

Sheep in wolf's clothing: host nestling vocalizations resemble their cowbird competitor's

Katie Pagnucco¹, Liana Zanette^{1,*}, Michael Clinchy² and Marty L. Leonard³

¹Department of Biology, University of Western Ontario, London, Ont., Canada N6A 5B7

²Department of Biology, University of Victoria, Victoria, BC, Canada V8W 3N5

³Department of Biology, Dalhousie University, Halifax, NS, Canada B3H 4J1

Nestlings of many avian brood parasites are virtuosos at mimicking host nestling vocalizations, which, like egg mimicry, presumably ensures acceptance by host parents. Having been accepted, parasitic nestlings then often exaggerate the aspects of the host's display to increase parental care. Host nestlings may, in turn, exaggerate their vocalizations to keep up with the parasite, though this possibility has not been evaluated. We experimentally parasitized song sparrow (*Melospiza melodia*) nests with a brown-headed cowbird (*Molothrus ater*) chick to evaluate how host nestlings respond. Vocalizations emitted from experimentally parasitized nests were higher in frequency, and louder, than those from unparasitized nests, consistent with the cowbird exaggerating its signalling. In response, host nestlings exaggerated the frequency and amplitude of their vocalizations, such that they resembled the cowbird's while they 'scaled back' on calls per parental provisioning bout. Sparrows in parasitized nests were fed equally often as sparrows in unparasitized nests, suggesting that exaggerating some aspects of vocalization while scaling back on others can help host nestlings confronted with a cowbird. Our results support the recently proposed hypothesis that signalling in parasitized nests involves a dynamic interaction between parasitic and host nestlings, rather than a one-way process of mimicry by the parasite.

Keywords: begging calls; brood parasitism; brown-headed cowbirds; song sparrows; vocal mimicry

1. INTRODUCTION

Numerous species of avian brood parasites lay eggs that precisely mimic the colour and egg patterning of their host to ensure their eggs are accepted by the host parents (Davies 2000; Payne 2005). Brood parasites can impose severe costs on the survival and reproduction of hosts or their offspring (Davies 2000; Smith *et al.* 2002; Payne 2005; Zanette *et al.* 2005, 2007; Hoover & Robinson 2007; Krüger 2007), so selection should favour hosts that can identify and eject the eggs of brood parasites from their nests (Brooke & Davies 1988; Davies & Brooke 1989; Moksnes & Roskaft 1995; but see Hoover & Robinson 2007).

Forgery by brood parasites also occurs at the nestling stage. Many parasitic cuckoo nestlings are virtuosos at mimicking the vocal calls of host nestlings, which, like egg mimicry, presumably ensures the cuckoo nestling is accepted and cared for by host parents (e.g. McLean & Waas 1987; Redondo & Arias de Reyna 1988; Langmore *et al.* 2003). Having been accepted, parasitic nestlings then often exaggerate those features of the host nestling's begging displays that are critical to attracting parental care, such as amplitude and call rate (Redondo 1993; Davies *et al.* 1998; Kilner *et al.* 1999). Among species where the brood parasitic nestling is reared together with host nestlings, such exaggeration helps explain why the brood parasite often receives the lion's share of parental food provisioning (Kilner *et al.* 2004).

Once the brood parasitic nestling has succeeded in being accepted and then begun exaggerating its signalling

to host parents, it may benefit host nestlings to, in turn, begin mimicking the brood parasite's exaggerations where the two are reared together. This novel idea, that the often very close resemblance between brood parasitic and host nestling signals may stem not only from mimicry by the brood parasite but also from mimicry of the brood parasite by host nestlings, was only very recently proposed by Hauber & Kilner (2007). Consequently, most studies to date have focused on mimicry by the brood parasitic nestling and have overlooked just how host nestlings are responding.

In this paper, we examine the begging calls of host (song sparrow, *Melospiza melodia*) nestlings in nests where we experimentally introduced a brood parasitic (brown-headed cowbird, *Molothrus ater*) nestling. We compare these calls with the begging calls of both the brood parasite and the host nestlings in unparasitized nests. We examine four components of vocalization: frequency; amplitude; the duration of each discrete vocalization (call length); and call rate. Previous studies suggest that cowbird nestlings exaggerate amplitude and call rate (Briskie *et al.* 1994; Dearborn 1999) and they may also exaggerate frequency in order to be better heard over ambient noise around the nest (Leonard & Horn 2005). Host nestlings in turn may exaggerate some or all of these components when together with a cowbird. Since the presumed benefit to the host nestling of mimicking the brood parasite is to prevent it from completely monopolizing parental provisioning (Hauber & Kilner 2007), we also compare the parental provisioning of host nestlings in both parasitized and unparasitized nests.

* Author for correspondence (lzanette@uwo.ca).

2. MATERIAL AND METHODS

(a) Cowbird nestling addition

We conducted this study near Victoria, Canada (48°26' N, 123°20' W) from May to July 2006. Details regarding study sites and song sparrows can be found elsewhere (Zanette *et al.* 2003, 2005, 2006a,b). When a nest was found, we candled the eggs to estimate the age of the nest. We monitored 42 unparasitized song sparrow nests and arranged for 12 nests to be parasitized with a single cowbird egg, deposited approximately 3 days prior to hatch (average 3.5 ± 0.64 days before hatch). The average difference in age between the song sparrows and cowbird was 0.7 ± 0.34 days. Brood sizes were comparable between treatments ($t_{41} = -1.5$, $p = 0.14$).

(b) Audio and visual recordings

One hour audio and visual recordings of nestlings were conducted between 07.00 and 12.00 hours on fine days when the nestlings were 6 days old. To record vocalizations, we used an Optimus 33-3003 lapel microphone positioned 10 cm above the centre of the nest, connected to a Marantz PMD-222 audio cassette recorder located 15 m from the nest. For simultaneous video recording, we used a National Electronics Bullet-C/IR camera (37 × 86 mm) positioned 10 cm from the edge of the nest, connected to a custom-built digital video recorder (Clinchy & Zanette 2004, unpublished data) also located 15 m from the nest. Once the equipment was installed, we waited at least 15 min to allow parents adequate time to resume usual activities.

(c) Nestling vocalizations

All begging calls recorded during provisioning (see below) were digitized at 44 kHz and 16 bits with RAVEN v. 1.2 software (Cornell Lab of Ornithology). We examined four components of vocalization including: (i) frequency, which consisted of two measures, minimum and maximum (the lowest and highest frequencies reached within a given call, measured in kHz), (ii) amplitude, which consisted of two measures, minimum and maximum amplitude reached within a given call minus background amplitude (measured in dB), (iii) call length, which was the average duration of each discrete vocalization, and (iv) call rate, which consisted of two measures, 'calls per trial' that was the total number of calls nestlings gave summed over each 1 hour trial and 'calls per bout' that was the number of calls given for each second of provisioning multiplied by 60 to convert seconds to minutes. All six variables in our four vocalization categories were measured from spectrograms (analysis bandwidth 699 Hz, display resolution 22 Hz × 3 ms) with the exception of amplitude that was calculated from oscillograms.

(d) Parental provisioning and food acquisition by song sparrow nestlings

We measured three components of parental provisioning behaviour including: (i) visits per hour, (ii) time spent provisioning when at the nest, and (iii) the number of times sparrows got fed in each treatment. Time spent provisioning was defined as the interval from when the parent placed its bill inside the gape of the first nestling to the moment the parent removed its bill from the gape of the last nestling.

(e) Statistical analyses

We present two sets of analyses. We first examine our vocalization measures on a per nest basis comparing experimentally parasitized versus unparasitized nests. We then separated

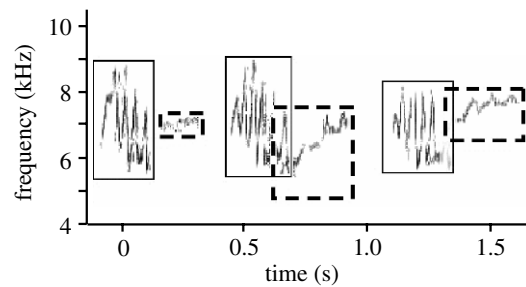


Figure 1. Representative spectrogram of the vocalizations of cowbirds (solid boxes) and their song sparrow nest-mates (dashed boxes).

song sparrow calls from cowbird calls (figure 1) using both our audio and video recordings and examined begging calls on a per individual basis, comparing sparrows in parasitized nests versus cowbirds versus sparrows in unparasitized nests. For both sets of analyses, we used stepwise discriminant function analysis (DFA) to determine whether and which combination of our vocalization variables could differentiate among groups on a per nest basis, and then on a per individual basis. In the latter case, if sparrows in parasitized nests exaggerated their vocalizations, then we expected their begging calls to deviate from that of sparrows in unparasitized nests, towards convergence with cowbirds. For this analysis, call rate was divided by the number of song sparrows or cowbirds in the nest to correct for there being several sparrows in each nest but only one cowbird.

We tested all variables for collinearity using Pearson's correlation coefficients and found that minimum and maximum frequencies were strongly and positively correlated ($F_{1,31} = 137.8$, $p > 0.0001$, $R^2 = 0.81$). Consequently, we excluded minimum frequency from our analyses, leaving five variables to enter in the DFA models. Checks were made for departures from normality and multivariate outliers. None were found, except for calls per trial that was normalized with a Box-Cox transformation. Each variable with $F \geq 1$ was entered sequentially into the analysis in the order of the greatest contribution to discrimination among groups. We restricted our interpretation of each discriminant function to those predictor variables that had correlations with the function that explained at least 5% of the variance (i.e. values greater than 0.22) to ensure we had adequately explored all potentially relevant predictors (Tabachnick & Fidell 2001). We subsequently analysed all such predictors using *t*-tests, one-way ANOVAs and Bonferroni *post hoc* tests, where appropriate, to further identify in which group the differentiation was the strongest for that variable.

We analysed parental provisioning and food acquisition by song sparrow nestlings with univariate parametric tests after checking for the normality and homogeneity of variances. All analyses were performed using STATISTICA v. 6.0. Means are presented \pm s.e.

3. RESULTS

On a per nest basis, vocalizations were very different in experimentally parasitized versus unparasitized nests ($\chi^2_5 = 29.4$, $p < 0.0001$). The predictors that best discriminated between our treatments were frequency (kHz; correlation with canonical root = 0.52) and amplitude (dB; correlation with canonical root = 0.40), with calls per trial being somewhat important (correlation with canonical root = 0.24). Vocalizations in experimentally

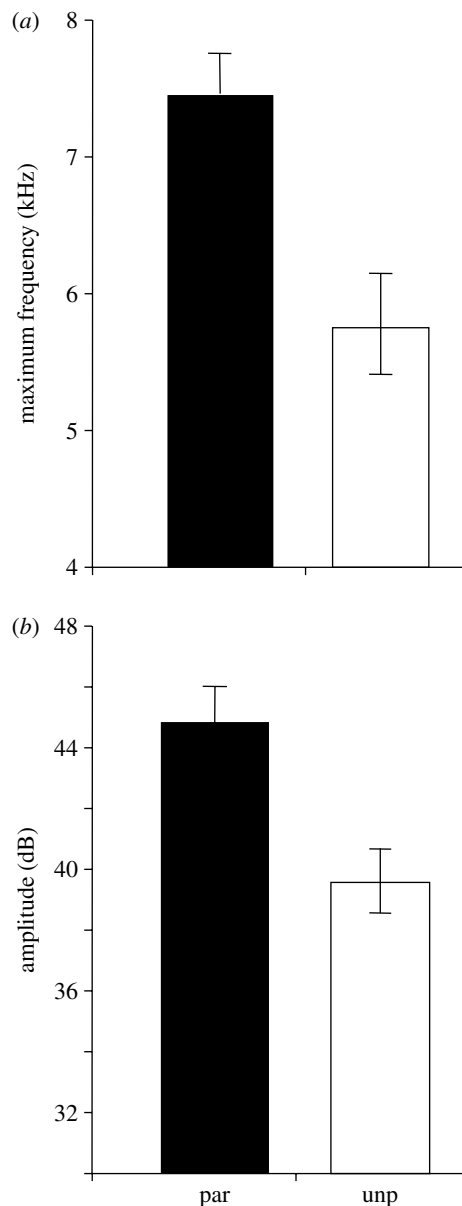


Figure 2. Components of nestling vocalizations in experimentally parasitized (black bars, $n=11$) and unparasitized nests (open bars, $n=22$). (a) Maximum frequency in kHz and (b) amplitude in dB. Values are means \pm s.e.

parasitized nests were higher in frequency (figure 2a; maximum frequency, $t_{31} = -4.0$, $p=0.0004$) and louder (figure 2b; amplitude, $t_{31} = -3.0$, $p=0.005$), and there tended to be more calls emitted per trial (parasitized, 163.3 ± 39.6 ; unparasitized, 103.4 ± 13.6 ; $t_{31} = -1.8$, $p=0.085$). The discriminant function correctly classified 100% of parasitized nests and 96% of unparasitized ones.

On a per individual basis, cowbirds were the first to vocalize in 80% of 340 feeding events. Not only the cowbird, but also the sparrow nestlings contributed to the exaggerated vocalizations emitted from experimentally parasitized nests. We found evidence that the sparrows altered some components of their vocalizations in parasitized nests such that the sparrow's calls more closely resembled the cowbird's. The DFA differentiated the three groups (figure 3; sparrows in parasitized nests versus cowbirds versus sparrows in unparasitized nests; $\chi^2_8 = 42.3$, $p < 0.0001$). After the removal of the first function, association using the second function was also

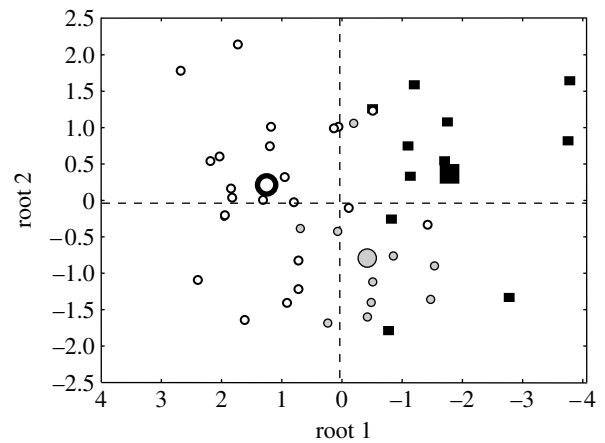


Figure 3. Discriminant function scores derived from the per individual vocalization variables, differentiating sparrows in parasitized nests (grey circles) versus cowbirds (black squares) versus sparrows in unparasitized nests (open circles). Small symbols represent individual scores and large symbols indicate centroids.

significant ($\chi^2_3 = 7.9$, $p=0.048$). The first and second discriminate functions accounted for 86.3 and 13.7% of the variation, respectively. The first discriminant function (root 1) separated sparrows and their cowbird nest-mates from sparrows in unparasitized nests (figure 3). The second discriminant function (root 2) separated sparrows in parasitized nests from both their cowbird nest-mates and sparrows in unparasitized nests (figure 3). The DFA correctly classified 70% of sparrows in parasitized nests, 82% of cowbirds and 94% of sparrows in unparasitized nests. Of the sparrows in parasitized nests incorrectly classified, 10% were classified as cowbirds and 20% as sparrows in unparasitized nests.

The variables that best discriminated sparrows and their cowbird nest-mates from sparrows in unparasitized nests (root 1) were frequency (kHz; correlation with canonical root = 0.63) and amplitude (dB; correlation with canonical root = 0.48). The maximum frequency differed significantly among groups (figure 4a; $F_{2,40} = 11.3$, $p=0.0001$). Sparrows and their cowbird nest-mates emitted calls of similar frequency (Bonferroni *post hoc*, $p > 0.05$) that were significantly higher than those given by sparrows in unparasitized nests (figure 4a; Bonferroni *post hoc*, sparrows in parasitized versus unparasitized nests, $p < 0.05$; cowbirds versus sparrows in unparasitized nests, $p < 0.0001$). Amplitude also differed significantly among groups (figure 4b; $F_{2,40} = 6.7$, $p=0.003$). Cowbirds were louder than sparrows in unparasitized nests (Bonferroni *post hoc*, $p < 0.01$), with amplitude being intermediate for sparrows in parasitized nests (figure 4b; Bonferroni *post hoc*: cowbirds versus sparrows in parasitized nests, $p > 0.05$; sparrows in parasitized versus unparasitized nests, $p > 0.05$). The second discriminant function (root 2) included only calls per bout (correlation with canonical root = 0.98) which differed significantly among groups (figure 4c; $F_{2,40} = 4.4$, $p=0.018$). Here, sparrows in parasitized nests emitted fewer calls per bout than either cowbirds or sparrows in unparasitized nests (figure 4c; Bonferroni *post hoc* tests: sparrows in parasitized nests versus cowbirds, $p < 0.05$; sparrows in parasitized versus unparasitized nests, $p < 0.05$; cowbirds versus sparrows in unparasitized nests, $p > 0.05$).

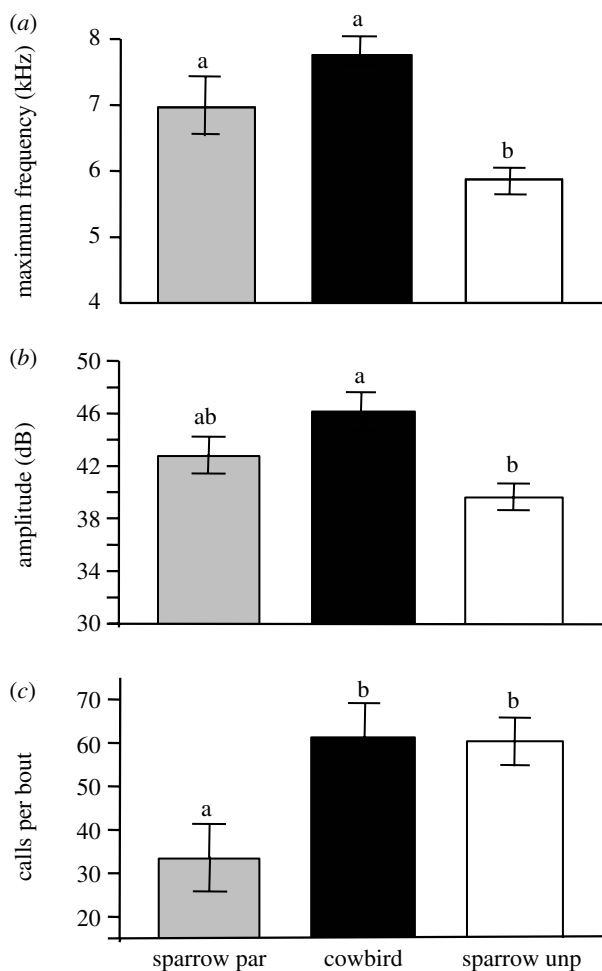


Figure 4. Components of vocalizations emitted by sparrows in parasitized nests (grey bars, $n=10$) versus cowbirds (black bars, $n=11$) versus sparrows in unparasitized nests (open bars, $n=22$). (a) Maximum frequency in kHz, (b) amplitude in dB and (c) calls per bout. Groups with different letters were significantly different from one another based on Bonferroni *post hoc* tests ($p < 0.05$). Values are means \pm s.e.

Whereas there was no difference in how frequently parents visited the nest ($t_{40} = -0.9$, $p = 0.35$), they spent 60% more time provisioning at experimentally parasitized nests (6.4 ± 0.53 s) than at unparasitized nests (4.3 ± 0.39 s; $t_{32} = 3.2$, $p = 0.002$). Sparrow nestlings got fed equally often regardless of treatment (parasitized versus unparasitized nests, 6.7 ± 1.17 versus 6.3 ± 0.99 ; $t_{10} = 0.3$, $p = 0.76$).

4. DISCUSSION

The frequency, amplitude and rate of vocalizations emitted from experimentally parasitized nests were all greater than those from unparasitized nests, consistent with the cowbird exaggerating its signalling to the host parents. This exaggeration, however, was not all on the part of the cowbird because the sparrows in parasitized nests also increased the frequency and amplitude of their vocalizations such that their calls more closely resembled that of the cowbirds. The presumed benefit to host nestlings of vocalizing like a cowbird is that this may help prevent the cowbird from completely monopolizing parental provisioning. Sparrows in experimentally parasitized nests not only succeeded in getting fed, but were also fed equally as often as sparrows in unparasitized nests.

In the only other study we are aware of that has compared the vocalizations from cowbird-parasitized and unparasitized nests, Dearborn (1999) showed that the amplitude and rate of calls emitted from cowbird-parasitized indigo bunting (*Passerina cyanea*) nests were exaggerated compared with those from unparasitized nests. Dearborn did not distinguish between cowbird and host calls in parasitized nests, but he did suggest that host nestlings could be contributing to the exaggerated calling coming from parasitized nests. If, like song sparrows, indigo bunting nestlings alter the structure of their calls, when together with a cowbird, this could explain why Dearborn was unable to distinguish between cowbird and bunting calls.

Rather than attempting to imitate the cowbird, sparrows in parasitized nests may have exaggerated the frequency and amplitude of their calls simply to be heard over the din made by the cowbird. Leonard & Horn (2005) showed that nestling tree swallows (*Tachycineta bicolor*) increase the frequency and amplitude of their calls as ambient noise increases, and parents preferentially feed those whose calls exceed ambient noise levels (i.e. those that can be heard over the din). Briskie *et al.* (1994) reported that cowbird nestlings are one of the loudest beggars among North American passerines. Consequently, the nestlings of most species of cowbird hosts must be faced with the challenge of making themselves heard over the cowbird. Studies on numerous species have shown that nestlings commonly alter the amplitude and structure of their begging calls when in competition with more, larger or more competitive conspecific nest-mates (Smith & Montgomerie 1991; Price *et al.* 1996; Leonard & Horn 2001; Rodríguez-Gironés *et al.* 2002; Neuenschwander *et al.* 2003). Thus, it would be very surprising if the nestlings of most host species do not also alter the amplitude and structure of their calls when confronted with a cowbird nestling that is necessarily an additional, and generally a larger and more competitive, nest-mate.

The sparrows in experimentally parasitized nests did not uniformly exaggerate every component of vocalization but in fact 'scaled back' their call rate (calls per bout) compared with sparrows in unparasitized nests (figure 4c). Sparrows in parasitized nests may be scaling back on call rate for at least two reasons. By sparing effort on call rate (figure 4c) while expending effort on increasing the frequency (figure 4a) and amplitude of their calls (figure 4b), sparrows in parasitized nests may be able to balance their total vocalization effort such that it does not differ greatly from that of sparrows in unparasitized nests. We found that parents provisioned sparrow nestlings in both parasitized and unparasitized nests at the same rate, and Zanette *et al.* (2005) reported that most song sparrow nestlings can maintain their mass when together with a cowbird. Sparrows in parasitized nests may also be able to scale back on call rate because the cowbird is calling enough for everybody. Cuckoos reared alone exaggerate their signalling solely to make host parents work harder (Davies *et al.* 1998; Kilner *et al.* 1999). Cowbirds may similarly exaggerate some signals to make parents work harder to bring food to the nest and exaggerate others to ensure they receive the lion's share when parents are at the nest. Host nestlings must exaggerate those signals that prevent the cowbird from monopolizing parental provisioning, but may

be able to let the cowbird 'work for them' by scaling back on those signals that make parents work harder.

The fact that sparrow nestlings in parasitized nests exaggerated some signals and scaled back on others (figure 4) reinforces the idea that signalling in parasitized nests may stem from a dynamic interaction between the brood parasitic and host nestlings, as opposed to a one-way process of mimicry by the brood parasite (Hauber & Kilner 2007). Rather than being a peculiarity of song sparrows, we expect future studies will find that the nestlings of numerous species of cowbird hosts become 'sheep in wolf's clothing', when together with a cowbird.

All procedures were conducted in accordance with the Canadian Council on Animal Care guidelines and were approved by the University of Western Ontario Council on Animal Care.

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