arctic and Arctic breeding sites where cold ambient temperatures cool eggs rapidly when the female leaves the nests to forage (Lyon & Montgomerie 1985, 1987). Male yellow warblers at our study site showed tremendous variation in feeding rates (0–19 visits/h; this study), but nest did not differ in hatching success (V. G. Rohwer, unpublished data). The degree to which male investment in mate feeding during incubation varies with environmental conditions (e.g. temperature), paternity and reproductive opportunities remains unknown, but yellow warblers are a good candidate species for addressing these questions as they breed in a diversity of environments (Lowther et al. 1999) and show geographical variation in the level of extrapair paternity (Yezerinac et al. 1999).

Our results suggest that females adjust the intensity at which they beg in response to energetic need and environmental factors (e.g. ambient temperature) that influence the possibility of future feedings from their mates in a sub-Arctic breeding passerine bird. Female begging behaviour functions to reduce the time between successive male feeding visits only during warm weather, suggesting that cold temperatures constrain the effectiveness of female begging. The ability of females to alter the intensity at which they beg may be an important adaptation that allows females to maintain sufficient food reserves during incubation and to spend less time away from the nest during cold weather, and may be especially important to breeding in sub-Arctic or unpredictable environments.

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Supplementary Material

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