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Carolina Chickadee (Aves, Paridae, *Poecile carolinensis*) Vocalization Rates: Effects of Body Mass and Food Availability under Aviary Conditions

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Abstract

We evaluated the effect of body mass and several environmental factors on vocalization rates of Carolina chickadees (*Poecile carolinensis*) housed in an aviary. Two different nonsong vocalizations (tseet and chick-a-dee) and song (fee-bee fee-bay) were recorded. Food was delivered from a feeder and three different levels of food access were presented to each bird: 10, 40 and 55 min/d. Two scales of body mass were measured: 'dawn mass' and 'focal mass' (mass during a focal observation divided by dawn mass). Across all birds, there was a significant negative correlation between both nonsong vocalization rates and body mass (both dawn and focal mass) and the effect of mass on call rate was greatest for days when food was relatively abundant. Nonsong vocalizations were also given at higher rates when food was limited (10 min/d) than when food was more abundant (40 and 55 min/d). No changes in call rates with time of day were observed. Overall, song rates were substantially lower than nonsong rates. Unlike nonsong rates, song rates were highest in birds that had relatively high dawn mass. No significant correlation between song rates and focal mass was observed, and no significant correlation between song rates and time of day was observed. Finally, vocalizations from nonfocal birds had little effect on vocalization rates of focal birds. Our results suggest that nonsong communicative signals are more important for birds facing energetic stress, while song is more important for birds that are not energetically stressed.

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Introduction

Information embodied in a vocal signal is to some extent a direct reflection of the external conditions under which the signal is given. Alarm calls are an example.

In some primates (Seyfarth & Cheney 1993) and birds (Marler & Evans 1996), different alarm vocalizations are given in response to different categories of predator (e.g. terrestrial vs. aerial), and playbacks of these vocalizations result in context-appropriate behavior by animals receiving the signals. Levels of resource availability may also play an important role in communication. For example, tamarins (*Leontopithecus rosalia*; Benz 1993; *Saguinus labiatus*; Caine et al. 1995), common ravens (*Corvus corax*; Heinrich et al. 1993), and black-capped chickadees (*Poecile atricapillus*; Ficken 1981) vocalize when they initially locate large amounts of food. Golden lion tamarins give different calls to preferred and nonpreferred food (Benz 1993).

Whether information is conveyed about the physiological state of the signaler is more equivocal. For example, there is little direct evidence of an effect of variation in body mass on vocalization rates; this lack of evidence presumably results from the difficulty of measuring body mass under field conditions. The majority of evidence we have on the relationship between physiological state and communication rates relates to mating behavior. Theoretical analyses indicate that signals given in the context of mating interactions should reflect the energetic state of the signaler, assuming that the energetic expenditure in the signal has fitness consequences (Grafen 1990). A number of empirical tests of this hypothesis have been performed. Bellowing in red deer (*Cervus elaphus*) supports this prediction; only males in good condition are capable of extended bouts of bellowing (Clutton-Brock et al. 1982; also see Reid (1987) and Møller (1991) for other examples). Crowing in red junglefowl (*Gallus gallus*) does not directly support this prediction, because there is no appreciable cost of crowing (Chappell et al. 1995). Results from great tits (*Parus major*; Weary et al. 1991) and Carolina wrens (*Thryothorus ludovicianus*; Gaunt et al. 1996; Eberhardt 1996) have been equivocal. Here we ask a broader question: does any category of vocal communication (mating or other) correlate with variation in energetic condition? To address this question, we describe vocalization rates of Carolina chickadees (*Poecile carolinensis*) observed under laboratory conditions where food access was manipulated and body mass could be monitored throughout the day.

Chickadees have a rich vocal repertoire of up to 15 different vocalizations (Smith 1972; Ficken et al. 1978, 1994). Here we focused on three of these vocalizations: fee-bee fee-bay, chick-a-dee, and tseet. Carolina chickadees sing a simple four-part song (fee-bee fee-bay) that is primarily used by males in territorial advertisement and is never used when birds are in close proximity with each other (Smith 1972; Ficken et al. 1978). Smith (1972) notes that fee-bee fee-bay vocalizations are primarily used in the spring by patrolling males, although they can be heard in other seasons (also see Kroodsma et al. 1995). The chick-a-dee and tseet calls are both nonsong vocalizations that are given under a variety of conditions. The tseet call is a contact call that appears to be used to maintain auditory contact with flockmates (Smith 1972). The chick-a-dee call is a complicated call exhibiting some syntactical characteristics of true language (Hailman & Ficken 1986). The call can be used as a contact call, threat display, alarm call, or as a call that coordinates group movement (Smith 1972; Ficken et al. 1978). In addition, the different functions of the chick-a-dee call are to some degree correlated with the call's syntax (Smith 1972; Gaddis 1985; Ficken et al. 1994).

Our experiment was designed to evaluate the effect of body mass and food availability on vocalization rates in Carolina chickadees. Predictions relating to this relationship are complicated in several ways. First, while we have some information about the social conditions under which chickadees vocalize (e.g. Smith 1972; Ficken et al. 1978; Gaddis 1985), the relationship between energetic conditions and vocalization rates has not been addressed. Second, we can assume that the chick-a-dee and tseet calls generally promote social interactions between birds (see discussion of the function of these calls outlined above), while song, if anything, decreases social interactions. Indeed, Smith (1972) notes that song is never given when birds are in close contact, and Ficken et al. (1978) state that males isolate themselves from the flock before singing. Thus, we can infer some general relationships between vocal behavior and flocking behavior. In addition, there is some empirical evidence indicating the relationship between energetic conditions and flocking behavior in the Paridae (see below). From these data we can extrapolate to generate predictions about the energetic conditions under which social cohesion should be preferred by a chickadee and, therefore, conditions under which vocalization rates might increase to facilitate social interactions.

This raises a third complication. There are a variety of factors that affect the fitness consequences associated with social interactions. Various combinations of these factors can, and do, generate the full range of relationships between flocking and energetic stress. For example, there is evidence for decreased flocking behavior under energetically stressful conditions (e.g. low food or low temperature; Samson & Lewis 1979; Ekman & Hake 1988), but there is also evidence for increased flocking behavior under energetically stressful conditions (Smith 1972; Berner & Grubb 1985; Hogstad 1988, 1989; With & Morrison 1990). With this background, we offer the following predictions.

1. Song rates should be positively correlated with an individual's body mass. This prediction results from a number of factors. As discussed above, song may be an energetically expensive behavior. If so, song rates may be limited by energetic stores. Even if song production itself is not energetically expensive, time budget considerations will make song relatively more costly to birds that are energetically stressed. Song is used in territorial advertisement and long-distance engagement. As such, song and foraging are mutually exclusive behaviors (e.g. see Hunt 1980 and Gaunt et al. 1996), and, therefore, lightweight birds should reduce song rates (and behaviors that covary with song) in order to devote more time to foraging. The prediction further assumes that, under our experimental conditions, birds that are relatively low weight are more energy stressed than those that are heavier (see Lucas et al. 1993 and Lucas 1994). We have evidence that low-weight Carolina chickadees spend more time in foraging-related activities than high-weight birds (Lucas 1994) and we have some evidence that total vocalization rates are lower for lightweight tufted titmice (*Baeolophus bicolor*; Lucas, unpubl. data), a bird related to the Carolina chickadee.

2. Predictions about the relationship between call (tseet and chick-a-dee) rates and body mass must invoke the additional issue of the tradeoffs involved in social interaction and, in turn, how these tradeoffs vary with energetic conditions. As a result, environmental conditions may dictate whether the birds exhibit a positive or a negative correlation between call rates and body mass. A negative correlation is expected if there is a net disadvantage of interactions resulting from calls (e.g. directly through fights caused by increased vocalization rates or indirectly through competition for food). For example, Ekman & Hake (1988) showed that birds on a negative energy budget shifted from flock to solitary foraging in order to increase variance in food access (a 'risk-prone' strategy; see Kacelnik & Bateson 1996). This shift presumably was accompanied by a decrease in vocalization rates, although vocalization rates were not measured. A negative correlation might also arise from a shift in the relative importance of starvation risk vs. predation risk as an individual shifts from a positive to a negative energy budget. For example, Szekely et al. (1991) provide theoretical evidence indicating that animals with low reserves should forage alone under conditions where flocking decreases predation risk but also decreases food availability. The assumption that hungry birds will adopt foraging behaviors that put them at higher risk of predation than sated birds has been verified in several studies (e.g. Hogstad 1988; Koivula et al. 1995).

A positive correlation between call rates and body mass is expected if there is a net advantage to interactions resulting from the calls. In this case, increased call rates may increase social contact and thereby provide a forager with more information about the location of food (e.g. Valone 1996) or about the risk of predators (McNamara & Houston 1992). As noted above, the potential for an increase in flock size under energetically stressful conditions is well documented, although we have little evidence that these changes in socialization are facilitated (or even accompanied) by increased vocal contact.

3. As a corollary of the predictions listed above, relationships between vocalization rates and food availability should be qualitatively similar to relationships between vocalization rates and body mass. This assumes that, for example, low food availability and low body mass both represent energetically stressful conditions, and that vocalization rates are generally responsive to energetic stress.

Methods

Capture and Holding Conditions

Chickadees were captured in sunflower seed-baited traps at Purdue University's Ross Biological Station, in West Lafayette, Indiana, USA. The birds were caught in two feeders that were $\approx 60\,\mathrm{m}$ apart; therefore, the birds were likely to have come from the same winter flock (e.g. Smith 1991), although we have no field evidence to substantiate this. All birds used in the experiment were adults (based on banding records), but their exact age was not known. Birds were used only if their wing chord length indicated that they were males (63–66 mm). Thirakhupt (1985) showed that in a sample of 30 birds of known sex, all birds in this range of wing chord length were males (12/15 males, and 0/15 females). All chickadees used in the experiments were held in 1 m^3 holding cages for 1 wk before being tested in the aviaries. Birds held in holding cages had auditory and visual contact, and were fed two mealworms daily, ad libitum sunflower seeds, grated carrot, and 'soft-bill' bird food.

Experimental Conditions

During the experiment, birds were housed individually in one of two $3 \times 3 \times 2$ m experimental aviaries. The birds had auditory contact (the aviaries were contiguous and had wire ceilings, so sounds easily passed between them) but not visual contact.

Four sets of two birds were tested in four separate observation periods starting in Dec., Feb., Apr. or Jun. Note that Apr. is approximately the time of mating in chickadees, although pair formation may occur throughout the winter (Smith 1991). Due to equipment failure, only one of the Jun. set of birds was monitored.

The light/dark cycle was 10/14 h and the aviary temperature was 19 ± 1°C throughout the experiment. Two sources of food were available in the experimental aviaries. Every day at 10.00h, the birds received 0.25 g of mealworms, 0.5 g grated carrot (which they rarely ate), 0.25 g 'soft-bill' bird food, and crushed egg shell. The second source of food was shelled sunflower seeds that were delivered from an electronic feeder.

The feeder access schedule was dictated by a parallel study of mass and cache regulation. The birds were given two different feeder schedules: variable or constant. All birds were given 12 d of the variable schedule followed by 12 d of the constant schedule, followed by 12 d of the variable schedule. During the variable schedule, they received either a total of 10 min of access to sunflower seeds all day or a total of 55 min of access; the sequence of 10 and 55 min days was generated using a random number generator, with the constraint that a 10 min day never followed another 10 min day. Thus, on average, 2 of 3 d were 55 min days, resulting in a mean daily food access of 40 min. In the constant schedule, the birds received a total of 40 min of feeder access every day. Previous results (Lucas 1994; Lucas & Zielinski 1998) showed that 10 min of daily access to the feeder is insufficient time for the birds to maintain body mass (in fact, birds lost mass in the experiments reported here), whereas 40 and 55 min are sufficient to do so. For this reason, we dichotomize days between those in which the birds were given limited access to food (10 min days) and those in which the birds were given relatively more abundant food (40 and 55 min days). However, we give separate regression coefficients (see Statistical Analysis below) for all three schedules where vocalization rates were significantly affected by feeder schedule. Irrespective of feeder schedule (i.e. on all 10, 40, and 55 min days), the feeder access time was divided into four equal access intervals. These access intervals were distributed randomly throughout the day (09.00–17.00h). When the feeder was on, a single seed was delivered into a cup.

Another seed was delivered on average 10 s after the seed in the cup was taken. No seeds were delivered when the feeder was off. The feeder schedules for both birds in a set were identical.

The birds were given six artificial trees with 10 cache sites in each (see Lucas 1994 and Lucas & Zielinski 1998). Caching rates are not directly relevant to this study; they will be addressed elsewhere (Lucas et al., unpubl. data). However, it is important to note that the birds typically had fewer than five seeds cached at lights-out (mean across birds 1.3 ± 1.8 standard deviation (SD), range 0.0–5.1). Therefore, they did not compensate for limited food experienced during 10 min days by caching excess seeds on the 55 min days that preceded 10 min days.

Body Mass

Body mass was recorded from two electronic balances located in each aviary. Mass and time were recorded automatically by a computer whenever a bird perched long enough for the balance to equilibrate. Body mass values were combined with behavioral observations collected during the focal animal samples (described below).

The analysis of mass-specific vocalization rates is complicated by the fact that chickadee body mass can vary enormously both within any given day (> 1 g for a 10 g bird) and between days (> 3 g). Previous results have shown that both time scales are relevant in foraging decisions (Lucas 1994) and, therefore, might be important in vocalization rates. For this reason, we used two mass-related variables in the regression models. Focal mass was the mass at the beginning of a focal sample divided by the mass at 09.00h. Dawn mass was body mass at 09.00h (interpolated with the regression equation; see below). We used the following equation to standardize dawn mass across birds:

$$\text{relative dawn mass} = (\text{maximum mass} - \text{dawn mass}) / (\text{maximum mass} - \text{minimum mass}),$$

where maximum and minimum mass are the highest and lowest mass values measured for an individual bird. Thus, dawn mass measured long-term (between-day) variation in body mass, whereas focal mass measured short-term (within-day) variation.

The balances typically recorded several hundred weights in a day, but nonetheless, we did not record mass continuously throughout the day. We used a fourth-order least-squares polynomial regression equation (PROC GLM; SAS Institute 1990) to estimate body mass during any given focal animal sample. A separate equation was generated for each day's data. Mass was estimated from two independent variables, time of day and time since the feeder last opened (or since 09.00h if the feeder had not opened yet). All interaction terms through the square of the independent variables were also used in the equation. The regression equation was used to reduce the amount of information required to interpolate body mass estimates (see Lucas 1994). The order of the regression equation (fourth) was the minimum required to generate an r^2 of 0.9 for all days.

Vocalization Rates

Vocalization rates were recorded in 15 min focal animal samples (Altmann 1974). We typically recorded two samples per bird per day; the samples were separated in time by at least 2 h. Three vocalizations (tseet, chick-a-dee, and fee-bee fee-bay; sonograms can be found in Smith 1972) given by the focal animal were recorded with an event recorder. The most common vocalization given by Carolina chickadees is the tseet call (Smith 1972). The chick-a-dee call is composed of four different note types, denoted A, B, C and D (e.g. Hailman et al. 1987). The number of elements in any given call can vary, and most calls given by Carolina chickadees do not consist of all note types (pers. obs.). There is some evidence that syntactically different chick-a-dee calls are given under different conditions (e.g. Smith 1972; Ficken et al. 1994). Unfortunately, it is difficult to distinguish subclasses of the chick-a-dee call without sonographic analysis, and we did not do so. A fourth call type, the gargle or t-slink call, was also recorded, but rates of this call were highly variable.

Vocalization rates by nonfocal birds could potentially affect vocalization rates of the focal birds. For example, high fee-bee fee-bay rates by the nonfocal bird might elicit high fee-bee fee-bay rates in the focal bird. To test for this, all but the tseet calls of the nonfocal bird were recorded during the focal animal samples. Both the observer and the focal bird could hear vocalizations of the nonfocal bird. Tseet calls are given at fairly low amplitude and were, therefore, difficult to monitor for nonfocal birds. The high combined rates of tseets from both birds made them impractical to record for all birds.

All observations were conducted by Curt Jackson and April Schraeder. We measured interobserver reliability by jointly observing birds for six of the 15 min focal samples. Cohen's kappa, $= (P_o - P_c)/(1 - P_c)$ ($P_o =$ proportion of agreement actually observed, $P_c =$ proportion expected by chance; Bakeman & Gottman 1986), exceeded 0.85 in all trials.

Statistical Analysis

Repeated measures analysis of covariance with a first-order autoregressive covariance structure (PROC MIXED; SAS Institute 1994) was used to test our predictions. Because the focus of the study was the effect of a bird's body mass and energetic environment on vocalization rates, all statistical tests used a within-subject design with $n = 7$ birds. The dependent variable was the number of calls of a specific type given by the focal animal in the 15 min sample. Seven independent variables were used in the repeated measures analysis. Six were treated as interval or continuous variables: focal mass, dawn mass, time of day, number of days the bird had been tested, nonfocal chick-a-dee rate, and nonfocal fee-bee fee-bay rate. One was treated as a nominal or class variable (with three levels as described above): duration of access to food. Q–q plots were used to test for normality in the residuals of the regression equations. For all call types, we log-transformed the dependent variable to normalize residuals. Nonlinear relationships between the dependent and independent variables were tested by adding squared terms for each independent variable. Two-way interaction terms between all independent variables were also added to the models. Nonsignificant ($p > 0.05$) interactions and squared terms were dropped from the models in order of increasing F value. Partial regression coefficients were generated using the estimate procedure in PROC MIXED (SAS Institute 1994). Note that the regression coefficients listed in the Results represent the mean change in the dependent variable (e.g. tseet rate) with a unit change in the independent variable (e.g. body mass), holding all other variables constant.

Results

Mean Vocalization Rates

We observed birds an average of 13.5 h each (54, 15 min focal samples). The most frequent vocalization during the focal observations was the tseet call and the least frequent vocalization was the fee-bee fee-bay, although individual differences in vocalization rates were evident (Fig. 1). Generally, birds tended to call more when light than when heavy, but they tended to sing more when heavy than when light. Below we address each vocalization separately.

Tseet Call

Generally, birds gave tseet calls more often when they were light than when they were heavy (Fig. 2). This relationship was found for both dawn (between-day)

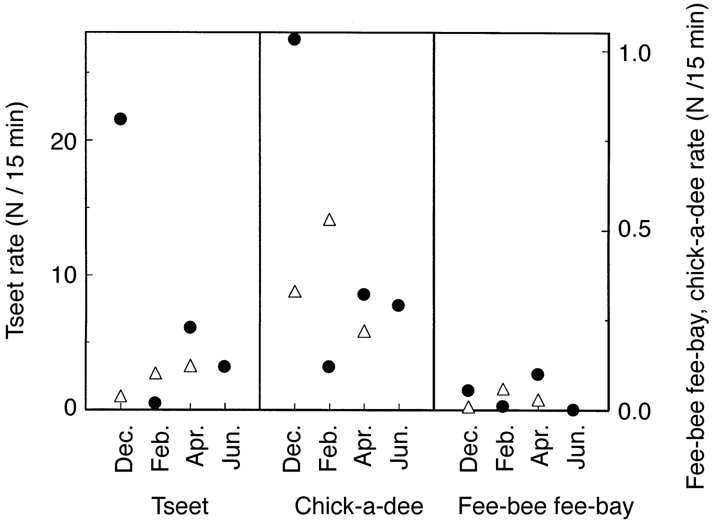

Fig. 1: Mean vocalization rates per 15 min focal animal sample for each of seven Carolina chickadees. Each symbol represents a separate bird; ●, bird with longer wing chord of the pair tested together; △, bird with smaller wing chord. The month indicated for each bird is the month observations started

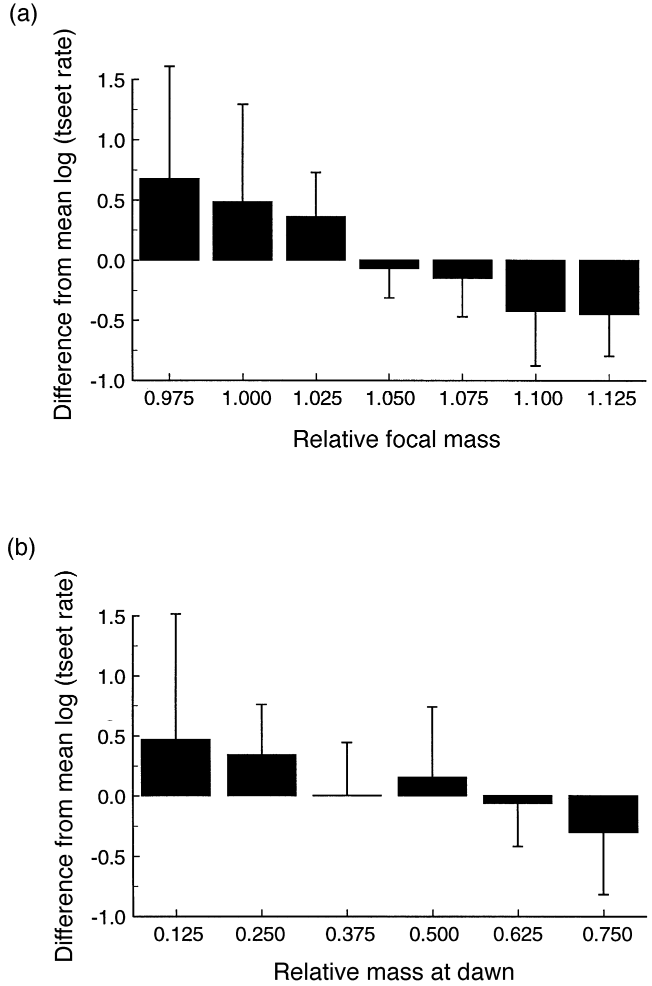

Fig. 2: Deviation from mean log-transformed (log[rate + 1]) tseet rates (n/15 min focal) as a function of a. relative mass during the focal, or b. relative mass at dawn. The mean of each bird was calculated as the mean log-transformed tseet rate at the given mass interval minus the mean across all data for this bird (in effect, generating the residual effect of mass on tseet rate). The values plotted here are ± standard deviation (SD) across birds (n = 7). See Fig. 1 for overall mean vocalization rates for each bird

mass ($\beta_{dawnmass} = -5.2 \pm 1.1$; $F_{1,6} = 23.42$, $p = 0.003$) and focal (within-day) mass. However, the effect of focal mass on tseet rate varied with the duration of access to food (focal mass: $F_{1,6} = 16.54$, $p = 0.007$; focal mass × duration interaction: $F_{2,11} = 3.99$, $p = 0.050$); the regression coefficient relating tseet rate with focal mass was higher (i.e. less negative) when food access was insufficient to maintain body mass (10 min days) compared with days when food was relatively more abundant (duration 10: $\beta_{\mathrm{fmass \times dur}} = -0.5 \pm 4.8$, df = 11, t = −0.10, ns; duration 40: $\beta_{\mathrm{fmass \times dur}} = -11.1 \pm 2.4$, df = 11, t = −4.62, p = 0.0007; duration 55: $\beta_{\mathrm{fmass \times dur}} = -14.4 \pm 2.2$, df = 11, t = −6.66, p = 0.0001). Thus, the tendency to tseet at low mass was greater when food was abundant.

Tseet rates tended to be higher when the birds had limited access to food (10 min/d: least-squares mean of log-transformed rate = 1.64 ± 0.42) than when food was more abundant (40 or 55 min/d; $F_{2,15} = 4.00$, p = 0.040; least-squares means for 40 min days = 1.44 ± 0.40 and for 55 min days = 1.56 ± 0.40). The overall higher tseet rate for 10 min days could have limited the relationship between mass and tseet rate discussed above. In effect, a higher intercept could cause a reduction in slope.

Holding other variables constant, there was no significant change in tseet rates during the day ($F_{1,6} = 2.8$, ns), nor was there a systematic change in tseet rates over the duration of the study ($F_{1,6} = 1.67$, ns). There was also no significant relationship between nonfocal vocalization rate and tseet rate (nonfocal chick-a-dee rate: $F_{1,6} = 0.01$, ns; nonfocal fee-bee fee-bay rate: $F_{1,4} = 0.42$, ns).

Chick-a-dee Call

The trends found with chick-a-dee rates were similar to those found with tseet rates. The birds gave more chick-a-dee calls when they were light than when they were heavy (Fig. 3). The relationship was significant and nonlinear for both dawn mass (dawn mass: $F_{1,6} = 9.54$, p = 0.021; dawn mass^2: $F_{1,6} = 6.73$, p = 0.041; regression coefficients: $\beta_{\mathrm{dmass}} = -0.40 \pm 0.45$; $\beta^2_{\mathrm{dmass}} = 1.07 \pm 0.41$) and focal mass (focal mass: $F_{1,6} = 14.12$, p = 0.009; focal mass^2: $F_{1,6} = 13.77$, p = 0.010; regression coefficients: $\beta_{\mathrm{fmass}} = -93.25 \pm 23.96$; $\beta^2_{\mathrm{fmass}} = 42.07 \pm 11.34$). The sign of the regression coefficients indicates that chick-a-dee rates decreased with increasing mass (both focal and dawn mass), but that the rate was asymptotic at high levels of mass.

The regression coefficient relating chick-a-dee rate with focal mass was higher (i.e. less negative) when the birds had 10 min of access to food compared with days when food was more abundant (focal mass × duration: $F_{2,11} = 13.94$, p = 0.001; duration 10: $\beta_{\mathrm{fmass \times dur}} = -76.7 \pm 22.4$, df = 11, t = −3.42, p = 0.006; duration 40: $\beta_{\mathrm{fmass \times dur}} = -80.3 \pm 22.8$, df = 11, t = −3.52, p = 0.005; duration 55: $\beta_{\mathrm{fmass \times dur}} =$ $\beta_{\mathrm{fmass \times dur}} = -80.3 \pm 22.8$, df = 11, t = −3.52, p = 0.005; duration 55: $\beta_{\mathrm{fmass \times dur}} =$ lower focal mass was greater when food was abundant.

Overall, birds tended to chick-a-dee more often when food was limited (10 min/d: least-squares mean of log-transformed rate = 0.54 ± 0.23) than when food was more abundant (40 or 55 min/d: $F_{2,17} = 14.7$, p = 0.0002; least-squares means for 40 min days = 0.32 ± 0.23, for 55 min days = 0.37 ± 0.22). As with tseet rates, a high overall chick-a-dee rate under food limitation (10 min days) could limit the effect of mass on chick-a-dee rates described above.

Chick-a-dee rates were not correlated with time of day ($F_{1,6} = 0.42$, ns), nor with the number of days the birds were tested in the aviaries ($F_{1,6} = 3.9$, ns). No correlation was shown between focal chick-a-dee rates and vocalization rates of

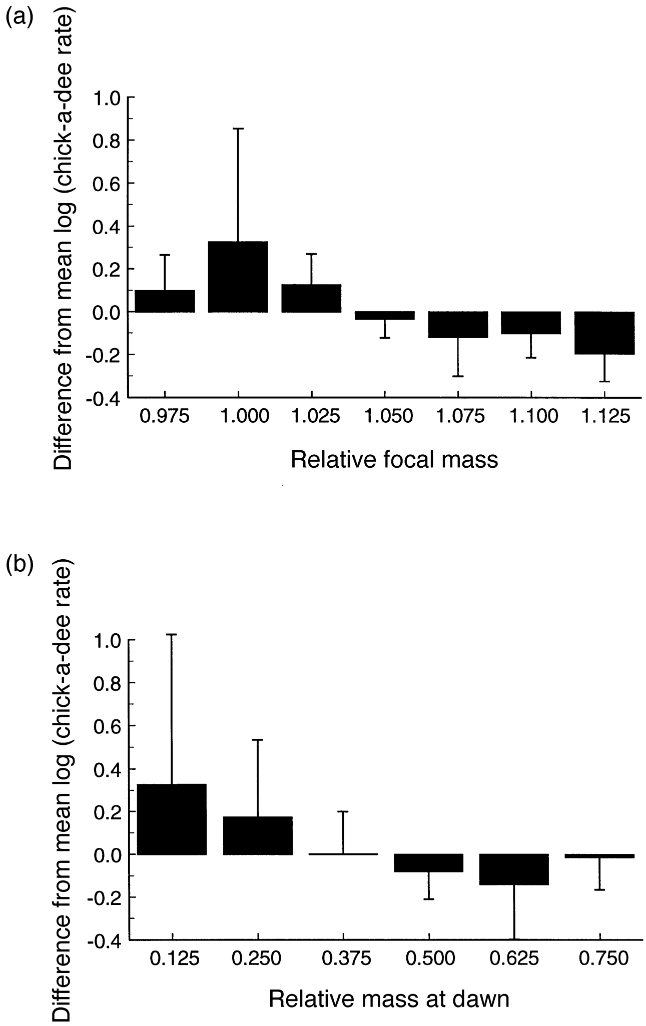

Fig. 3: Deviation from mean log-transformed chick-a-dee rates (n/15 min focal) as a function of a. relative mass during the focal, or b. relative mass at dawn. The values plotted here are ± standard deviation (SD) across birds (n = 7)

the nonfocal birds (nonfocal chick-a-dee rates: $F_{1,6} = 4.50$, ns; nonfocal fee-bee fee-bay rates: $F_{1,4} = 1.29$, ns).

Fee-bee Fee-bay

Unlike both nonsong vocalization rates, fee-bee fee-bay rates increased with an increase in dawn mass (Fig. 4; $F_{1,6} = 7.18$, $p = 0.036$). Focal mass was not correlated with fee-bee fee-bay rates ($F_{1,6} = 0.29$, $p = 0.61$).

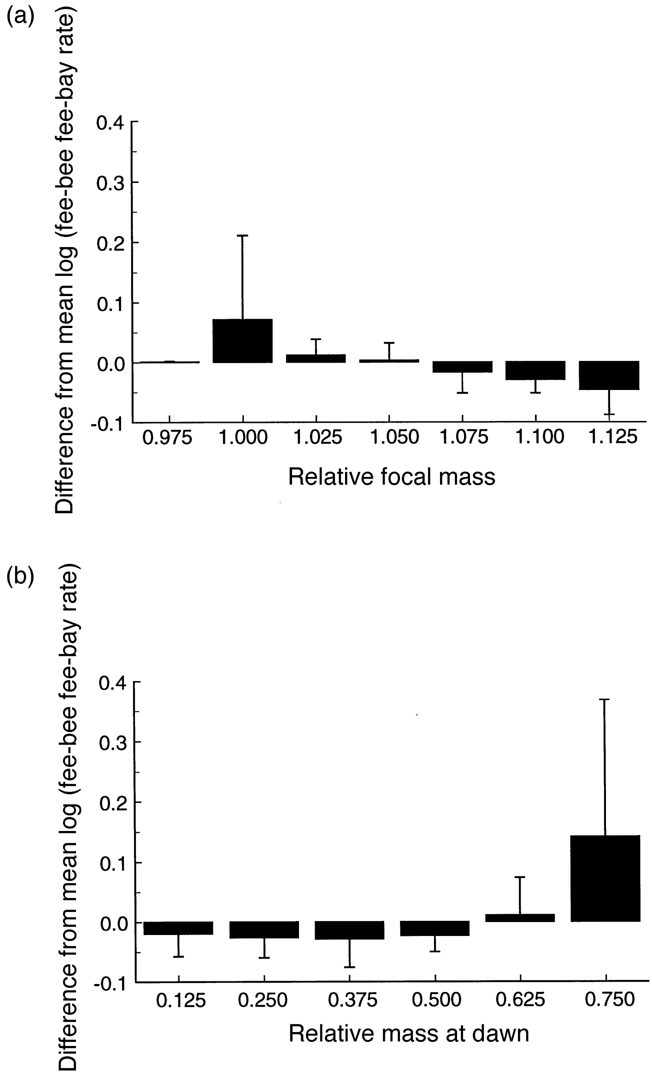

Fig. 4: Deviation from mean log-transformed fee-bee fee-bay rates (n/15 min focal) as a function of a. relative mass during the focal, or b. relative mass at dawn. The values plotted here are ± standard deviation (SD) across birds (n = 7)

No significant relationship was found between fee-bee fee-bay rates and the duration of food access ($F_{2,17} = 2.30$, ns), or with the number of days the birds were tested in the aviaries ($F_{1,6} = 0.12$, ns). Even though the highest fee-bee fee-bay rates were given in the morning (compared, for example, with tseet rates: compare Fig. 5a and b), fee-bee fee-bay rates were not significantly correlated with

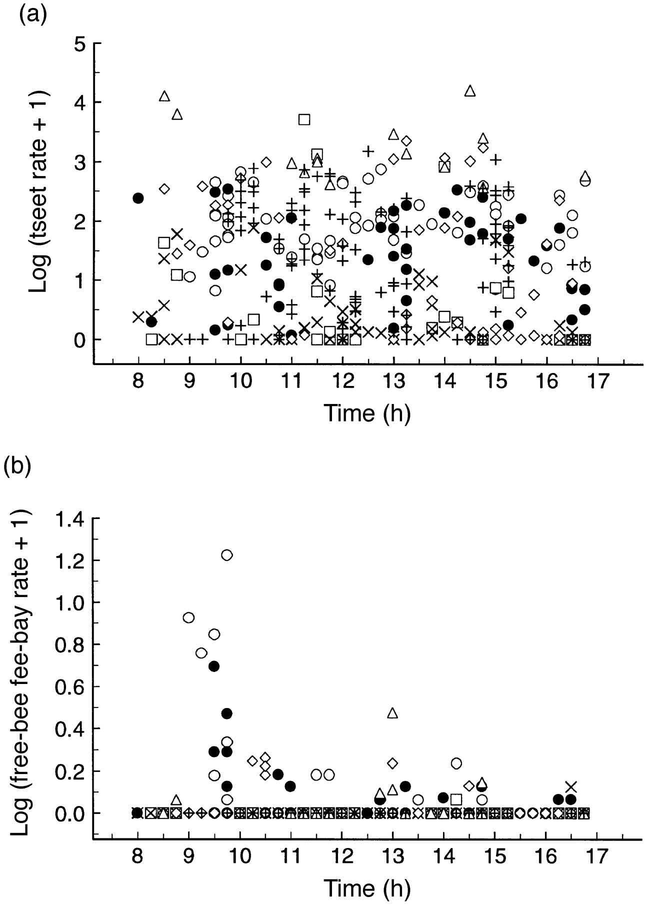

Fig. 5: Scatterplot of a. log-transformed tseet rates (n/15 min focal) and b. log-transformed fee-bee fee-bay rates (n/15 min focal). Each symbol represents one 15 min focal and each symbol type represents a different bird

time of day ($F_{1,6} = 0.42$, ns). No correlation was found between the fee-bee fee-bay rate and nonfocal vocalization rates (nonfocal chick-a-dee rate: $F_{1,6} = 1.61$, ns; nonfocal fee-bee fee-bay rate: $F_{1,4} = 0.25$, ns).

Discussion

Nonsong vocalizations (tseet and chick-a-dee) were given more frequently by birds that were lightweight. This result holds for two temporal scales of body mass: within-day (focal mass) and between-day (dawn mass). In contrast, song vocalizations (fee-bee fee-bay) were given more frequently when dawn mass was relatively high. Thus, our original prediction that song rates should increase for relatively heavy birds is correct, although individual differences in overall song rates were observed. The fact that nonsong communication rates increased for relatively lightweight birds rules out the prediction that, under the conditions we provided in our experiment, call rates decline with increased energetic stress due to risk-prone behavior or to a reduced emphasis on vigilance. Also, vocalizations from nonfocal birds had no consistent effect on the vocalization rates of the focal birds, suggesting that the birds in each pair did not respond vocally to variability in vocalization patterns that they heard in the aviaries.

One intriguing aspect of our results is that both calls analyzed showed similar mass dependence: call rates increased when the birds were relatively lightweight. This is intriguing because these calls are typically given under a variety of circumstances. The tseet call is a short-range contact call given under a wide range of circumstances, and, according to Smith (1972), is used to keep pair or flock members appraised of each others' position. The chick-a-dee call has a number of potential functions, including predator or mobbing call, food call, or mild alarm call (Smith 1972; Ficken et al. 1978; Mammen & Nowicki 1981). Our data suggest that the value of both calls increases for relatively lightweight birds.

Why should call output increase in relatively lightweight birds? Our results imply that the social context of nonsong vocal communication is more important for birds facing energetic stress. High call rates were recorded when food was most limiting, when the birds were relatively lightweight within a day, and when they were relatively lightweight at dawn. The reduction in call rates at higher body mass was also greatest when the birds had more access to food (40 or 55 min/d vs. 10 min/d), and therefore when the potential for energetic stress was minimized. Krebs (1973) demonstrated the potential for social learning about food resources both within and between species in mixed species flocks (also see Vickery et al. 1991). Energetic stress may promote the requirement for social interaction. However, theoretical analyses are equivocal on this point, because several opposing factors can govern the relative value of social behavior (McNamara & Houston 1990). For example, sociality is beneficial in several respects. Sociality can decrease predator risk (and indirectly increase time available for foraging) if animals can share information derived from predator vigilance (McNamara & Houston 1992). Sociality can also potentially cause an increase in food finding rates and decrease the variance in food availability if animals can observe flockmates that have found food or if flockmates share information about food (Valone 1996). However, sociality can also be detrimental in several respects. Sociality may enhance competition for food (Milinski & Parker 1991), decreasing the amount of food available and increasing the variance in food availability, and it may increase competition for favorable foraging sites (especially for subordinates; Clark & Ekman 1995).

This discussion underscores the point that there are many tradeoffs associated with sociality that produce complex predictions regarding the net benefits of sociality on the fitness of animals. However, a number of empirical studies show that stressful conditions may generally enhance social behavior and set the context for increased social communication. Severe weather induces flocking in blackbirds (*Turdus merula*; Elkins 1988). Individuals in several species of *Poecile* are less likely to flock when given supplemental food (Berner & Grubb 1985; Hogstad 1988, 1989; but see Samson & Lewis (1979) for a counter example where provisioning increased flock size) and when natural resource abundance is relatively high (Smith 1972; With & Morrison 1990). Also, both primates (e.g. tamarins) and birds give calls that are related to food acquisition. In both taxa, these calls are given at higher rates when food is located in large quantities (e.g. red-bellied tamarins, Caine et al. 1995; black-capped chickadees, Ficken 1981). Our data suggest that an additional dimension to this problem is the physiological state of the participating individuals.

Why should song output increase in relatively heavy birds? There is little evidence that song in passerines is an honest signal with a high energetic cost (Weary et al. 1991; Chappell et al. 1995; Gaunt et al. 1996). However, song rates may provide at least indirect advertisement of male quality. A number of studies have shown that increasing food availability through provisioning correlates with an increase in song rates (e.g. pied flycatchers, *Ficedula hypoleuca*, Gottlander 1987; Ipswich sparrows, *Passerculus sandwichensis*, Reid 1987). In addition, the first song production of the breeding season of a number of bird species peaks on warm-weather days, when energetic conditions are presumably favorable (Slagsvold 1976). Galeotti et al. (1997) failed to find a correlation between song rates and body condition in barn swallows (*Hirundo rustica*), but they did find that at least one property of the call (the pitch of the 'rattle') correlated with condition. Finally, dominant black-capped chickadees (*P. atricapillus*) sing at higher rates than subordinates (Otter et al. 1997). Clearly, song output rates could provide cues to females about male condition even if song production, per se, is not costly.Slater (1983) suggested that communication in some way describes the state of the animal. If this is true, then an understanding of physiological conditions that regulate communication should provide some insight into the information embodied in the signal. In contrast, Smith (1972) published the most complete description of the vocal patterns of the Carolina chickadee, and she described conditions under which these vocalizations are given; hunger levels or body mass effects were never mentioned in that paper and are typically not mentioned in analyses of vocal patterns in most publications. Nonetheless, variation in energetic condition does indeed appear to be an important correlate of vocal communication in this species.

The data we have described here are not definitive. A 3 × 3 m aviary is not a 3000 × 3000 m woodlot. On the other hand, it is difficult to collect data in the field at the resolution required to address the issues we have raised here. The artificial social conditions under which our birds were housed (visual, but not acoustic, isolation) may have affected the results of our studies. In particular, adding females to the aviaries may increase fee-bee fee-bay rates. Indeed, song rates were somewhat higher in a previous study we conducted in which both males and females were housed in our aviaries (see Lucas 1994). We are currently conducting additional studies with flocks of four, and under these conditions t-slink (or gargle) calls are more common than recorded for the isolated birds in the study described here. Nonetheless, our results provide an interesting glimpse into bird communication that raises a number of hypotheses about tradeoffs associated with communication.

Ultimately, we need to go into the field to evaluate these ideas. Our data suggest that this would be a venture worth undertaking.

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