Offspring development mode and the evolution of brood parasitism

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In the evolution of interspecific social parasites, the shift from facultative to obligate brood parasitism is thought to be driven by the cost of parental investment. Accordingly, avian brood parasites with precocial young are almost exclusively facultative parasites, whereas those with altricial young are almost exclusively obligate parasites. Surprisingly, then, North American cuckoos (*Coccyzus* spp.) have altricial young but are described as facultative brood parasites. Because little is known about parasitism by *Coccyzus* cuckoos, we explored the potential importance of heterogeneric brood parasitism to their reproductive strategy. In contrast to the existing set of anecdotal reports of cuckoos parasitizing songbirds, we found no evidence of cuckoo parasitism in 10 197 songbird nests, despite spatial and temporal overlap between cuckoos and potential hosts and despite varied food availability. Experiments revealed a lack of egg-rejection behavior in some of the most common potential hosts, suggesting that parasitic eggs would be accepted if laid and that we would detect cuckoo parasitism if it occurred regularly. We propose that reports of *Coccyzus* cuckoos parasitizing songbirds stem from errant attempts to parasitize other cuckoos. This resolves a theoretical paradox about interspecific parasitism and mode of offspring development, as we suggest that *Coccyzus* cuckoos have not evolved to parasitize other species. *Key words:* altricial, brood parasitism, cuckoo, facultative, obligate, precocial. *[Behav Ecol 20:517–524 (2009)]*

Parental investment lies at the heart of fundamental trade-offs in life-history traits (Clutton-Brock 1991; Stearns 1992). Social parasites can avoid a major component of parental investment by laying eggs in the nests of other species, where the offspring are reared and defended by unwitting foster parents. This strategy of interspecific brood parasitism has evolved in insects (Tallamy 1986; Hölldobler and Wilson 1994; Lenoir et al. 2001; Als et al. 2004), fish (Taborsky 1994; Avise et al. 2002), and birds (Payne 1977; Rothstein and Robinson 1998; Davies 2000).

The relative benefits of brood parasitism—and hence the evolution of this life-history strategy—should be a function of the cost of parental care, and this cost varies widely across taxa. In birds, this cost is tied to the development mode of offspring. For species with precocial offspring (e.g., most ducks), parental care after hatching is minimal and fecundity is generally limited by the nutritional costs of egg production (Starck and Ricklefs 1998)—a cost that must be paid regardless of whether the eggs are laid parasitically. In contrast, in species with altricial young (e.g., most songbirds), individuals pay a high cost for the extensive parental care performed after eggs hatch (Lack 1947; Nur 1984; Starck and Ricklefs 1998). Consequently, because of the energy saved by not providing parental care, altricial species potentially can reap large fecundity benefits by laying eggs parasitically. In addition, eggs of altricial species are smaller relative to body size than those of precocial species (Starck and Ricklefs 1998), so females of altricial species could lay an additional parasitic egg with a smaller incremental increase in the cost of egg production (Lyon and Eadie 1991; Davies 2000). For these reasons, the advantages of laying parasitic eggs are potentially very large for altricial species.

The costs, benefits, and opportunities for parasitism will ultimately determine the balance between parasitic and parental reproduction in a population. At an extreme are obligate brood parasites such as European cuckoos (*Cuculus canorus*; Wyllie 1981), which reproduce only by laying eggs in the nests of other species. Toward the other end of the spectrum are facultative brood parasites, such as redhead ducks (*Aythya americana*; Yerkes and Koops 1999), which often not only care for their own eggs but also may deposit some eggs parasitically. Facultative parasitism is generally believed to be an initial step in the evolution of a brood parasitic lineage from an ancestral state of parental reproduction (Darwin 1859, p. 217; Hamilton and Orians 1965; Yamauchi 1995; but see Robert and Sorci 2001). An evolutionary transition from facultative parasitism to obligate parasitism could be favored if there were both frequent opportunities for parasitism and consistently high benefits for not performing posthatching parental care (Hamilton and Orians 1965; Payne 1974; Yamauchi 1995). Such a scenario should be more likely in species with altricial, rather than precocial, offspring because of the high cost of posthatching care (Hamilton and Orians 1965; Lyon and Eadie 1991).

Consistent with this theoretical framework, there is a coupling of mode of parasitism and mode of offspring development in the approximately 122 bird species that exhibit interspecific brood parasitism (Lyon and Eadie 1991). Eighty-six of 88 brood parasitic species with altricial young are obligate brood parasites (with probably 7 independent origins of brood parasitism; Sorenson and Payne 2002), and 33 of 34 brood parasitic species with precocial young are facultative parasites (with an unresolved number of origins of brood parasitism; Lyon and Eadie 1991). Three species are inconsistent with this paradigm: the black-headed duck

(*Heteronetta atricapilla*), which has precocial young but is an obligate brood parasite (Weller 1968; Lyon and Eadie 2004), and the yellow-billed and black-billed cuckoos (*Coccyzus americanus* and *Coccyzus erythropthalmus*), which have altricial young but are facultative brood parasites (Hughes 1999, 2001). Here, we explore the reproductive mode of yellow-billed and black-billed cuckoos and assess the robustness of our theoretical framework about the evolution of interspecific brood parasitism.

Facultative parasitism by *Coccyzus* cuckoos was reported first nearly 150 years ago (Darwin 1859, p. 217; Darwin 1872, p. 212), but the dynamics of this behavior are still poorly understood. Previous studies have documented occasional cases in which yellow-billed and black-billed cuckoos have parasitized conspecifics, congeners (i.e., yellow-billed and black-billed cuckoos parasitizing each other; Nolan and Thompson 1975; Fleischer et al. 1985), and a set of 17 more distantly related species (Appendix A). Many of these reports are simply anecdotal descriptions of finding a cuckoo egg in another species' nest; thus, the frequency and success of interspecific brood parasitism by *Coccyzus* species remain unclear.

Understanding the evolution of brood parasitism requires a phylogenetic framework, but historically there has been disagreement about the phylogenetic placement of *Coccyzus* cuckoos (Beddard 1885; Berger 1960; Sibley and Ahlquist 1990; Avise et al. 1994; Hughes 1996; Aragon et al. 1999; Hughes 2000; Sorenson and Payne 2002; Sorenson and Payne 2005) and about the corresponding implications for the evolutionary pathway of brood parasitism in this clade (Aragon et al. 1999; Hughes 2000; Sorenson and Payne 2002; Sorenson and Payne 2005). There is also little evidence about the circumstances under which *Coccyzus* cuckoos reproduce parentally versus parasitically. One hypothesis has been that food availability is a key determinant of reproductive mode. Specifically, Nolan and Thompson (1975) proposed that episodes of extreme food abundance cause females either to lay eggs in excess of the capacity of their nests or to lay eggs without any nest in which to put them; either situation would then lead to parasitic deposition of those "extra" eggs. However, it seems equally plausible that parasitism could be a best-of-a-bad-job strategy that is used when cuckoos' food is too limited to meet the demands of parental care (as suggested by Hamilton and Orians 1965 as a predisposing cause for the evolution of parasitism in Old World cuckoos).

Here, we investigate the parasitic behavior of yellow-billed and black-billed cuckoos to examine why they depart from the hypothesized life-history framework for brood parasitism. We present nest data from potential hosts to assess the frequency, circumstances, and success of heterogeneric parasitism by yellow-billed and black-billed cuckoos. At a subset of study sites, we mapped cuckoo territories and measured food abundance on those territories to test whether parasitism varies with food availability. In addition, we used egg-rejection experiments to assess the extent to which parasitic eggs would be accepted by potential host species. Egg-rejection experiments would shed light on the potential effectiveness of parasitic egg laying by cuckoos in addition to revealing whether researchers might misclassify songbird nests as unparasitized simply because of rapid, widespread egg rejection by hosts.

METHODS

Natural parasitism of potential host nests

We located and monitored nests of potential cuckoo hosts at study sites in Pennsylvania, Illinois, and Missouri. At our Pennsylvania sites, we also collected detailed data on cuckoo territory locations (see next section). Study sites in each region

were a mix of mature deciduous forest, dominated by oaks (*Quercus* spp.), hickories (*Carya* spp.), and maples (*Acer* spp.); regenerating forest stands as a result of even- or uneven-aged timber harvest; edges of pasture or agricultural row crops; and shrub habitats, including riparian strips, powerline right-of-ways, old fields, and dolomite glades. In central Pennsylvania, we worked on State Game Lands and adjacent private lands in the Ridge and Valley physiographic region, using two 150-ha study sites in 2003 and three 150-ha study sites in 2004. In Illinois, we worked at sites in Alexander, Jackson, Union, Johnson, Ogle, Will, Pope, Lee, Hardin, Shelby, St Clair, Vermillion, Carroll, and Jo Daviess counties in 1985–1986, 1989–1998, and 2000–2003. These sites were located in the Wisconsin Driftless Section, Rock River Hill Country, Wheaton Moraine Country, Bloomington Ridged Plain, Springfield Plain, and Shawnee Hill physiographic regions. In Missouri, we worked on 16 sites in 1997 and 14 sites in 1998 and 1999 in the Glaciated Plains, Ozark Border, and Ozark physiographic regions. These sites were managed by the US Forest Service, the Missouri Department of Conservation, and the University of Missouri and ranged in size from 5 (small dolomite glades) to 400 ha.

Breeding Bird Survey (BBS) data from 1994–2004 (Sauer et al. 2007) indicate that densities of *Coccyzus* cuckoos are highest at the Missouri sites (ca. 10 detections per BBS route), followed by Illinois (3–10 detections per route), and Pennsylvania (1–4 detections per route). Illinois is, in fact, the location of an early account of a cuckoo nestling being raised by a blue jay (*Cyanocitta cristata*), as reported by Darwin (1872, p. 212).

At all sites, we searched for nests of species that had been reported anecdotally in the literature as *Coccyzus* hosts and we searched for nests of other songbird species with similar body size and life-history traits; we excluded data from species that nested in cavities or did not have habitat overlap with *Coccyzus* cuckoos. Nests were monitored every 2 days for the presence of cuckoo eggs or young. In all potential host species' nests, cuckoo eggs would be easily recognizable by researchers, based on egg size, shape, and color, and cuckoo nestlings would be easily recognizable based on their unusual morphology and rapid development. During nest monitoring, we also checked the ground beneath nests for ejected eggs, as some avian hosts (e.g., of brown-headed cowbirds) are known to eject parasitic eggs onto the ground near the nest.

We calculated confidence limits (CLs) on the observed parasitism levels according to Zar (1996). Because no nests were parasitized (see Results), we used the alternate formula for the upper CL as $CL = 1 - (\alpha/2)^{1/n}$.

Spatial distribution of cuckoos

At our sites in Pennsylvania in 2003 and 2004, *Coccyzus* cuckoos were located visually and by their vocalizations from mid-May through early August. Locations of cuckoo sightings and of potential host nests were plotted on a combination of topographic maps and digital orthophoto quarter quadrangles using visual reference points, terrain features, and handheld Global Positioning System units. These locations were then entered into ArcView for spatial analysis.

Food abundance

The synchronous emergence of periodical cicadas comprises an enormous resource pulse that has been shown to affect broad ecosystem processes (Williams and Simon 1995; Yang 2004) and the reproductive behavior of birds (Anderson 1977; Murphy 1986; Strehl and White 1986; Steward et al. 1988; Stephen et al. 1990). Like many forest-breeding land birds,

Coccyzus cuckoos will eat periodical cicadas and also will feed them to nestlings (Nolan and Thompson 1975; Dearborn DC, MacDade LS, personal observation). Thus, we recorded the presence or absence of periodical cicada emergences at our study sites, predicting that those site-years with periodical cicadas would show higher levels of brood parasitism by cuckoos.

In years without periodical cicadas, the diet of *Coccyzus* cuckoos is primarily composed of lepidopteran larvae (Hughes 1999, 2001). At our Pennsylvania sites, lepidopteran larvae abundance was measured in 2003 and 2004 (Anders and Post 2006). Randomly located fixed transects were surveyed, covering a 50 × 1 × 1 m strip within each cuckoo territory ($n = 10$ territories in 2003 and 8 territories in 2004) during a 2- to 4-day period in mid-June and again in late June. Lepidopteran larvae were surveyed by counting the number of larvae per 1000 understory leaves, and length of each caterpillar, which was left in place on the vegetation, was recorded to the nearest millimeter.

Egg-rejection experiments

Egg-rejection experiments were conducted from late May through late July in 2003 and 2004 at study sites in Pennsylvania. We used model cuckoo eggs in a manner similar to that used in studies of cowbird parasitism (e.g., Lorenzana and Sealy 2001), and experiments with cowbirds have shown that cowbird hosts respond similarly to real and model eggs (Rothstein 1975; Peer et al. 2000, 2002). Model yellow-billed cuckoo eggs were either wooden (for most species) or a puncturable design (for wood thrush and northern cardinals, which might be unable to eject by grasping). Wooden eggs were sculpted on a belt sander, yielding an egg suitable for grasp ejection. Puncturable eggs consisted of a foam core covered with either Sculpey modeling clay or plaster of paris. All model eggs were made to the dimensions and mass of yellow-billed cuckoo eggs (30.4 × 23.0 mm, 9.1 g; Hughes 1999) and painted to match the immaculate pale greenish blue of freshly laid cuckoo eggs. Note that black-billed cuckoo eggs are more similar in size to potential host eggs than are yellow-billed cuckoo eggs (Table 1), so rejection rates for black-billed cuckoo eggs are likely to be similar or lower, relative to the model eggs used in our experiment.

One model egg was experimentally added to the nest of a potential host in the morning (when *Coccyzus* cuckoos lay; Spencer 1943) during either the laying period or the first half of the incubation period. Because there is no clear evidence that *Coccyzus* cuckoos remove a host egg in conjunction with parasitic laying, we did not alter the number of host eggs in

the nest (Lorenzana and Sealy 2002). After the addition of the model cuckoo egg, we monitored the nest contents daily for 5 days (Rothstein 1982; Briskie et al. 1992; Peer et al. 2002). Acceptance was determined by the continued presence of the model egg during the 5-day experimental period. The disappearance of a model egg from the nest during the experimental period, despite continued presence of host eggs, was considered as a rejection by the host species. If the egg was missing from the nest, the area around the nest was searched in an attempt to locate the model egg. Nests that were depredated during the 5-day period were excluded from analysis, regardless of whether ejection had occurred prior to depredation; inclusion of these nests could cause a downward bias in estimating the frequency of egg rejection.

RESULTS

Natural parasitism of potential host nests

We located and monitored 10 197 nests of potential cuckoo hosts: 120 at our Pennsylvania sites, 559 in Missouri, and 9518 in Illinois (see Appendix B for sample size by species). In all nests, we found no evidence of cuckoo parasitism. No nests contained cuckoo eggs or nestlings, and no ejected cuckoo eggs were found beneath nests of potential hosts.

For all nests pooled, the 95% confidence interval (CI) on parasitism frequency was 0–0.0003617, assuming that any parasitic eggs would have been found prior to any possible ejection by hosts. If we exclude completely all nests of potential hosts that are known or suspected to reject model cuckoo eggs at least sometimes (i.e., excluding brown thrasher, gray catbird, northern mockingbird, and northern cardinal; see Table 1), the 95% CI is 0–0.0004132; this is a conservative approach because 1) these species did not reject every model egg in our experiments and 2) many egg rejections in our experiments did not occur until several days after artificial parasitism, implying that naturally laid eggs that are ultimately rejected by hosts might be detected first by field researchers.

Spatial overlap of cuckoos and hosts

At our sites in Pennsylvania, we mapped 510 detections of yellow-billed cuckoos in 2003 and 395 detections in 2004. Black-billed cuckoos were uncommon at these sites, with 3 detections in 2003 and 18 detections in 2004. The detections of yellow-billed cuckoos appeared to comprise a minimum of 19 and 21 territories in 2003 and 2004, respectively. Of the

Table 1
Egg characteristics and results of egg-rejection experiments with model cuckoo eggs

Species	Egg appearance	Egg size (mm)	Accepts cowbird eggs?	Percentage of eggs accepted (n)
Yellow-billed cuckoo	Pale greenish blue	30.4 × 23.0	Yes	—
Black-billed cuckoo	Greenish blue	27.2 × 20.6	Yes	—
Brown-headed cowbird	White with brown dots	21.5 × 16.4	—	—
Eastern towhee	Creamy with reddish brown dots	23.1 × 17.0	Yes	100 (3)
Mourning dove	White	28.4 × 21.5	Usually	100 (1)
Wood thrush	Pale blue or bluish green	25.4 × 18.6	Yes	100 (14)
Northern cardinal	Off-white with brown blotches	25.3 × 18.2	Yes	67 (9)
Brown thrasher	Pale bluish white with red spots	26.5 × 19.4	Rarely	33 (3)
Gray catbird	Deep greenish blue	23.3 × 17.5	Rarely	20 (30)

Egg descriptions from Harrison (1975). All species in this experiment have extensive sympatry with the brown-headed cowbird, an obligate brood parasite. Behavioral responses to cowbird eggs were compiled from Friedmann 1963, Rothstein 1975, Friedmann and Kiff 1985, and Peer and Bollinger 1998.

potential host nests that we monitored at these sites, 95% (114 of 120) were within 100 m of a cuckoo detection during the same season, based on our spot map data. Mapping of cuckoos in Illinois likewise revealed the presence of cuckoos and cuckoo nests at all sites in all years, in the same areas where we located nests of potential hosts. Although cuckoo territories were not mapped in Missouri, we observed cuckoos and cuckoo nests at those sites (Dowling Fink AD, Fink ML, personal observation), and BBS data (Sauer et al. 2007) indicated substantially higher densities of cuckoos in both Missouri and Illinois than in Pennsylvania, increasing the likelihood of overlap between cuckoos and potential hosts at those study sites.

Food abundance

In Missouri, periodical cicadas emerged in 1998 but not in 1997 or 1999; at the central Missouri study sites, the 1998 season was characterized by the rare simultaneous emergence of 13- and 17-year cicadas, creating an extremely large resource pulse during which we monitored 191 potential host nests. In Illinois, periodical cicadas emerged at a subset of our sites in 1985, 1989, 1998, and 2002; at site-years with cicadas, we monitored 1582 potential host nests. In Pennsylvania, 17-year cicadas emerged at one of our sites in 2004, where we monitored 28 potential host nests. At that site, detailed sampling of cicada abundance revealed densities of periodical cicadas (predominantly *Magicicada septendecim*) up to 10 individuals per square meter, with large spatial variation in cicada densities (coefficient of variation [CV] between survey points = 128.9%).

Lepidopteran abundance at our Pennsylvania sites generally decreased from early June to late June, considering all territories and both years ($F_{1,16} = 15.99$, $P = 0.001$, partial $\eta^2 = 0.500$), though it decreased more markedly in 2004 than in 2003 (year $\times$ date interaction: $F_{1,16} = 10.66$, $P = 0.005$, partial $\eta^2 = 0.400$). There was variation between territories (CV = 96.7%), and overall abundance of lepidopteran larvae ranged from 1.9 to 30.6 individuals per 1000 leaves. Thus, our Pennsylvania study sites exhibited spatial and seasonal variation in food abundance for both lepidopteran larvae and, in 2004, periodical cicadas.

Egg-rejection experiments

Model eggs were added to 83 nests at our Pennsylvania sites; experiments at 8 of those nests were begun too late in the incubation period to meet our criteria, and an additional 15 nests failed due to predation or severe weather. Thus, successful experiments during the proper stage of incubation were completed at a total of 60 nests (Table 1). Overall, the species we tested were either partial or complete accepters of model cuckoo eggs.

DISCUSSION

Contrary to expectations, we found no evidence of *Coccyzus* cuckoos parasitizing songbirds. Before exploring what this might mean, we begin by considering our likelihood of detecting such parasitism if indeed it were occurring. First, we had a large sample of more than 10 000 nests of potential hosts, yielding a very narrow CI on our estimate of 0% parasitism. Second, cuckoos were present at all our study sites, overlapping temporally and spatially with nesting by potential hosts (Dearborn DC, MacDade LS, Robinson S, Dowling Fink AD, Fink ML, personal observation). Spot-mapping data from our Pennsylvania sites showed that 95% of potential host nests

were within 100 m of a cuckoo detection. Although data were less detailed in Missouri and Illinois, cuckoos were present at all sites in all years, and long-term data from the BBS indicate that cuckoos are at least twice as abundant at those sites than at our sites in Pennsylvania. Detailed temporal data on cuckoo and host abundance were not collected, but previous accounts of breeding phenology of these species indicate nearly complete overlap, with cuckoos breeding May through August (Payne 2005); even if some hosts escaped the possibility of parasitism by breeding very early or very late in the summer, this cannot account for the absence of cuckoo parasitism in thousands of songbird nests. Third, we monitored hosts' nests during both low and high food availability—factors that have been hypothesized (under 2 different mechanisms) to favor facultative parasitism. We documented extensive variation in the abundance of food at a variety of spatial and temporal scales: seasonal, among territories, among years, and among study sites. Cuckoo parasitism has been hypothesized to be linked to abundance of caterpillars and periodical cicadas (Nolan and Thompson 1975; Fleischer et al. 1985), and work at our Pennsylvania sites has shown a link between food availability and parental reproduction by yellow-billed cuckoos (Anders and Post 2006). However, we found no parasitic egg laying at any level of food availability, including 1801 songbird nests monitored during periodical cicada emergences. Fourth, many of our site-years had a high probability of nest predation, another factor suggested to increase the likelihood of cuckoo parasitism. Fifth, our egg-rejection experiments did not reveal widespread or rapid rejection behavior by potential hosts; for example, wood thrush—a common songbird across eastern North America and a regular host of brown-headed cowbirds—accepted all our model cuckoo eggs. A key implication of the egg-rejection data is that an apparent absence of cuckoo eggs in songbird nests is not likely to be simply a consequence of hosts rejecting cuckoo eggs before they are detected by researchers nor is the absence of parasitic eggs attributable to cuckoos' evolution of a very narrow host range in response to many hosts' evolution of defenses against parasitism.

Overall, these pieces of evidence suggest that we had good opportunity to detect *Coccyzus* parasitism of songbirds if it were occurring regularly. We now attempt to reconcile our findings with previous research that viewed yellow-billed and black-billed cuckoos as species with a long history of parasitizing other birds. In an interspecific analysis of brood parasites, Lyon and Eadie (1991) demonstrated an association between mode of interspecific brood parasitism (facultative vs. obligate) and mode of offspring development (precocial vs. altricial), classifying yellow-billed and black-billed cuckoos as facultative parasites with altricial young. Others have gone further, hypothesizing that *Coccyzus* cuckoos have evolved egg mimicry as part of a long coevolutionary history with North American songbird hosts (Hughes 1997, but see Lorenzana and Sealy 2002). Our data, though, suggest that such parasitism is extraordinarily rare. Thus, we propose a new hypothesis: heterogeneric brood parasitism in *Coccyzus* cuckoos is a rare event resulting from errant attempts to parasitize conspecifics or congeners. Our study did not measure the frequency of congeneric parasitism, and this is an area in need of more investigation using genetic markers and large samples. However, a small genetic data set (Fleischer et al. 1985) and observations of occasional large clutches with sporadic egg-laying sequences (Fleischer et al. 1985; Hughes 1997) suggest that conspecific parasitism—and parasitism of yellow-billed and black-billed cuckoos by each other in areas of sympatry (Nolan and Thompson 1975)—may be common, at least under certain ecological conditions.

Cuckoo parasitism of songbirds via errant attempts to parasitize other cuckoos is consistent with findings from this and previous studies: 1) extremely infrequent parasitism of heterogeneric hosts (this study); 2) a likelihood for parasitized nests to contain host eggs that resemble *Coccyzus* eggs (Hughes 1997); 3) a tendency for heterogeneric parasitism to be observed under superabundant food (Nolan and Thompson 1975), when the laying of more eggs in total causes a concomitant increase in the number (but not proportion) of mislaid eggs; 4) a general lack of egg rejection or other evolved defenses by hosts (this study; Lorenzana and Sealy 2002); 5) a lack of differential rejection by hosts of white versus blue eggs (Lorenzana and Sealy 2002); and 6) an ongoing rarity of heterogeneric parasitism over the course of many generations (this study, in relation to Darwin 1859, p. 217).

The "mistaken identity" hypothesis is an alternative to 3 previously proposed hypotheses for the evolution of songbird parasitism by *Coccyzus* cuckoos. First, some phylogenies have suggested an obligately parasitic ancestor to the *Coccyzus* lineage, leading to an interpretation that *Coccyzus* cuckoos are longtime parasites that have subsequently been reevolving traits associated with parental reproduction (Aragon et al. 1999; Hughes 2000). Such a scenario seems unlikely, in part because several lines of evidence suggest that there has not been coevolution of egg rejection and egg mimicry (Lorenzana and Sealy 2002, Grim 2005). Furthermore, 2 recent phylogenies based on larger data sets (Sorenson and Payne 2002, 2005) suggest that the ancestral state of *Coccyzus* cuckoos is one of parental reproduction, rather than obligate parasitism. This is consistent with a second hypothesis that yellow-billed and black-billed cuckoos had a parentally reproducing ancestor, subsequently became facultative parasites, and are currently in the process of evolving obligate parasitism from facultative parasitism, as originally envisioned by Darwin (1859, p. 217). However, our data revealed that heterogeneric parasitism is quite rare,

despite the fact that it was observed in early naturalists' surveys of the New World (Darwin 1859, p. 217; Darwin 1872, p. 212) and could have spread quickly had it conveyed a fitness advantage. A third hypothesis is that facultative parasitism of songbirds by yellow-billed and black-billed cuckoos was derived from a parentally reproducing ancestor (Sorenson and Payne 2005) and that this strategy is currently evolutionarily stable because parasitism is favored only under some ecological circumstances (Nolan and Thompson 1975). Because host nests are widely and routinely available, the 2 factors that might vary enough to impact the reproductive mode of a facultative parasite are food availability (laying parasitically when food is very high or very low) and nest predation (laying parasitically when one's own nest is depredated during the egg-laying stage). We did not find any evidence of parasitism, despite broad variation in food availability and moderate to very high levels of nest predation; thus, our data support neither of these factors as an ecological determinant of heterogeneric parasitism by these species.

Even if these rare heterogeneric parasitism events are truly cases of mistaken identity, such behavior could be favored by natural selection and thus could become more common, if this tendency is heritable and if parasitically laid eggs are successful. We have shown that several potential hosts will accept *Coccyzus* eggs at least sometimes; a key next test would be to experimentally compare the hatching and fledging success of heterogeneric parasitism attempts relative to self-reared eggs, relative to conspecific parasitism, and relative to congeneric parasitism, through egg and nestling translocations. Perhaps, the development or reproductive ecology of *Coccyzus* cuckoos is sufficiently unusual that songbirds are not appropriate hosts. Regardless, it is clear that heterogeneric parasitism by yellow-billed and black-billed cuckoos is rare despite the proximity and availability of suitable hosts, and mistaken identity may be a plausible explanation for this behavior.

Appendix A

Species with previous documentation of parasitism by yellow-billed or black-billed cuckoos (reviewed in Hughes 1997; Lorenzana and Sealy 2002)

Species	Egg appearance	Egg size (mm)	Accepts cowbird eggs?
Yellow-billed cuckoo	Pale greenish blue	30.4 × 23.0	Yes
Black-billed cuckoo	Greenish blue	27.2 × 20.6	Yes
Mourning dove (*Zenaida macroura*)	White	28.4 × 21.5	Unknown
Eastern wood-pewee (*Contopus virens*)	Creamy with brown blotches	18.2 × 13.6	At least sometimes
Blue jay (*Cyanocitta cristata*)	Olive with grayish brown dots	28.0 × 20.4	No
Veery (*Catharus fuscescens*)	Pale blue	22.4 × 16.7	Yes
American robin (*Turdus migratorius*)	Blue	28.1 × 20.0	Rarely
Wood thrush (*Hylocichla mustelina*)	Pale blue or bluish green	25.4 × 18.6	Yes
Gray catbird (*Dumetella carolinensis*)	Deep greenish blue	23.3 × 17.5	Rarely
Cedar waxwing (*Bombycilla cedrorum*)	Pale bluish gray with few brown spots	21.8 × 15.6	Sometimes
Yellow warbler (*Dendroica petechia*)	Bluish or greenish white with brown markings	16.6 × 12.6	Sometimes
Yellow-breasted chat (*Icteria virens*)	White with brown spots	21.9 × 16.9	Usually
Eastern towhee (*Pipilo erythrophthalmus*)	White with reddish brown spots	23.1 × 17.0	Yes
Chipping sparrow (*Spizella passerina*)	Pale bluish green with few dark marks	17.6 × 12.9	Usually
Black-throated sparrow (*Amphispiza bilineata*)	Bluish white	18.0 × 13.7	Usually
Dickcissel (*Spiza americana*)	Pale blue	20.8 × 15.7	Yes
Northern cardinal (*Cardinalis cardinalis*)	Off-white with brown blotches	25.3 × 18.2	Yes
Red-winged blackbird (*Agelaius phoeniceus*)	Pale bluish green with dark scrawls	24.8 × 17.6	Yes
House finch (*Carpodacus mexicanus*)	Pale bluish green with few black dots	18.8 × 13.8	Usually

Egg descriptions are from Harrison (1975). Most of these species have extensive sympatry with the brown-headed cowbird, an obligate brood parasite. Behavioral responses to cowbird eggs were compiled from Friedmann 1963, Rothstein 1975, Friedmann and Kiff 1985, and Peer and Bollinger 1998.

Appendix B

Sample sizes of potential host nests monitored for *Coccyzus* parasitism in this study

		Number of nests monitored		
Potential host species		Illinois	Missouri	Pennsylvania
Passeriformes—Tyrannidae				
Eastern wood-pewee[a]	*Contopus virens*	23		
Acadian flycatcher	*Empidonax virescen*	1658		
Willow flycatcher	*Empidonax traillii*	27		
Eastern phoebe	*Sayornis phoebe*	81		
Eastern kingbird	*Tyrannus tyrannus*	60		
Passeriformes—Laniidae				
Loggerhead shrike	*Lanius ludovicianus*	6		
Passeriformes—Vireonidae				
White-eyed vireo	*Vireo griseus*	155	22	
Bell's vireo	*Vireo bellii*	17		
Yellow-throated vireo	*Vireo flavifrons*	10		
Warbling vireo	*Vireo gilvus*	3		
Red-eyed vireo	*Vireo olivaceus*	28		9
Passeriformes—Corvidae				
Blue jay[a]	*Cyanocitta cristata*	96		
Passeriformes—Troglodytidae				
Carolina wren	*Thryothorus ludovicianus*	80		
Passeriformes—Sylviidae				
Blue–gray gnatcatcher	*Polioptila caerulea*	4		
Passeriformes—Turdidae				
Veery[a]	*Catharus fuscescens*	31		
Wood thrush[a]	*Hylocichla mustelina*	1302	168	30
American robin[a]	*Turdus migratorius*	160		
Passeriformes—Mimidae				
Gray catbird[a]	*Dumetella carolinensis*	56		48
Northern mockingbird	*Mimus polyglottos*	1		
Brown thrasher	*Toxostoma rufum*	217	2	4
Passeriformes—Bombycillidae				
Cedar waxwing[a]		24		
Passeriformes—Parulidae				
Blue-winged warbler	*Vermivora pinus*	7	6	
Yellow warbler[a]	*Dendroica petechia*	42		
Chestnut-sided warbler	*Dendroica pensylvanica*	1		
Yellow-throated warbler	*Dendroica dominica*	1		
Prairie warbler	*Dendroica discolor*	32	54	
Black and white warbler	*Mniotilta varia*	4		
American redstart	*Setophaga ruticilla*	46		
Worm-eating warbler	*Helmitheros vermivorum*	214		
Ovenbird	*Seiurus aurocapilla*	46		
Kentucky warbler	*Oporornis formosus*	698		
Common yellowthroat	*Geothlypis trichas*	69		
Hooded warbler	*Wilsonia citrina*	50		
Yellow-breasted chat[a]	*Icteria virens*	117	92	
Passeriformes—Thraupidae				
Summer tanager	*Piranga rubra*	35		
Scarlet tanager	*Piranga olivacea*	25		
Passeriformes—Emberizidae				
Eastern towhee[a]	*Pipilo erythrophthalmus*	226	11	6
Chipping sparrow[a]	*Spizella passerina*	53		
Field sparrow	*Spizella pusilla*	1070	60	1
Lark sparrow	*Chondestes grammacus*	42		
Song sparrow	*Melospiza melodia*	51		
Dickcissel[a]	*Spiza americana*	48		
Passeriformes—Cardinalidae				
Northern cardinal[a]	*Cardinalis cardinalis*	895	28	21
Rose-breasted grosbeak	*Pheucticus ludovicianus*	104		
Blue grosbeak	*Passerina caerulea*	8		
Indigo bunting	*Passerina cyanea*	1167	116	1
Passeriformes—Icteridae				
Red-winged blackbird[a]	*Agelaius phoeniceus*	183		
Orchard oriole	*Icterus spurius*	147		
Baltimore oriole	*Icterus galbula*	2		
Passeriformes—Fringillidae				
American goldfinch	*Carduelis tristis*	96		
Total		9518	559	120

[a] Species with anecdotal reports of parasitism by *Coccyzus* cuckoos.

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