Are begging calls of generalist parasitic cowbirds adapted for brood parasitism?

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Introduction

Avian brood parasites lay their eggs in the nests of other birds, and leave the care of their offspring entirely to the foster-parents or hosts. Some host species have evolved the ability to recognize and eject foreign eggs (Rothstein 1975). To counter possible rejection by the host, brood parasitic eggs and nestlings may be selected to mimic those of the hosts to reduce the likelihood of rejection (Redondo and Arias de Reyna 1988). Mimicry of host eggs has been reported in many brood parasitic species (Rothstein 1990), and nestlings of some parasitic species have evolved mimicry of host young (Davies and Brooke 1988), mouth patterns (Payne 1982), and/or begging calls (Redondo and Arias de Reyna 1988). Mimicry not only may deter the ejection of the parasitic nestlings, but also acts effectively to stimulate the host to bring food to the nest (Mundy 1973).

Vocal mimicry in nestlings and fledglings has been suggested to occur in at least 14 parasitic species (Morton and Farabaugh 1979; Redondo 1993). Most workers have judged by ear the similarity between the begging calls of parasite and host nest-mates; however, the similarity has been quantified spectrographically for some parasitic species. No generalist species are known to practice vocal mimicry (reviewed by Sealy and Lorenzana, unpublished data). Generalist parasites should be less likely to evolve mimetic behavior because they must beg in association with a wide range of hosts (Gochfeld 1978). The brown-headed cowbird (*Molothrus ater*), for example, has been recorded parasitizing 220 host species (Friedmann and Kiff 1985). Broughton *et al.* (1987) provided evidence that this species does not mimic the begging call of host nestlings.

Broughton *et al.* (1987) suggested that the wide frequency range of cowbird calls may cover a sufficient spectrum to trigger feeding behaviour in many hosts, thus, eliminating the need to mimic specific calls. There is also evidence that cowbird nestlings beg more loudly than non-parasitic icterines (Briskie *et al.* 1994). The begging call of the cowbird is assumed to be an effective feeding stimulus because 144 host species have been recorded to have fledged cowbirds (Friedmann and Kiff 1985).

The purpose of this study was to determine whether the acoustic structure of the nestling cowbird's begging call evolved specifically to subserve brood parasitism or whether it is merely a reflection of the cowbird's phylogeny (see Hamilton and Orians 1965). The cowbird belongs to the subfamily Icterinae (the blackbirds). The acoustic structure of begging calls should reflect phylogenetic history (Popp and Ficken 1991). Thus, if the cowbird's begging call is substantially different from that of the other nonparasitic icterine species, this will provide evidence that the difference is an adaptation evolved by the cowbird for brood parasitism. The structure of the begging call of another generalist parasite species, the shiny cowbird (*M. bonariensis*), was also analyzed using a published spectrogram (Fraga 1985) to gain more insight regarding which begging call charactersitics are important for generalist brood parasites.

Methods

This study was conducted at the University of Manitoba Field Station (Delta Marsh) from 1 June through 15 July 1996. Begging calls were recorded from the following nonparasitic icterine species: red-winged blackbird (*Agelaius phoeniceus*, n=17 individuals), yellow-headed blackbird (*Xanthocephalus xanthocephalus*, n=20), Brewer's blackbird (*Euphagus cyanocephalus*, n=6), common grackle (*Quiscalus quiscula*, n=5), orchard oriole *(Icterus spurius*, n=2), and Baltimore oriole (*I. galbula*, n=6). The yellow warbler (*Dendroica petechia*, n=17) was recorded for use as a sister group (i.e. a non-icterine emberizid), and the American robin (*Turdus migratorius*, n=18) for use as a non-emberizid outgroup. Cowbird nestlings used in this study were raised in yellow warbler (n=4) and red-winged blackbird (n=2) nests. All cowbird recordings were pooled because Broughton *et al.* (1987) demonstrated that the structure of the cowbird's begging call is the same regardless of the host species. Characteristics of the begging call of the shiny cowbird were measured from a spectrogram of four calls of a seven-day-old nestling presented in Fraga (1985). Although the orchard oriole and shiny cowbird were

not included in any of the statistical analyses, they were included in this study because they provide additional icterine species to use for comparative purposes. Previous spectrographic studies have involved sample sizes that ranged from one to eight nestlings (e.g. Broughton et al. 1987; McLean and Griffin 1991; Popp and Ficken 1991).

We controlled for developmental stage by recording nestlings on the day when at least one primary had emerged from its sheath (unsheathed vanes *ca*. 1 mm). We did not use absolute age because growth rates differ among species; however, using this criterion ensured that all birds were at the same stage of physical development (see Briskie *et al*. 1994). Nestlings varied from five to nine days of age when recorded. One nestling was recorded per nest, regardless to hatching order, and all nests were used, regardless of brood size. Only the nestling at the desired developmental stage was left in the nest. We removed all other nestlings from the nest because a brood contained a range of developmental stages and we wanted to control for developmental stage because begging call characteristics change with development (*e.g*., Broughton *et al*. 1987; Popp and Ficken 1991).

A tie-clip microphone was tied above the nest. Distance from the microphone to the nestling was standardized at 15 cm. The microphone was attached to the Sony TCM-5000EV cassette-recorder with an extension cord. The cassette-recorder had the narrowest frequency response of all the equipment (90-9000 Hz). The recording level of the cassette-recorder was standardized at 4. TDK high bias SA90 IEC II/type II cassettes were used. The recorder was left recording at the nest for 45 minutes. The calls recorded were ensured to be begging calls because they occurred only when an adult visited the nest (the landing and the rustling of the adult visiting the nest could be heard). The nestlings that were removed from the nest were kept warm by the sun or a heat lamp, and were fed chironomids, mosquitoes, or mealworms.

Spectrograms were produced using the computer program, Canary 1.2. A pure tone of known frequency (1.0 kHz) and loudness (-10 dB) was recorded at the beginning of each tape at a recording level of 4.0. The tone was generated using a Fostex model TT-15 test tone oscillator, and used to calibrate Canary so that absolute loudness measurements could be obtained.

The following characteristics of each call were measured using Canary: 1) call duration, 2) frequency range, 3) peak frequency (i.e. frequency that is uttered the loudest), 4) number of syllables (i.e. number of frequency peaks or units in a begging call), 5) loudness, and 6) call rate. Five of the first 20 calls from each individual were sampled randomly from the recordings and the mean of the above characteristics was calculated. A multiple discriminant analysis (MDA, see Green 1978 for details) was conducted using the program, Syn-Tax 5.02, to determine whether call characteristics differed among the six icterine species and the two outgroups.

Each call was categorized into one of the six call types used by Popp and Ficken (1991) in their analysis of passerine nestling calls: (1) 'tonal', calls with a single narrow frequency band, (2) 'arched', calls with a semi-arched or arched shape, (3) 'repeated', calls with short repeated units, (4) 'multiple-banded', calls with more than one narrow frequency band, (5) 'complex', calls with frequency modulation and/or multiple dissimilar units, and (6) 'noisy', calls that lack tonal structure. We modified this classification system slightly by defining multi-complex calls as complex or repeated calls with more than one band.

The "outgroup rule" was used to determine whether a particular call characteristic (e.g. short call duration) is a plesiomorphic (i.e. ancestral) or apomorphic (i.e. derived) trait. This criterion states that the character found in the sister group is the plesiomorphic character, whereas the character found only within the monophyletic group is the apomorphic character (Wiley 1981).

Results

There was much variation in call types among species (Table 1). 'Arched' was the most common call type for Brewer's blackbirds and Baltimore orioles, whereas 'repeated' was the most common for brown-headed cowbirds and yellow-headed blackbirds, 'complex' for shiny cowbirds, 'multiple-banded' for orchard orioles, 'multi-complex' for common grackles, and 'noisy' for red-winged blackbirds. The most common call type of American robins and yellow warblers was 'multiple-banded' and 'arched', respectively (Table 1, Fig. 1). There was also much variation in call types within species. For example, yellow-headed blackbirds uttered five of seven call types (Table 1). There was also variation in call types within individuals. For example, out of five spectrograms sampled for one yellow-headed blackbird individual (YH-96-19), four different call types were present.

According to univariate F-ratios, all six begging call characteristics differed significantly among the species (number of syllables: $F = 35.1$, duration: $F = 33.7$, peak frequency: 12.6, loudness: 10.2, call rate: 9.4, frequency range: 4.9; $df = 6, 105$, $p<0.00005$ in each case). Figure 2 graphically represents the 95% confidence intervals for all of the species with respect to the call characteristics. The 95% confidence intervals for the red-winged blackbird, Brewer's blackbird and Baltimore

Table 1. The structural type of each begging call sampled for eight icterines and two outgroups.

	Percent of calls in a species with particular call type[1]						
Species	Tonal	Arched	Repeated	Complex	Multiple-banded	Multi-complex	Noisy
American robin	6	29	0	1	**54**	5	5
Yellow warbler	0	**94**	0	0	6	0	0
Red-winged blackbird	0	42	0	0	14	0	**44**
Yellow-headed blackbird	0	3	**72**	6	2	17	0
Brewer's blackbird	5	**73**	5	0	18	0	0
Common grackle	4	24	0	20	0	**48**	4
Shiny cowbird[2]	0	0	0	**100**	0	0	0
Brown-headed cowbird	0	0	**83**	17	0	0	0
Orchard oriole	0	0	0	0	**90**	0	10
Baltimore oriole	0	**53**	0	0	30	0	17

[1] Sample sizes differed among species. Each individual was sampled five times. Bolded percentages indicate the most common call type for a given species.

[2] Information derived from spectrogram of four begging calls of a seven-day old shiny cowbird nestling presented in Fraga (1985).

oriole overlap, which indicates that these species have similar begging calls. The calls of these species are short, monosyllabic, fast, and have a high frequency (Fig. 2, Tables 2 and 3). The remaining five species had calls that differ significantly from all others. The yellow warbler's call is similar to those of the red-winged blackbird, Brewer's blackbird and Baltimore oriole except that it is particularly quiet and uttered at a high rate. The American robin's call has a low frequency. The calls of both the yellow-headed blackbird and cowbird are long and polysyllabic; however, the yellow-headed blackbird's call has a low frequency. The common grackle's call is long, but has only a few syllables (Fig. 2, Tables 2and 3).

The call of the orchard oriole, which was not included in the multiple discriminant analysis, is similar to that of the American robin in that it is quiet and has a low frequency, and is similar to the red-winged blackbird, Brewer's blackbird, and Baltimore oriole being short and monosyllabic with a narrow frequency range. The call of the shiny cowbird, which also was not included in the analysis, was similar to the common grackle in every respect (Table 3).

Generally, species with a long call had a slow call rate (correlation = -0.66). For this reason, only character states of call duration (and not call rate) were polarized. The plesiomorphic traits of the icterine begging call are short duration, a low number of syllables, quiet, high frequency, and narrow frequency range. The yellow-headed blackbird possesses the most apomorphic traits (four of five). The apomorphic traits of the brown-headed cowbird are long duration and polysyllables, and of the shiny cowbird, long duration and loudness range (Table 3). Figure 3 indicates the points along two hypothesized phylogenies for the icterines (Freeman 1990; Lanyon in Webster 1992) where apomorphic begging call traits evolved. According to Lanyon's phylogeny, loudness was lost by the brown-headed cowbird and Brewer's blackbird.

Discussion

The apomorphic traits of the brown-headed cowbird begging call are long call duration and polysyllables. In fact, this species had the longest mean duration and highest mean number of syllables (Table 2). The begging call of the shiny cowbird is also long and polysyllabic, although it has only an average number of syllables. As these characteristics have seldom evolved among nonparasitic icterines, they may have evolved in these species to facilitate brood parasitism. Muller and Smith (1978) and Bengtsson and Rydén (1983) found that playbacks of begging calls at active nests increased the number of parental feeding visits. This suggests that parents respond to an increased level of vocalization (i.e. increased rate of calling, loudness, or both). If adults cue into begging call rate, a begging call that is polysyllabic may act as a super-stimulus by compressing more 'arched' calls into a given length of time. Redondo and Arias de Reyna (1988) commented that a call with repetitive units mimics the begging call of a hungry chick, thus deceiving the host to bring more food to the nest. Collias (1952) found that American robins uttered polysyllabic calls only when they were hungry. There

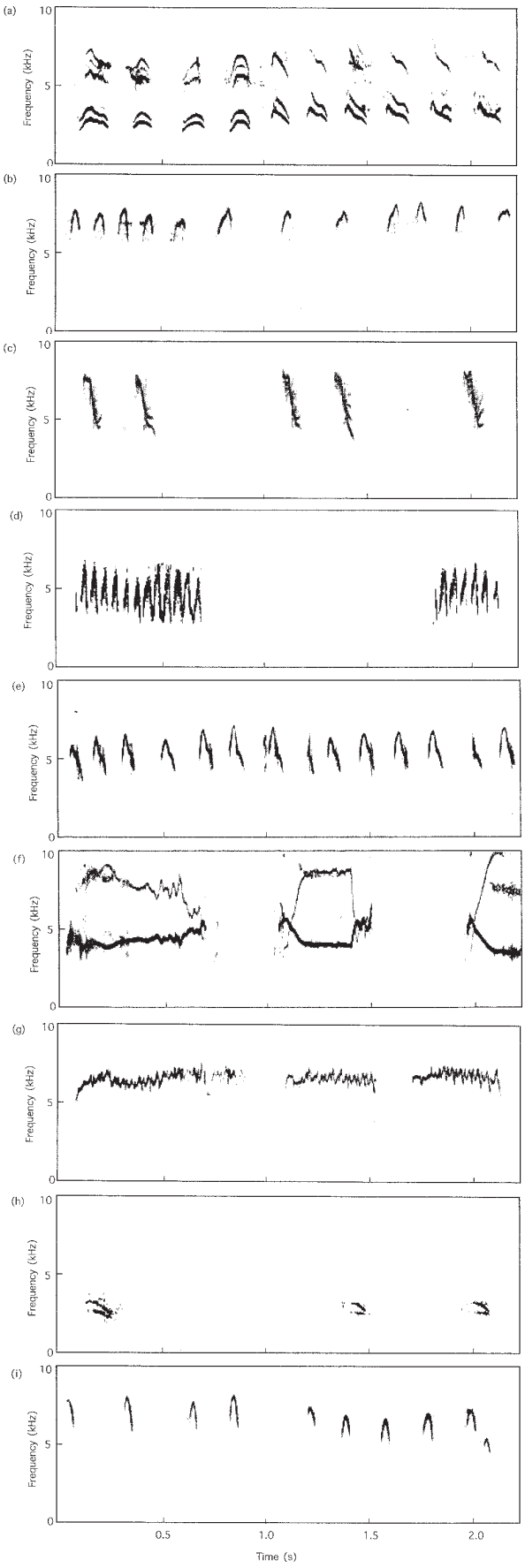

Figure 1. Representative spectrograms of the most frequent begging call type uttered by: (a) American robin, 'multiple-banded'; (b) yellow warbler, 'arched'; (c) red-winged blackbird, 'noisy'; (d) yellow-headed blackbird, 'repeated'; (e) Brewer's blackbird, 'arched'; (f) common grackle, 'complex'; (g) brown-headed cowbird, 'repeated'; (h) orchard oriole, 'multi-banded'; and (i) Baltimore oriole, 'arched'. Spectrograms are not necessarily representative of the average duration, frequency range, or call rate for the species.

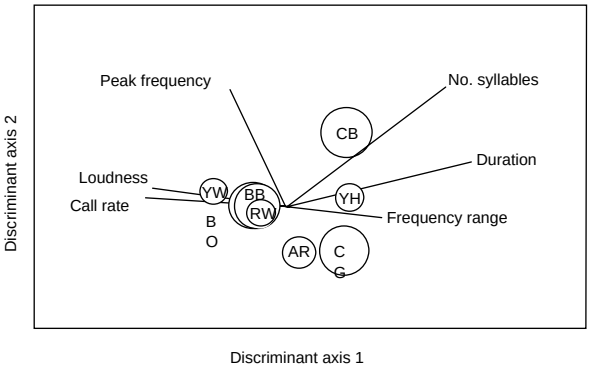

Figure 2. Multiple discriminant analysis of begging call characteristics. Circles delineate the 95% confidence interval surrounding the centroid position of the species: AR, American robin; YW, yellow warbler; RW, red-winged blackbird; BB, Brewer's blackbird; CG, common grackle; CB; brown-headed cowbird; and BO, Baltimore oriole. The relative length of the vectors indicate the relative importance of the variables in differentiating between species, and the direction of the indicates the direction the variable is increasing vector with respect to the discriminant axes.

appears to be a trade-off between call duration and call rate, because species with long calls generally had a low call rate. Presumably, a long polysyllabic begging call is more effective than a short begging call that is uttered at a high rate because the former is the more derived character.

Had the parasitic cowbirds been the only icterine species to have evolved long call duration and polysyllables, this would have been stronger evidence that these characters evolved in response to brood parasitism. The question remains as to why the yellow-headed blackbird possesses these two traits. Phylogenetic history does not explain these synapomorphies because according to the two hypothesized phylogenetic relationships among the Icterinae (Freeman 1990; Lanyon in Webster 1990), the yellow-headed blackbird is not a sister species to the

Table 2. Mean begging call characteristics (± standard deviation) for nine icterine species and two outgroups.

Species	No. syllables	Duration (ms)	Peak freq. (kHz)	Loudness (dB)	Call rate (/ms)	Frequency range (kHz)	Low freq. (kHz)	High freq, (kHz)
Red-winged blackbird	1.0	52	5.6	-23	2.1	3.2	4.2	7.4
	(0)	(18)	(0.6)	(9)	(1.5)	(0.9)	(0.6)	(0.9)
Yellow-headed blackbird	5.2	268	4.7	-33	0.7	4.2	3.2	7.4
	(1.7)	(74)	(0.8)	(9)	(0.3)	(0.9)	(0.7)	(1.0)
Brewer's blackbird	1.1	83	6.2	-28	3.4	2.0	5.1	7.0
	(0.2)	(27)	(1.3)	(14)	(2.7)	(1.0)	(1.3)	(1.4)
Common grackle	2.3	315	5.7	-26	1.1	2.8	4.3	7.1
	(0.4)	(55)	(0.8)	(6)	(0.2)	(0.7)	(0.5)	(0.9)
Shiny cowbird[2]	2.8	200	7.1	U	0.00 (2)	2.6	5.5	8.1
Brown-headed cowbird	7.7	330	6.6	-33	1.1	2.7	5.5	8.0
	(4.1)	(141)	(0.4)	(5)	(0.5)	(1.0)	(0.6)	(1.5)
Orchard oriole	1.0	102	3.2	-48	0.3	1.1	2	3.8
	(0)	(9)	(0.6)	(7)	(0)	(0.2)	(0.5)	(0.6)
Baltimore oriole	1.0	61	5.8	-28	3.9	2.4	4.6	7.0
	(0)	(15)	(0.7)	(12)	(2.2)	(1.9)	(1.2)	(0.8)
Outgroups								
Yellow warbler	1.0	44	5.8	-43	4.4	1.8	5.0	6.7
	(0)	(17)	(1.6)	(4)	(2.4)	(1.5)	(1.5)	(1.8)
American robin	1.2	120	3.4	-38 (11)	2.0 (1.0)	3.0 (2.0)	2.2 (0.5)	5.2 (2.1)
	(1.0)	(99)	(0.9)	(11)	(1.0)	(2.0)	(0.5)	(2.1)
Mean (icterines only)	**2.8**	**176**	**5.6**	**-31**	**1.6**	**2.6**	**4.3**	**7.0**

[1] Measurements estimated from spectrogram of four begging calls of a seven-day old shiny cowbird nestling presented in Fraga (1985). U = unknown.

Table 3. Summary of plesiomorphic and apomorphic begging call characteristics possessed by each species.

	Begging call characteristic[1]					
Species	Number of syllables	Duration	Peak frequency	Loudness	Frequency range	Number of apomorphic traits
Red-winged blackbird	low	short	average	loud*	wide*	2
Yellow-headed blackbird	high*	long*	low*	average	wide*	4
Brewer's blackbird	low	short	high	average	narrow	0
Common grackle	average	long*	high	loud*	average	2
Shiny cowbird	average	long*	high	average	average	2
Brown-headed cowbird	high*	long*	high	average	average	2
Orchard oriole	low	short	low*	quiet	narrow	1
Baltimore oriole	low	short	high	average	average	0

[1] Begging call characteristics are categorized as low/high, short/long, quiet/loud, slow/fast, and narrow/wide relative to the mean calculated for the icterines.

[2] The loudness of the shiny cowbird was not measured using the same methodology as in this study. It was classified as loud based on a qualitative description in Gochfeld (1978).

* denotes apomorphic (derived) traits.

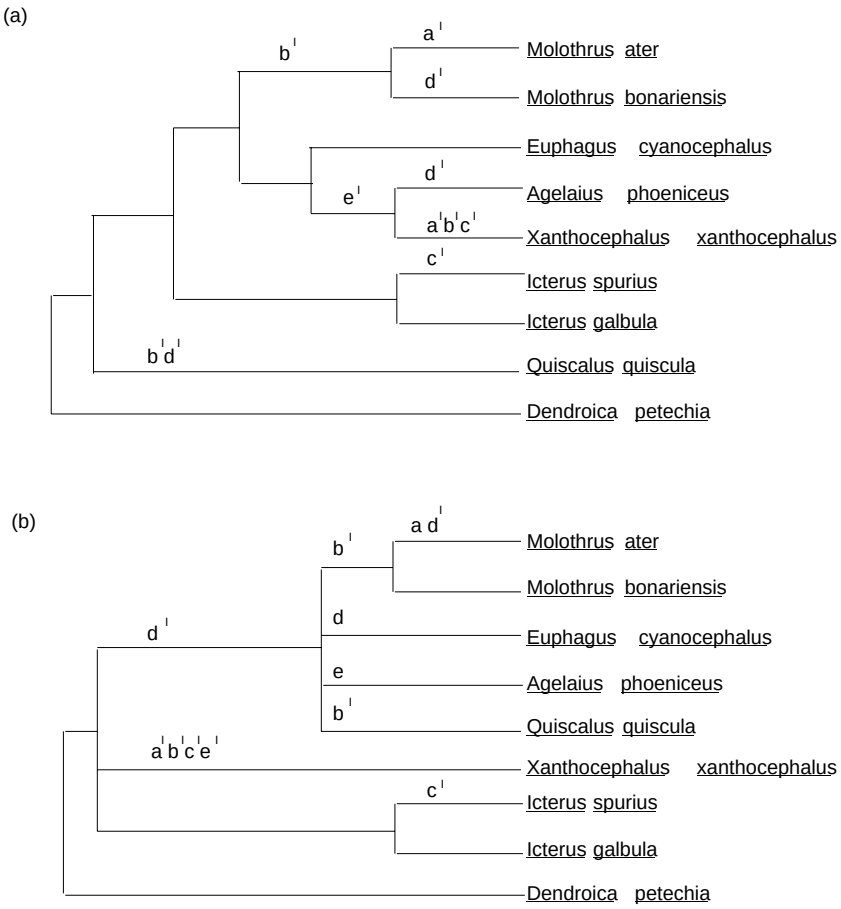

Figure 3. Hypothesized phylogenetic relationships among the Icterinae, based on (a) mitochondrial restriction fragment length polymorphism (Freeman 1990), and (b) sequencing of the Cytochrome B region of mitochondrial DNA (Lanyon in Webster 1992). The outgroup rule was used to determine apomorphic begging call characteristics, with the yellow warbler as a member of a sister group, Parulinae. The points along the cladogram where an apomorphic trait evolved are indicated: a', high number of syllables; b', long duration; c', low frequency; d', loud; and e', wide frequency range. In (b), loud calling was lost by *Molothrus ater* and *Euphagus cyanocephalus*.

parasitic cowbirds. The brown-headed cowbird infrequently parasitizes this species (Friedmann *et al*. 1977; Ortega and Cruz 1991; Neudorf and Sealy 1994; but see Dufty 1994), in spite of doing well in yellow-headed blackbird nests (Ortega and Cruz 1991); therefore, mimicry is not a possible explanation. However, it is noteworthy that the calls of the yellow-headed blackbird are not exactly the same as those of the cowbirds because yellow-headed blackbirds uttered calls that were significantly lower in frequency. Presumably, calls of low frequency are not as an effective feeding stimulus as calls of high frequency (Morton 1977).

The begging calls of the parasitic cowbirds had the highest frequencies (Table 2), but this characteristic has not been specifically selected for brood parasitism because this is a plesiomorphic trait. Begging calls of high frequency effectively stimulate adults to bring food to the nest (Morton 1977; Redondo and Arias de Reyna 1988), so it is not surprising that high frequency is a common characteristic among the begging calls of icterines.

The frequency ranges of both cowbird species were average (Tables 2 and 3), which contradicts Broughton *et al*.'s (1987) suggestion that the brown-headed cowbird has a wide frequency range to trigger feeding behaviour in many hosts. The red-winged blackbird, yellow-headed blackbird and American robin had a wider frequency range than both cowbird species. This suggests that the frequency range of the parasitic cowbirds is not been specifically adapted for brood parasitism. This is not to say that frequency range is not important in eliciting feedings from hosts. It would be useful to determine the frequency ranges of parasitized species to see if they fall within the frequency range of the brood parasite. The only species in this study that

have the potential of being raised in the company of the brown-headed cowbird are yellow warblers, red-winged blackbirds and Brewer's blackbirds. The other species are not parasitized frequently or they eject cowbird eggs (Neudorf and Sealy 1994, unpubl. data). The cowbird's frequency range corresponds closely to those of the yellow warbler and Brewer's blackbird (Table 2).

An unexpected finding of this study was that red-winged blackbirds called the loudest, whereas brown-headed cowbirds were not particularly loud (Tables 2, 3). This contrasts strongly with Briskie *et al.*'s (1994) finding that brown-headed cowbirds beg significantly louder than red-winged blackbirds. Others have also described the cowbird's begging call as being loud (Nice 1939; Broughton *et al*. 1987; Payne 1991; Burhans 1996). We did not obtain a comparable loudness measurement for the shiny cowbird, although Gochfeld (1978) stated that the begging call of the shiny cowbird nestling was so loud that it often revealed the location of its host's well-concealed nest.

Briskie *et al.* (1994) obtained their recordings at nests that contained a full brood, whereas our recordings were of single nestlings, with nestmates experimentally removed. This strongly suggests that nestlings beg louder when in the company of nestmates (see also Muller and Smith 1978). The methodology used in this study, therefore, does not give a true indication of the loudness at which a nestling begs when in the company of nestmates. Nonetheless, the results from this study are indicative of a baseline loudness at which a nestling begs and all of the loudness measurements were standardized as they were taken when the nestling was alone. It is still surprising that the brown-headed cowbird nestling was not among the loudest. One might argue that there is no benefit in vocalizing loudly if there are no nestmates with which to compete, especially if there are predatory and energetic costs associated with begging. However, McCarty (1996) found the energetic cost of begging by European starlings (*Sturnus vulgaris*) and tree swallows (*Tachycineta bicolor*) to be quite low, and the only experimental study determining whether begging calls attract predators was unreliable due to the calls being played back at an unrealistic rate. Haskell (1994) played back calls at a rate of 25 begging calls per minute from dawn to dusk. Nestlings do not beg continuously, but only during parental feeding visits to the nest (Briskie *et al*. 1994, pers. obs.). Furthermore, because parental feeding rate is affected by the loudness of calls of an entire brood (Bengtsson and Rydén 1983), there is presumably selection pressure for solitary nestlings to beg loudly to maintain a high parental feeding rate, especially if the cost of begging is negligible.

Our study suggests that nestling brown-headed cowbirds have evolved polysyllabic calls of long duration, presumably to subserve brood parasitism. Experiments are still required to establish the fact that these characteristics allow the cowbird to elicit feedings from a wide range of species. It has been argued that the cowbird would be fed regardless of the structure of the begging call as long as it were to make any noise at all. Craig and Jamieson (1990) argue that there is a strong selective pressure for all birds to feed begging nestlings; therefore, their neurological system is such that they react regardless of whether the young is their own. Indeed, Eastzer *et al*. (1981) demonstrated that four of five nestlings of nonparasitic species were as successful as the cowbird when experimentally placed in barn swallow (*Hirundo rustica*) nests. Their study suggests that species that do not recognize their young feed any nestling in their nests. Except for the case of colonial nesting and brood parasitism, there is little selection pressure for birds to recognize their young (reviewed in Redondo 1993), and in the case of brood parasitism, recognition occurs more often at the egg stage than the nestling stage (Lotem 1993). However, the structure of parasitic begging calls cannot be completely inconsequential because some brood parasites have evolved mimicry of the begging call of the host nestling.

Unless a host species has evolved nestling recognition, the begging call of a brood parasite may not be as important during the nestling stage as it is during the fledgling stage. Parasitic fledglings must communicate their location to their adult host(s). Adults should be selected to respond only to species-specific calls; therefore, it is puzzling that parasitic fledglings are fed. Eastzer *et al.* (1987) found that red-winged blackbirds and gray catbirds (*Dumetella carolinensis*) that successfully fledged from experimental barn swallow nests were not fed as fledglings, whereas the cowbird was. All three species begged loudly but the cowbird begged at a substantially higher rate. There are also accounts of cowbird fledglings being fed by adults of species other than the fosterers (e.g. Klein and Rosenberg 1986; Scott 1988). Woodward (1983) found that eight host species fed fledgling cowbirds more than they fed an equivalent mass of their own young. He commented that the cowbird's loud, persistent begging call is likely their main adaptation for brood parasitism. A comparative analysis of the begging calls of icterine fledglings would be useful.

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