HOST USE BY SYMPATRIC COWBIRDS (*MOLOTHRUS AENEUS* AND *M. ATER*)

BY

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A Thesis
Submitted to the Faculty of Graduate Studies
in Partial Fulfillment of the Requirements
for the Degree of

Ph.D. in Zoology

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THE UNIVERSITY OF MANITOBA

FACULTY OF GRADUATE STUDIES
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DOCTOR OF PHILOSOPHY

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ABSTRACT

Obligate brood parasites are characterized as host specialists or host generalists based on the number of hosts regularly parasitized within avian communities. For instance, despite parasitization of several species' nests, individual cuckoo demes, or gentes, are maintained by matrilinear specialization on one host species (Gibbs et al. 2000). By contrast, individual Brown-headed Cowbirds (*Molothrus ater*) parasitize multiple host species (Gibbs et al. 1997, Alderson et al. 1999, Hahn et al. 1999). These findings, combined with phylogenetic trends in host number and divergence time (Rothstein et al. 2002) lead to the central question whether generalism is a stable strategy or a pre-condition along an evolutionary pathway to specialism. More simply put, would every obligate brood parasite species become a host specialist given enough time for host-parasite coevolutionary cycles? The molothrine cowbirds comprise a recently derived (3.8 - 0.8 mya) group of brood parasites, whereas the Cuculinae have been extant 3-4 times as long and are highly specialized (Rothstein et al. 2002). Cowbirds range from specialists that use one host species to generalists that use >200 species as hosts. Therefore the cowbirds provide an excellent opportunity to study the derivation of reproductive strategies, especially fecundity, selectivity of hosts and mating systems.

The three most recently derived cowbirds (Bronzed [*M. aeneus*], Brown-headed, and Shiny [*M. bonariensis*] cowbirds) are host generalists. Host use by these species has been described as ranging from random (Rothstein 1976, Kattan 1997) to relatively selective (Wiley 1988, Grant and Sealy 2000, Woolfenden et al. 2003). These opposing characterizations stem from differential attention to the apparent wasting of inappropriately laid eggs and relatively specific host use within diverse avian

communities. However, the costs and benefits of cowbird behavior rarely have been assessed holistically. First, what is the relative value of an egg to an individual cowbird? How appropriate are laying decisions relative to the availability of alternative nests not parasitized? How much time is budgeted for locating host nests relative to feeding and social activities? These are the questions I have addressed through the analysis of Brown-headed and Bronzed cowbird life histories (overview in Chapter 1).

Specifically, I compared theoretically host generalist and specialist strategies to determine whether either strategy is more evolutionarily stable (Chapter 2, see also Ney-Nifle et al. in press). This information is vital to viewing appropriately the evolution of host use and assessing whether either strategy must be preceded by the other. I found generalism was more often sustainable than specialism and that specialist ancestors may have given rise to generalists. Combined with the phylogenetic analysis by Mermoz and Ornelas (2004) it appears clear that the molothrine cowbirds are not following the coevolutionary trajectory outlined by Rothstein et al. (2003). Instead, I suggested that phylogenetic trends in host specificity reflect differing degrees of host imprinting (Chapters 1 and 2). Therefore, Lanyon's (1992) phylogenetic trajectory hypothesis appears to best explain host use among *Molothrus*.

Next, I analyzed host use data to demonstrate that sympatric Brown-headed and Bronzed cowbirds differentially use some hosts and do so in a manner that is fit poorly by random series (Chapter 3). This was primarily because hosts of Bronzed Cowbirds often reared more than one cowbird. If cowbirds do not randomly distribute their eggs among hosts' nests when in sympatry, then competition between cowbird species may affect host use (Chapter 4). In Chapter 4, I examined host use by cowbirds

geographically to show cowbirds compete for host nests and that interspecific competition best explains the lack of host overlap I found in Texas. In particular, each species may differentially parasitize hosts that better match the growth requirements of their young. Likewise, non-random host use may affect cowbird sex ratio. Because cowbirds produce sexually size-dimorphic young, they may benefit by differentially placing eggs of either sex among certain host nests. Therefore, I examined host use relative to the destined sex of cowbird eggs (Chapter 5). I found that despite producing eggs of each sex equally, cowbird sex ratios may become male-biased among hatching-year birds rather than adults as previously thought. This finding has implications for understanding cowbird life history, as the male-bias was previously attributed to differential mortality of females associated with extraordinary annual egg production.

I discuss the results of my analyses with respect to host use among *Molothrus* and the implications for study of other brood parasites (Chapter 6). Primarily, through the more refined understanding of cowbird host use that I have provided, cowbird evolution can be better understood. Foremost, I outlined that determining whether more basal *Molothrus* imprint on aspects of hosts would clarify whether ancestral cowbirds were specialists (phylogenetic hypothesis, Lanyon 1992) or generalists (coevolutionary hypothesis, Rothstein et al. 2002). In practical application, my results can be used to refine cowbird control programs and focus funds at the most appropriate process to mitigate songbird declines. For instance, because individual cowbirds lay fewer eggs than previously estimated, trapping efforts may be reconsidered incorporating revised

fecundity estimates. Indeed, habitat restoration or predator control may represent a better option than broadcast trapping efforts.

Finally, my data suggest that sympatric cowbirds will partition hosts, therefore, preventive measures may be taken in advance of expanding cowbird populations where vulnerable host populations occur. For example, small songbirds such as endangered Black-capped Vireos may face elevated use by Brown-headed Cowbirds if Bronzed Cowbirds compete for larger host species, thereby increasing Brown-headed Cowbird dependence on small hosts.

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CHAPTER 1. OVERVIEW OF THE EVOLUTION OF HOST USE BY MOLOTHRINE COWBIRDS

Interactions between organisms are central determinants of niche space within ecosystems. For instance, animal diets may vary from specialized to generalized dependent upon the behavior or physiology of prey (Futuyma and Slatkin 1983, Godfray 1994). Despite the frequency of interactions between organisms, few clear examples of coevolution are evident, i.e. those where evolution is reciprocal and paired traits and counter-defenses can be identified (Rothstein 1990, Futuyma 1998, Fig. 1.1). Instead, coevolutionary relationships generally are difficult to detect, as coevolution may be diffused by interactions between more than two primary co-actors and, thus, coevolution is more apparent among specialists than generalists. Analyses of coevolution are also constrained by the evolutionary "snapshots" provided by the fossil record and relationships among extant forms.

Brood parasitic birds provide an excellent system for studying coevolution (see review by Rothstein 1990). Individual Common Cuckoos (*Cuculus canorus*) produce distinct egg morphs that approximate the appearance of host eggs (Moksnes and Røskaft 1995, Gibbs et al. 2000) as a result of the removal of discordant eggs by hosts (detected through experimental egg addition), a trait presumably selected to ameliorate costs of parasitism (Davies and Brooke 1989, Davies 2000).

One hundred species of brood-parasitic birds among seven genera exhibit a diversity of host use strategies (reviewed by Davies 2000, Sorenson and Payne 2002). Common Cuckoos and Brown-headed Cowbirds are two well-studied brood parasites for which host use patterns are often compared (Davies 2000, Rothstein et al. 2002).

Parasite   **Host**

```
┌─────────────────────┐                    ┌─────────────────────┐
│      Step 1          │                    │      Step 2          │
│                      │ ─────────────────▶ │   Defense 1,         │
│    Use of host       │                    │                      │
│                      │                    │    e.g. egg          │
│                      │                    │   discrimination     │
└─────────────────────┘                    └─────────────────────┘
                                                     │
                                            ◀────────┘
┌─────────────────────┐                    ┌─────────────────────┐
│      Step 3          │                    │      Step n          │
│  Counter-defense 1,  │ ─────────────────▶ │    Defense n,        │
│  e.g. egg mimicry    │                    │  repetitious cycle   │
└─────────────────────┘                    └─────────────────────┘
                                                     │
                             ◀───────────────────────┘
┌─────────────────────┐
│                      │
│  Counter-defense n   │
│                      │
└─────────────────────┘
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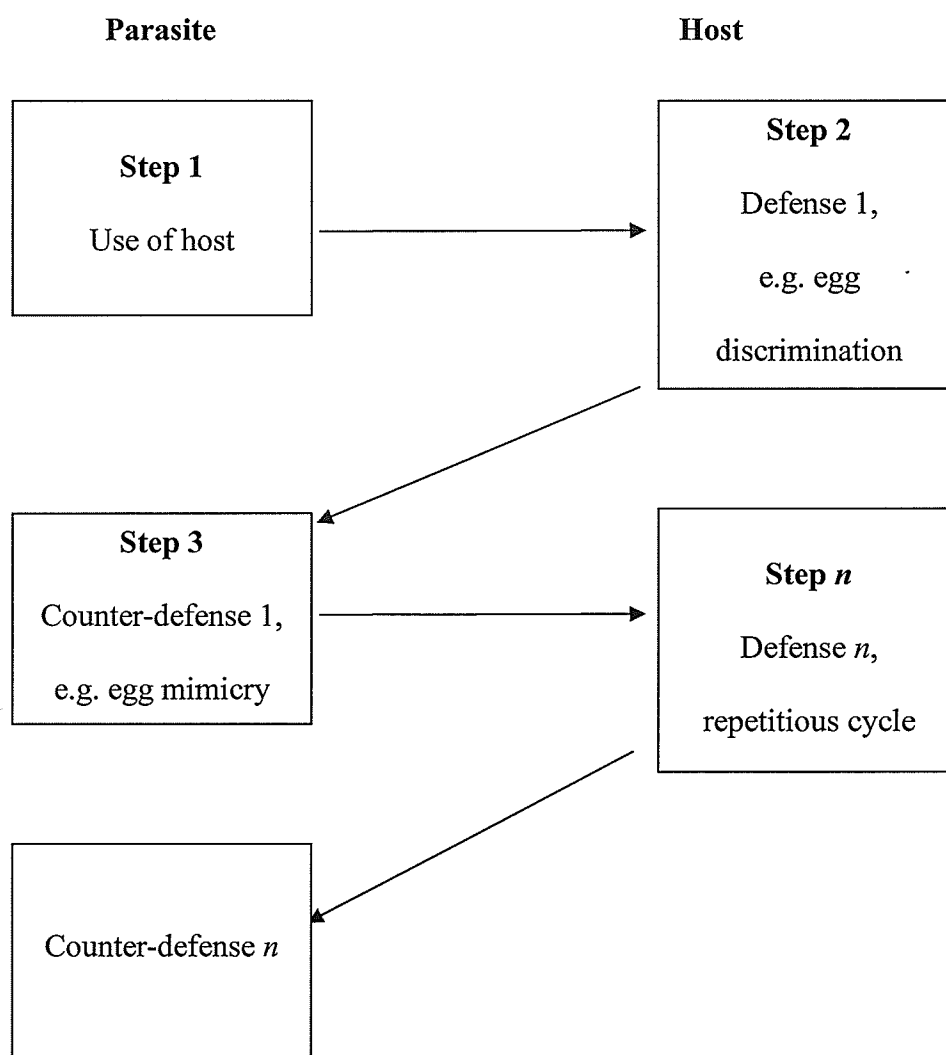
Fig. 1.1. Schematic representation of the steps during host-parasite coevolution. Each solid line represents a cost imparted upon the other party, arising in response to costs imposed by the other party.

This is particularly so, because individual cuckoos parasitize a single host species (Moksnes and Røskaft 1995, Edvardsen et al. 2001) frequently enough to have accrued host-based genetic differences (Gibbs et al. 2000). By contrast, individual Brown-headed Cowbirds regularly use multiple hosts and have not differentiated genetically (Gibbs et al. 1997).

Comparisons among *Molothrus* species (following nomenclature of American Ornithologists' Union, 2000), which range from host-specialists to those using over 100 host species (Table 1.1), have contributed to the development of evolutionary hypotheses for the strength and mechanisms of coevolutionary relationships (Rothstein 1990, Lanyon 1992, Rothstein et al. 2002, Mermoz and Ornelas 2004). For instance, host use by cuckoos and cowbirds has been attributed to coevolution (Rothstein 1990, Rothstein et al. 2002), whereas Lanyon (1992) suggested host generalism is a derived character state among cowbirds.

As derived states, both generalism and specialism are considered equally tenable as explanations for trophic interactions, including coevolutionary interactions (reviews in Futuyma and Slatkin 1983, J. N. Thompson 1994). However, host use by brood parasites has been considered to reflect one-way, rather than more labile, changes in characters. Thus, I analyzed whether host use among the molothrine cowbirds reflects predominantly adaptations for a brood-parasitic lifestyle or more refined and direct coevolution with hosts. I studied host use among *Molothrus* to better understand evolution in this genus and provide insights for comparisons with other brood parasites. I used theoretical models to demonstrate that shifts between host specialism and generalism are possible

Table 1.1. The five parasitic cowbirds, genus *Molothrus*, listed from most basal to recently derived, based upon Lanyon's (1992) mtDNA phylogeny. Number of host species known to have fledged young of each cowbird. Number of host species' nests in which eggs have been found, but fledging has not been observed, is given in parentheses. The numbers of potential host species shared by sympatric cowbirds are represented in the non-identity terms of the matrix.

	rufoaxillaris	*oryzivorus*	*aeneus*	*ater*	*bonariensis*	Sources
rufoaxillaris	3	--	--	--	--	Mermoz and Reboreda (1996)
oryzivorus	0	8	--	--	--	Ortega (1998), Lowther (2004)
aeneus	0	1 (1)	42 (53)	--	--	Sealy et al. (1997), this study
ater	0	0	19 (24)	162 (77)	--	Ortega (1998)
bonariensis	3	0 (1)	4 (9)	4 (4)	88 (155)	Lowther and Post (1999)

and that generalism provides benefits that may make such transitions more likely. Also, I

collected field data on host use by two sympatric generalists, the Bronzed Cowbird

(*Molothrus aeneus*) and the Brown-headed Cowbird (*M. ater*), for analysis of the

attributes of the species used and not used as hosts. Prior to a more detailed discussion,

however, I provide a synopsis of life histories for *Molothrus* in the following section.

MOLOTHRINE NATURAL HISTORIES

Historically, cowbirds fed in association with native grazing herbivores, i.e. capybaras

(*Hydrochoerus hydrochoerus*) and plains bison (*Bison bison*), which have been replaced

today largely by livestock and agricultural lands (Jaramillo and Burke 1999). Therefore,

cowbirds are mobile and most exhibit dynamic daily activity patterns that depend upon

the movements of herbivores (Curson and Matthews 2003) or human land-use practices

(Mayfield 1960, Skutch 1996, Clotfelter 1995, Evans and Gates 1997). Cowbirds also

exhibit considerable variation in pairing and reproductive success (Carter 1984,

Woolfenden et al. 2002, Curson and Matthews 2003), which likely explains their

investment of substantial time in development, maintenance, and defense of access to

mates (Yokel and Rothstein 1991, Clotfelter 1995).

Molothrine cowbirds share several characteristics associated with reproduction

that are unique from most songbirds: seasonally increased hippocampus and

telencephalon volumes in females (*M. rufoaxillaris*, *M. bonariensis*, *M. ater*: Sherry et al.

1993, Clayton et al. 1997), rapid egg laying prior to sunrise (*M. bonariensis* and *M. ater*:

Scott 1991, Sealy et al. 1995, McMaster et al. 2004, *M. aeneus*: Peer and Sealy 1999a),

and temporally random sequences of follicular production (*M. ater*: Payne 1965, 1973,

1976; Scott and Ankney 1983, *M. bonariensis*: Kattan 1993, *M. aeneus*: Appendix 1).

Cowbird eggs vary from immaculate to heavily maculated between individuals (Table

1.2) and are more thickly shelled and more round than those of non-parasitic species

(Rahn et al. 1988, Picman 1989, Mermoz and Ornelas 2004).

Screaming Cowbird (*M. rufoaxillaris*)

Screaming Cowbirds (*M. rufoaxillaris*, hereafter, cowbirds are referred to by species'

names alone) specialize largely on the Bay-winged Cowbird (*Agelaiodes badius*),

formerly included among *Molothrus* (Lanyon 1992, Lowther 2001). Because *badius*

often usurps or reuses primarily domed nests constructed by other species, attempts by

rufoaxillaris to synchronize laying with *badius* are complicated. *Badius* may often have

helpers at the nest and aggressively defend nests (Fraga 1998).

When laying, male-female pairs of *rufoaxillaris* overcome nest defense when the

male distracts the hosts (Fraga 1998). Such nest defense results in poor synchronization

of laying with the host. Fraga (1998) suggested that individual females overcome this by

laying many eggs per nest, because many are ejected due to laying before the host. He

formulated this hypothesis based on observed numbers of daily visits to nests by

individuals and numbers of eggs deposited per day (no bird is known to lay more than

one egg per day, Sturkie 1976). The eggs of *rufoaxillaris* do not mimic those of *badius*

(Fraga 1978, 1983, 1998). Therefore, costs and benefits of egg ejection apparently

restrict *badius* to ejecting eggs laid before its own (Fraga 1998) and many *rufoaxillaris*

eggs are wasted during attempts to synchronize laying with hosts (Hoy and Ottow 1964,

Mason 1980, Fraga 1998). Thus, mechanisms that promote increased egg production

Table 1.2. Cowbird attributes associated with number of hosts used.

	Breeding range (10^3 km^2) [a]	Female size (g) [b]	Sexual size-dimorphism [c]	Egg markings [d]	Host number [e]
M. rufoaxillaris	24	50	1.27	1	3 (3)
M. oryzivorus	114	162	1.35	0/1	8 (8)
M. aeneus	38	57	1.21	0	95 (42)
M. ater	153	36	1.26	1	239 (162)
M. bonariensis	155	32	1.21	0/1	243 (88)

[a] Calculated from maps in Johnsgard (1997), see also Fig 1.2.

[b] Body masses from Dunning (1993), Carter (1986), Lowther and Post (1999), this study.

[c] Ratio of male and female masses.

[d] 0 = immaculate, 1 = maculated, varied amount of spotting (Dufty 1983, Lyon 1997).

[e] Species parasitized by cowbirds and number that have reared cowbirds in parentheses (sources, Table 1.1).

and/or ways of defeating host defenses, such as egg mimicry (Fraga 1998), may have been favored by natural selection. However, *badius* accepts several foreign egg types (Mason 1980, Fraga 1983), including those of *bonariensis*, which vary from maculated to white. Thus, the only parasite countermeasures documented clearly include frequent and gregarious nest visits and a close resemblance or "mimicry" between parasite and host young (Fraga 1983, 1998; Jaramillo 1993; Lichtenstein 2001a).

Chick mimicry, particularly in the juvenal plumage, is a remarkable feature of this parasite-host association. However, *rufoaxillaris* chicks do not approach the levels of mimicry found in other systems such as the mimetic mouthparts of parasitic finches (Nicolai 1964, Reed and Freeman 1991) or cuckoo begging calls that mimic begging by host broods (Butchart et al. 2003). Indeed, human observers can accurately distinguish parasitic young from host young because *rufoaxillaris* young have orange skin, lack a dark subterminal spot on the bill, and have partially occluded nares (Fraga 1979, 1998; Lichtenstein 2001a).

Similarities between *rufoaxillaris* and *badius* may in part reflect phylogenetic similarity (Lanyon 1992), as phenotypic convergence is common among the icterine relatives of *Molothrus* (Johnson and Lanyon 1999, Omland and Lanyon 2000), and more distantly related species (Moynihan 1968). Moreover, mechanisms underlying such mimicry are unclear as two other species are known to rear *badius* chicks (Sick 1993, Mermoz and Fernández 2003). Thus, further study is required to more clearly understand the similarities in nestling appearance.

Rufoaxillaris breeds in sympatry with *oryzivorus* and *bonariensis*, however, the degree of overlap among hosts used appears minimal (Mermoz and Fernández 2003, Fig.

1.2). The size of *oryzivorus* (three times as large) likely precludes much overlap in host use between these species (Skutch 1996). By contrast, *rufoaxillaris* and *bonariensis* are similarly sized and share three hosts, both faring equally in nests of Brown-and-yellow Marshbirds (*Pseudoleistes virescens*) (8-10% eggs produce fledglings) (Mermoz and Fernández 2003), Chopi Blackbirds (*Gnorimopsar chopi*) (Table 1.3) (Sick 1993, Fraga 1996), and *badius* (7% and 5% of eggs produced fledglings, for *rufoaxillaris* and *bonariensis*, respectively) (Fraga 1998). However, excluding improperly timed eggs, *rufoaxillaris* fared twice as well, as 11% of eggs produced fledglings (Fraga 1998).

Moreover, *bonariensis* chicks, which do not mimic *badius*, fledged from natural and manipulated *badius* broods (Fraga 1998). In preference tests with caged fledglings, *badius* exhibited a mixed response, once feeding *bonariensis* preferentially over *rufoaxillaris* (Fraga 1998). Although the power of these tests was extremely low, the tests demonstrated that *badius* does not always discriminate between allospecific young and its own. Thus, host specialization by *rufoaxillaris* is not fixed, as host use is not constrained by egg appearance nor is host discrimination against parasites well refined as predicted for coevolution (see Rothstein et al. 2002). Perhaps the *rufoaxillaris-badius* system is better described as parasite imprinting (see Fig. 1.3) followed by coevolutionary modification of chick appearance to enhance, rather than to facilitate success. This view is supported by the successful use of alternative hosts, but again, further study is required.
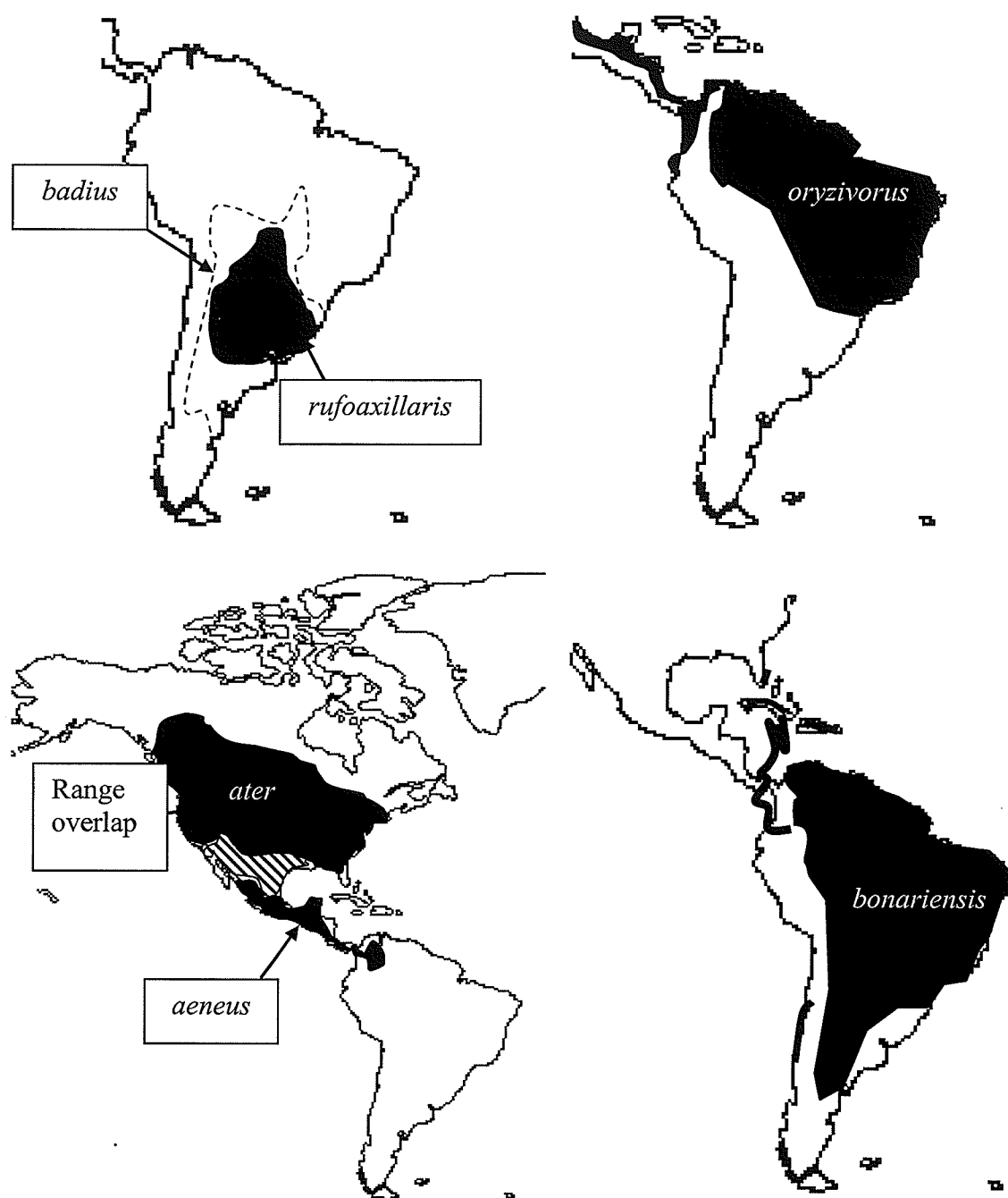
Figure 1.2. Breeding ranges for *badius* and *Molothrus* spp. (after Johnsgard 1997).

Table 1.3. Success of *rufoaxillaris* and *bonariensis* with the same host species.

Host species	Number of young fledged			Number of broods	Source
	rufoaxillaris	*bonariensis*	Host		
Brown-and-yellow Marshbird	1	0	ND[a]	2	Mermoz and Fernández (2003)
	1	1	ND	1	
	0	1	ND	4	
Chopi Blackbird	≥1	0	ND	0	Sick (1993)
	1	3	0	1	
	1	3	1	1	
	3	0	1	1	
	0	4	0	1	
	1	0	0	1	Fraga (1996)
	2	0	1	1	
Bay-winged Cowbird	0	1[b]	> 1	5	Fraga (1998)

[a] "ND" indicates data not provided. [b] Four nests fledged a 2-day old *bonariensis* chick added experimentally, along with at least one host young (Fraga 1998).
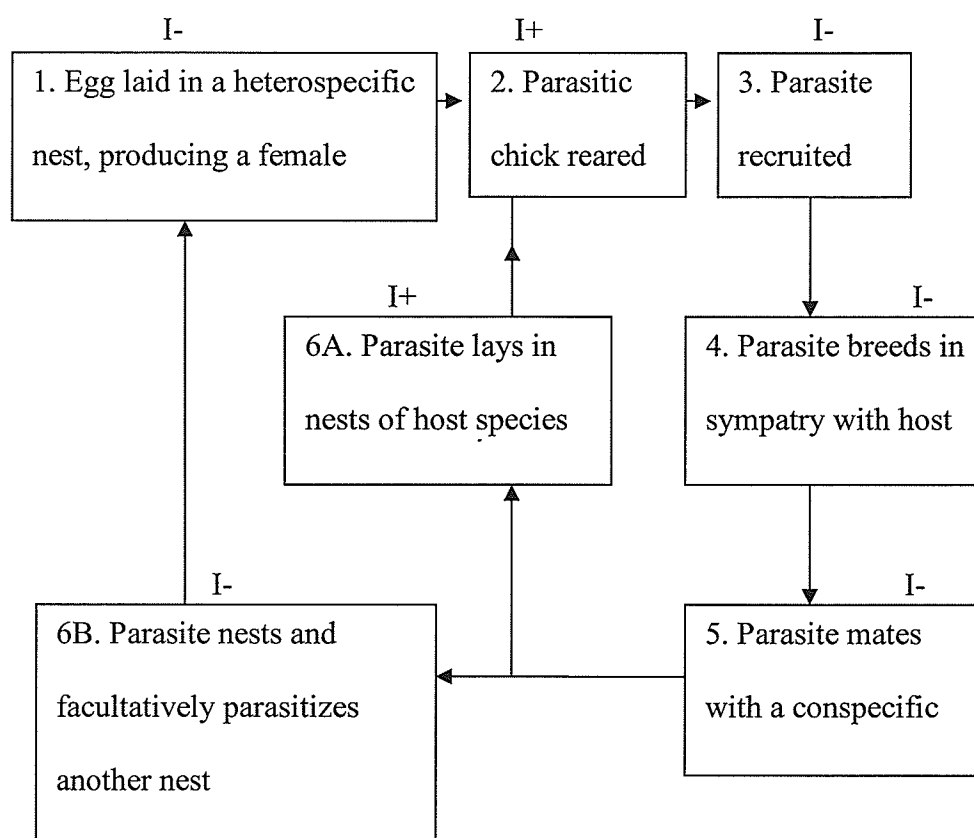
Figure 1.3. Hypothetical pathways to obligate brood parasitism involving imprinting, steps 1-6A or B (after Slagsvold and Hansen 2001). Imprinting on social parents may increase (I+) or decrease (I-) the likelihood of events one through six. Parasites that specialize on few hosts may imprint more strongly on hosts. Thus, for generalists, the strength of imprinting would have decreased at steps 2 and/or 6A.

Giant Cowbird (*M. oryzivorus*)

Oryzivorus has been the subject of only two detailed studies, both conducted in Panama (Smith 1968, Fleischer and Smith 1992). Nonetheless, *oryzivorus* has been characterized as a specialist brood parasite based largely on egg collections (Friedmann 1929, Friedmann 1963). Indeed, because females are two to three times larger than other *Molothrus*, *oryzivorus* may have access to fewer potential hosts that can rear its young (Table 1.1; Wetmore et al. 1984, Johnsgard 1997). The large size is unique in *Molothrus*, despite being similar to *aeneus* in appearance (see Friedmann 1929).

Rothstein et al. (2002) considered *oryzivorus* as a specialist with traits unique among *Molothrus* that have resulted from coevolution. Specifically, they referred to scrawled eggs, chick allo-preening, and the lightly colored bill in juveniles as specialist traits, although the function of each trait requires confirmation. Furthermore, *oryzivorus* eggs range from unmarked to heavily speckled and scrawled (Haverschmidt 1968, Fleischer and Smith 1992).

Smith (1979) described a remarkable system in which hosts whose nests were not protected from ectoparasites by wasps, benefited from parasitism by *oryzivorus*, whose chicks feed on ectoparasites. Thus, cowbird parasitism was tolerated at colonies without wasps, but not at colonies with wasps (Smith 1979). However, subsequent studies have not replicated Smith's findings (Robinson 1988, Webster 1994). Likewise, suggested egg mimicry in *oryzivorus* and two hosts (Smith 1968) was not found upon re-analysis (Fleischer and Smith 1992). Also, among icterids, only non-parasitic species (*badius* and Yellow-shouldered Blackbird, *Agelaius xanthomus*) have been confirmed to preen nestmates (Post 1981; Fraga 1984, 1998). Finally, the lightly colored bill may not be an

adaptation, as other bill color traits among *Molothrus* did not affect success with hosts (Fraga 1998, Appendix 2), however, this remains to be tested through manipulation (*sensu* Stevens 1982). Therefore, despite a basal position within *Molothrus*, *oryzivorus* does not appear highly specialized toward its hosts. It co-occurs with *rufoaxillaris*, *aeneus* and *bonariensis*.

Bronzed Cowbird (*M. aeneus*)

Few studies have focused on host use by *aeneus* (Friedmann 1929; Carter 1984, 1986; Sealy et al. 1997; Peer and Sealy 1999b; Chace 2001, 2004). *Aeneus* is known to parasitize nests of 95 species (Table 1.2). Friedmann (1929) noted a tendency for differential parasitism on orioles (*Icterus*). However, most subsequent studies focused on non-oriole hosts in areas where orioles were rare (Carter 1986, Peer and Sealy 1999b, Chace 2004, Sealy and Underwood 2004; but see Brush 2000). Moreover, where present, oriole nests are frequently not monitored, likely due to their placement high in the canopy (Flood 1990, Skutch 1996, Hathcock and Brush 2004). Therefore, use of orioles as hosts may be under reported and further study is required in areas where nests of orioles and other species are present to test Friedmann's (1929) hypothesis.

Aeneus breeds in sympatry with *oryzivorus* and *ater*. Because host use by sympatric *oryzivorus* and *aeneus* appears associated with body size, host overlap with *ater* may be similarly influenced. One study suggested no differential use of hosts relative to body size occurs where *aeneus* and *ater* co-occur (Peer and Sealy 1999b), whereas another did (Chace 2001). However, both studies were restricted by small sample sizes (33 and 18 nests parasitized by *aeneus*, in Peer and Sealy's (1999b) and

Chace's (2001) studies, respectively). Furthermore, the presence of *aeneus* at Peer and

Sealy's (1999b) site varies dramatically and in some seasons, few, if any individuals,

breed there (B. D. Peer pers. comm., H. R. McGaha unpubl. data). Similarly, there were

essentially no *ater* at Carter's (1986) site (only eight eggs/young were found 1980-1981).

Historically, the degree to which these two species have co-occurred has varied.

Breeding in sympatry was less common in the early 1900s than presently (Kostecke et al.

2004), but *ater* was likely more restricted within North and Central America until

relatively recently, when expansion across much of North America took place (Mayfield

1965, Rothstein et al. 1980, Rothstein1994). It is likely that Pleistocene glaciation events

(see Avise and Walker 1998) affected cowbird distribution and therefore the extent of

earlier co-occurrence is not known (Lowther 1995, Rothstein et al. 2002). Nevertheless,

throughout recent history, each cowbird species has evolved largely in the absence of

another on their breeding grounds.

Shiny Cowbird (*M. bonariensis*)

Recently, *bonariensis* has undergone the greatest breeding range expansion among

Molothrus (Cruz et al. 1998, Sykes and Post 2001). Thus, analysis of the extreme

generalist host use (up to 243 host species) by *bonariensis* must take this expansion into

account (Table 1.2). Still, the high number of hosts used within areas (Wiley 1988, Fraga

2002, Mermoz and Fernández 2003) most likely indicates generalist host use by

individual *bonariensis*, as determined genetically among *ater* (Gibbs et al. 1997). Like

oryzivorus, egg appearance in *bonariensis* is believed to vary among individuals, ranging

from immaculate to spotted (Fraga 1985). Despite differential rejection by some hosts of

immaculate versus spotted eggs, both types are laid in these nests (Mermoz and Reboreda 1999). Therefore, *bonariensis* does not appear remarkably specialized for parasitism of any particular hosts. *Bonariensis* breeds in sympatry with *rufoaxillaris* and *oryzivorus*. More recently, *bonariensis* may co-occur with *ater* in Florida (Lowther and Post 1999) and *aeneus* in Colombia (Lowther 1995).

Mason (1980, 1986a) tested whether any hosts of *bonariensis* differentially rejected *rufoaxillaris*-type eggs, thus effectively reducing competition between the two cowbirds. He found no species, through its rejection behavior, protected *bonariensis* from potential competition with *rufoaxillaris* (Mason 1986a). Likewise, *badius*, the primary host for *rufoaxillaris*, did not reject eggs representing either morph of *bonariensis* egg (spotted or not) and, thus, *badius* does not act to reduce competition between the two parasitic species. Nevertheless, *bonariensis* generally parasitizes *badius* at a lower frequency than expected, however, this may reflect poor matching for parasite-host body size (see Lichtenstein 1998) or avoidance due to low success with this species.

Brown-headed Cowbird (*M. ater*)

M. ater has been the primary subject of hundreds of studies (reviews by Lowther 1993, Ortega 1998, Hauber and Dearborn 2003). Therefore, the characterization of molothrine life-histories has been greatly influenced by studies of this species. As the northernmost of the five brood-parasitic cowbirds, *ater* ranges across numerous habitat types, where it encounters a great diversity of potential hosts and has laid eggs in nests of 239 species (Ortega 1998, Table 1.2). As mentioned, *ater* breeds in sympatry with *aeneus* and also possibly with *bonariensis* (Cruz et al. 1998).

Brown-headed Cowbirds are believed to lay far more eggs than species that nest and provide parental care, but data are mixed, as captive cowbirds, fed *ad libitum*, produced 40-77 eggs (Jackson and Roby 1992), whereas a maximum of 17 eggs/year was found among genetic-based estimates for free-ranging cowbirds (Alderson et al 1999a, Shonk 2001, Strausberger and Ashley 2003, Woolfenden et al. 2003). Differences in fecundity estimates may be due to energetic costs during reproduction, as free-ranging cowbirds regularly exhibited atretic ova (Scott and Ankney 1983, Curson and Matthews 2003), more so than non-parasitic birds (Pearson and Rohwer 1998). This may be expected, however, with increased egg production (Payne 1965, 1973; Kattan 1995; Curson and Matthews 2003). Disparity in fecundity estimates prompts debate over the degree of selectivity cowbirds exhibit when laying eggs. Several studies have found that the number of cowbird eggs per host nest did not differ from that expected from Poisson series and therefore concluded cowbird-laying does not differ from a random process (Lowther 1984, Lea and Kattan 1998). However, more community-oriented studies have suggested that despite the use of multiple hosts by individuals, cowbirds do not use nests of all species (Post and Wiley 1977, Briskie et al. 1990, Gibbs et al. 1997, Strausberger and Ashley 1997, Underwood et al. 2004, Woolfenden et al. 2004).

EVOLUTIONARY HYPOTHESES

Both Old World Cuckoos (*Cuculus* spp.) and cowbirds have been characterized as occurring at extremely different points along similar coevolutionary trajectories (Rothstein et al. 2002), such that cuckoos are highly coevolved specialists and cowbirds are generalists. However, the results of several recent studies suggest it is unclear

whether such comparisons are valid and whether wholly different trajectories are tenable. For instance, molecular genetic techniques have facilitated measurement of host use by individuals (reviewed by Sorenson and Payne 2002, Hauber and Dearborn 2003). This is central to determining how parasites and hosts have coevolved. For instance, through functional demes, called "gentes," individual cuckoos use single host species and produce host mimetic eggs whose appearance appears to be maternally determined (Gibbs et al. 2000). By contrast, individual cowbirds (*ater* and *bonariensis*) use multiple host species and lack mimetic egg types (Gibbs et al. 1997, Lyon 1997).

Lanyon (1992) and Rothstein et al. (2002) combined species' trends in the number of hosts used with re-constructed phylogenies for *Molothrus* and the Cuculinae. Lanyon (1992) proposed a phylogenetic trend concurrent with speciation (Fig. 1.4a; Lanyon 1992), whereas others favored coevolution after speciation (Fig. 1.4b; Friedmann 1929, Rothstein et al. 2002). Having established that the cuckoo clade is up to three times older than the *Molothrus* group, 6.3- 8.4 my versus 2.8-3.8 my, Rothstein et al. (2002) proposed host generalism as a shared ancestral state from which members of both groups had host number winnowed by coevolution, i.e. via cycles of improved host egg discrimination/ parasite egg mimicry (Fig. 1.1). Thus, the apparent specialism among only the basal species of *Molothrus* suggested generalists persist due to their relatively recent origins and, hence, lack of time for coevolutionary cycles with hosts. By contrast, the phylogenetic hypothesis posits a shift from specialism to generalism with each speciation event (Lanyon 1992). The hypothesis assumes a specialist ancestor from which more generalist species have been derived (Lanyon 1992, Rothstein et al. 2002).

More information is needed to compare these hypotheses. First, although
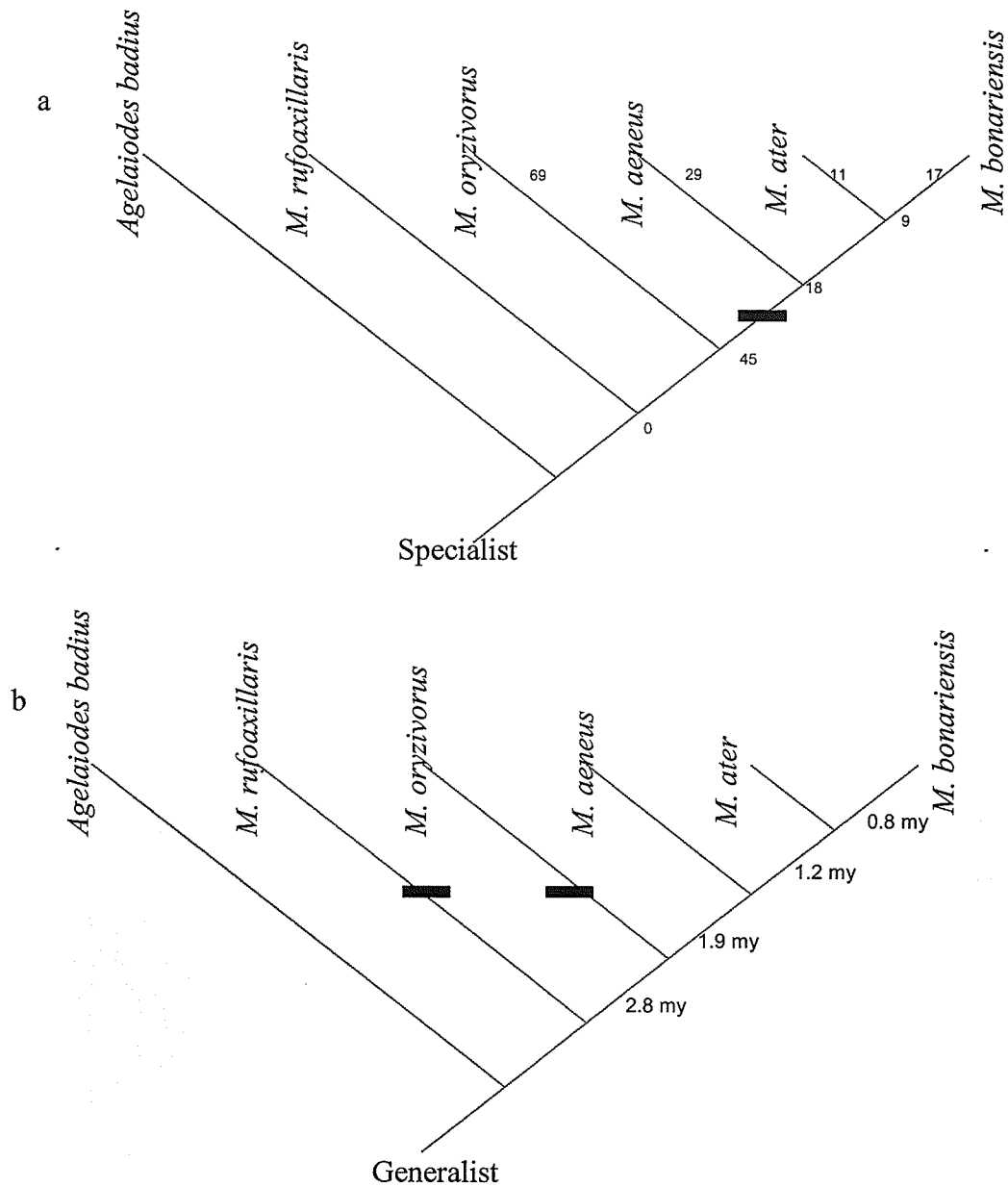
Figure 1.4. The most parsimonious evolutionary histories and transitions (solid bars) for

Molothrus based on few versus many hosts as a single character state under (a) the

phylogenetic (Lanyon 1992) and (b) coevolutionary (Rothstein et al. 2002) hypotheses.

Phylogeny based on cytochrome-*b* gene sequence (Lanyon 1992, Johnson and Lanyon

1999). Branch lengths (a) represent the result of a 250-replication bootstrap and

divergence times at nodes of (b) were estimated (*sensu* Rothstein et al. 2002).

individual cuckoos produce eggs of one maternally inherited type, one host is not always used, and in some cases poorly matching cuckoo eggs appear among hosts' eggs (Gärtner 1982, Alvarez 1999, Edvardsen et al. 2001).

In Europe, only 44% of 11,870 host clutches contained a cuckoo egg of the appropriate morph (Moksnes and Røskaft 1995). Still, 77% of the poorly matched cuckoo eggs occurred in nests of species with nest sites similar to those of the appropriate egg morph. These findings have been corroborated through studies using radio telemetry (Honza et al. 2002, Vogl et al. 2002) and molecular genetics (Sjkelseth et al. 2004), which found some individuals use more than one host species. Thus, while cuckoos are not "perfect" parasites, their use of hosts has been relatively refined by some form of imprinting on hosts or habitat (Teuschl et al. 1994, 1998, Vogl et al. 2002). This is associated with the matrilineal inheritance of genes for egg appearance (Gibbs et al. 2000) and the effects of subsequent host-parasite coevolution are clear and have accrued genetically to form gentes (Davies and Brooke 1989, Gibbs et al. 2000).

By contrast, individuals of two cowbirds, *ater* and *bonariensis*, use multiple hosts with a variety of nest sites (Fleischer 1985, Fraga 1985, Lyon 1997, Strausberger and Ashley 2003, Woolfenden et al. 2003) and do not appear to imprint on nest features as cuckoos do (Moksnes and Røskaft 1995, Teuschl et al. 1998, Vogl et al. 2002). Thus, among cowbirds, at least *ater* has not accrued genetic differences with respect to hosts as cuckoos have (Gibbs et al. 1997, 2000). Also, molothrine cowbirds frequently parasitize nests multiply (Carter 1986; Mason 1986a,b; Lea and Kattan 1998; Goguen 1999; Trine 2000) and have been described as employing random, or 'shotgun', laying strategies among hosts' nests (Rothstein 1975, Kattan 1997). Therefore, host use by cowbirds is

more generalized and few clear examples of coevolution exist (Rothstein 1990, Mermoz and Ornelas 2004).

Previously, these differences were attributed to disparate estimates of the number of eggs laid in nests by individual cowbirds, hereafter referred to as "realized fecundity" (Table 1.4). However, several genetic-based studies suggest cowbirds lay close to the same number of eggs as cuckoos (Hahn et al. 1999, Strausberger and Ashley 2003, Woolfenden et al. 2003). It would appear that reduced realized fecundity should be associated with selective host use. However, lacking constraints of imprinting (see Slagsvold and Hansen 2001) and widespread rejection by hosts, a generalist strategy may still be favored over a specialist one (Mason 1986b).

Indeed, without costs from host rejection or genetic cohesion associated with imprinting and/or inheritance of egg traits, little scope exists for specialists to derive from generalists. Differential success of either strategy would be minimized by nest predation, nest availability, and competition among brood parasites. Despite coevolved egg mimicry, individual cuckoos use alternative hosts (Moksnes and Røskaft 1995) and more than one gens and species parasitizes the same host (Higuchi and Sato 1984, Nakamura et al. 1998). Thus, provided selection against cuckoos using alternative hosts is weak, some gentes may not be selected to discriminate between hosts at the species level.

Similarly, cowbirds appear to have relatively equal reproductive success with different hosts (Kilpatrick 2002, Mermoz and Fernández 2003) and thus cowbirds may be under selection only to discriminate at a much coarser level, between certain groups of hosts. For instance, use by cowbirds does not merely reflect potential host abundance

Table 1.4. Estimates for egg production by cowbirds (number of eggs/female/breeding season). Potential fecundity is the estimated number of eggs a female may produce based on snapshot measurements of follicular development multiplied by season length. Realized fecundity represents the number of eggs successfully laid among host nests (*sensu* Hahn et al. 1999).

Maximum per year (peak rate eggs/ d)	Technique	Location	Mean season length (d)	Source(s)
Potential fecundity				
Bonariensis				
120 (0.66)	POF[a]	Colombia	182	Kattan (1993, 1997)
Ater				
30.0 (0.83)	POF	California	81	Payne (1965, 1973, 1976)
25.0		Oklahoma	85	
11.3 (0.75)		Michigan	45	
≤ 40.0 (0.79)	POF	Ontario	60	Scott and Ankney (1980)
25 – 50 (0.36-0.70)	POF	New Mexico	72	Curson and Matthews (2003)
35.2 – 49.8 (0.78)	Palpation[b]	California	60	Fleischer et al. (1987)

Maximum per year (peak rate eggs/ d)	Technique	Location	Mean season length (d)	Source(s)
16.4 (0.18 - 0.91)	Captivity	Illinois	68	Jackson and Roby (1992)
26.3 (0.09 - 0.87)	Captivity	Illinois	89	Holford and Roby (1993)
Realized fecundity				
ater				
8.2	Genetic [c,d]	New York	60	Hahn et al. (1999)
13	Genetic [e]	Illinois	81	Strausberger and Ashley (2003)
16	Genetic [b,e]	Manitoba	50	Woolfenden et al. (2003)
17	Genetic [d,e]	Manitoba	50	Shonk (2001)

[a] Intact and ruptured post-ovulatory follicles (post-mortem) averaged across specimens.

[b] Oviducal eggs felt by hand in live birds.

[c] Maternal assignment using DNA fingerprinting; fecundity estimate corrected with point-count density data.

[d] Females radio-tracked.

[e] Maternal assignment using microsatellite DNA loci.

(Post and Wiley 1977, Barber and Martin 1997, Strausberger 1998, Grant and Sealy 2002, Woolfenden et al. 2003) and in some communities, the use of inappropriate hosts apparently has declined in response to poor reproduction using them (Table 1.5).

Origins of Specialism

Based on species' current patterns of host use, it is unclear whether ancestral brood parasites were generalists or specialists, or even whether all species evolved similarly from one state to the other. Thus, discussion of such trends is largely semantic; however, the directionality of each hypothesis differs and therefore they may be contrasted. The coevolutionary hypothesis is rooted in a transition from generalism to specialism and the phylogenetic hypothesis predicts the reverse. The coevolutionary hypothesis is favored over the phylogenetic explanation because it provides a mechanism for evolutionary transition and does not relegate number of host species to a phylogenetic character in the quantitative sense, i.e. it posits a shift from qualitatively less to more specialized rather than considering host number *per se* (Rothstein et al. 2002).

Nonetheless, the most basal and specialist cowbirds and their hosts do not clearly exhibit the traits expected during a coevolutionary arms race that has winnowed host numbers. Instead, *rufoaxillaris* is reared by alternative hosts and its primary host(s) care for non-mimetic eggs and young (Fraga 1998, Mermoz and Fernández 2003). Because *rufoaxillaris* is equally successful parasitizing nests of *badius* (Fraga 1998), Brown-and-yellow Marshbirds (Mermoz and Fernández 2003), and Chopi Blackbirds (Sick 1993, Fraga 1996), the remarkable nestling similarity between *rufoaxillaris* and *badius* young may be a secondarily derived trait rather than one associated with exclusive

Table 1.5. Low use of some potential hosts relative to others associated with poor cowbird reproductive success. For rejecting species, use may be under-estimated as rejected eggs may not be detected by observers (Scott 1977).

Species	Use by *ater* This spp.	Other spp.	Cowbird Success [a]	Presumed Mechanism	Source
Eastern Kingbird	< 5% (279)	12 - 64% [b]	Poor	Rejection	Sealy and Bazin (1995)
Brown Thrasher	1 % (525)	Common	Poor	Rejection	Goertz (1977), Haas and Haas (1998)
House Wren	0.2 % (900)	Common [c]	Poor	Poor Host	Pribil and Picman (1997)
American Robin	4 % (92)	Common	Poor	Rejection	Lowther (1981)
Northern Mockingbird	0 % (607)	5-70 %	Poor	Rejection	Goertz (1977)
Gray Catbird	5 % (101)	10-80 %	Poor	Rejection	Neudorf and Sealy (1994)
Bullock's Oriole	9 % (34)	Common	Poor	Rejection	Friedmann and Kiff (1985)
House Finch	≈ 0%	Common	Very poor	Seed Diet	Friedmann and Kiff (1985)
American Goldfinch	6 % (802)	Common	Very poor	Seed Diet	Middleton (1991)

[a] Fledging information from cited source and/or Friedmann and Kiff (1985).

[b] Neudorf and Sealy (1994) and Underwood et al. (2004).

[c] Burgham and Picman (1989).

use due to a lack of alternative hosts.

Alternatively, I suggest that host specialization within *Molothrus* resulted from a form of host imprinting which subsequently weakened or was lost among the generalists (Figs. 1.3, 1.4). Evidence for a link between specialist use by obligate brood parasites and imprinting is clear among *Cuculus* cuckoos, viduine finches, and perhaps honeyguides (Indicatoridae) that imprint upon aspects of their fosterers, and/or natal habitats/nests (Wyllie 1981, Brooker and Brooker 1992, Moksnes and Røskaft 1995, Teuschl et al. 1998, Vogl et al. 2002, Sorenson et al. 2003, Skjelseth et al. 2004). Indeed, some amount of host-imprinting should be expected as a similar process is common for species recognition among the non-parasitic ancestors of brood parasites (Hamilton and Orians 1965, Rothstein and Robinson 1998, Slagsvold and Hansen 2001).

For *Molothrus*, imprinting would have been lost, possibly through selection for generalism (see Chapter 2), among the more recently derived members (Fig. 1.4) as in the obligately parasitic Black-headed Duck (*Heteronetta atricapilla*) (Weller 1968) and facultatively parasitic ducks (*Aythya*: Mattson 1973, Eadie et al. 1998). This hypothesis de-emphasizes coevolution, which indeed may be a secondary process that undoubtedly has refined host use for some species, however, it favors the evolutionary history that Lanyon (1992) posed (Fig. 1.4a). Recent studies that have found Common Cuckoos laying in nests of more than one species strongly suggest that cuckoo egg appearance reflects an amalgam due to egg discrimination by more than one species of host (Edvardsen et al. 2001, Honza et al. 2002, Vogl et al. 2002). Cuckoos produce eggs that poorly match those of some hosts (Edvardsen et al. 2001), yet these eggs of the 'wrong'

type are accepted. Thus, because host discriminatory abilities vary, cuckoos may be viewed as more generalized than commonly believed.

Based on host- or habitat-imprinting, selection would have resulted in the cuckoo gentes/races we recognize today. Coevolution would have played a more secondary role, such as enhancing parasite mimicry of host eggs or young. Genetic differentiation of gentes and races would have occurred via the genetic cohesion implicit in imprinting and maternally linked genes for egg appearance under selection from hosts (Davies and Brooke 1989, Gibbs et al. 2000). To apply this model to *Molothrus*, we must consider evolutionary pathways to generalism as a derived state.

The assumption that *rufoaxillaris* imprints on its hosts appears a reasonable explanation for the use of one primary host species. Host number for the nearest molothrine relative, *orizyvorus*, is limited by the cowbird's size (126 g, Dunning 1993) and, thus, the use of few hosts may or may not involve some form of post-natal imprinting. By contrast, the three generalist cowbirds, *aeneus*, *ater* and *bonariensis*, are distinct from other brood parasites because they do not imprint upon hosts or nest and habitat types (Lyon 1997, Hahn et al. 1999, Strausberger and Ashley 2003, Woolfenden et al. 2003, Chapter 2). Therefore, they lack within-species genetic cohesion associated with using a certain host or group of hosts (Gibbs et al. 1997). Theoretically, lacking genetic cohesion and, hence, maintaining far greater population sizes (Fig. 1.5), coevolution among generalist cowbirds and their hosts would take much longer to occur (Nakamura et al. 1998). I suggest that *rufoaxillaris* is in a dynamic specialization with its hosts and thus has not attained a high degree of egg mimicry or genetic differentiation between individuals using different hosts. Imprinting could be tested by determining
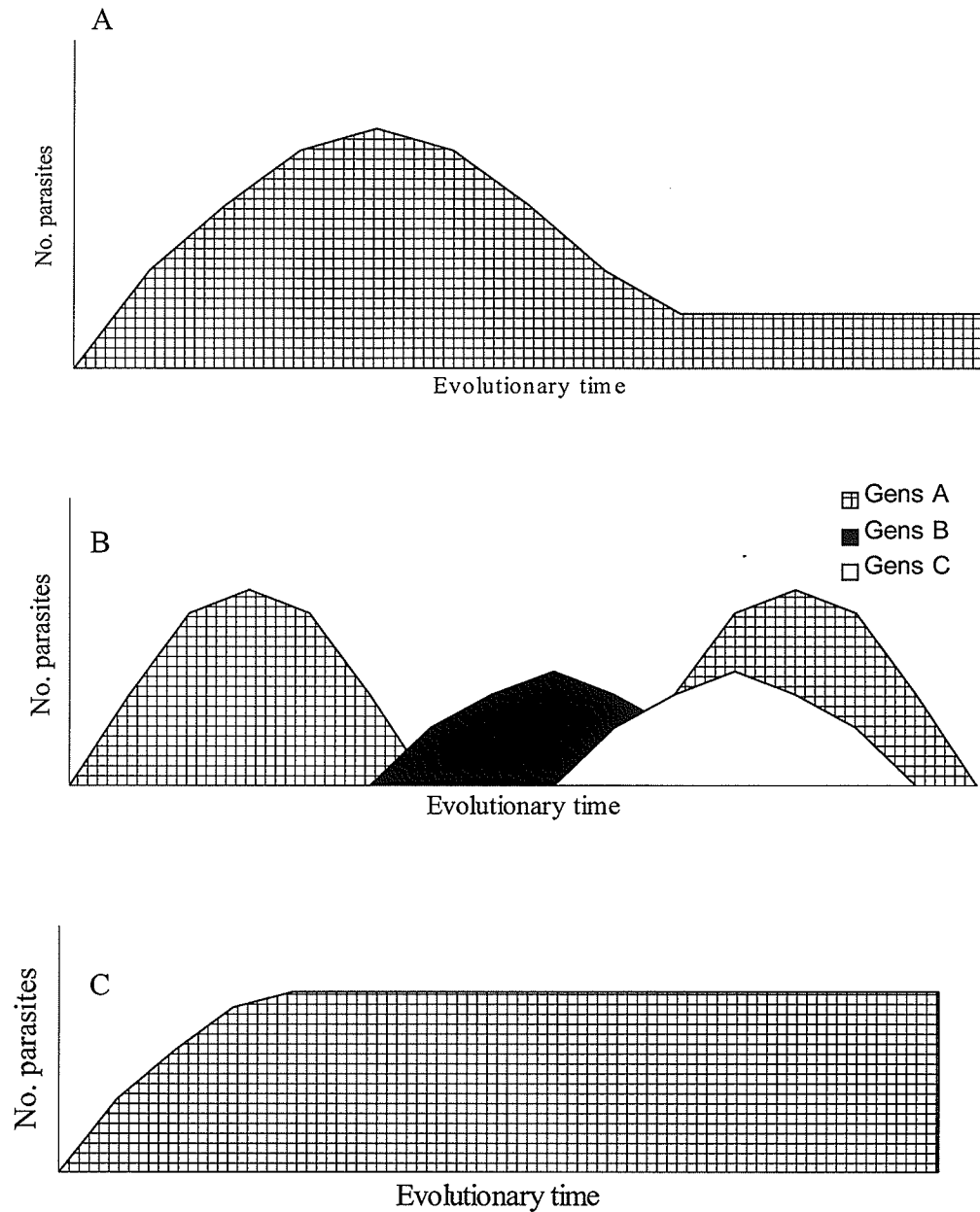
Figure 1.5. Theoretical models for parasite population size relative to host use (after

Nakamura et al. 1998). A. Stable specialization: represents Common Cuckoo use of one

gens with population reduction due to coevolutionary arms race. B. Dynamic

stabilization: parasite success changes with time and parasites switch between gentes. C.

Lack of coevolutionary arms race: parasite population size determined by factors other

than host behavior.

whether individuals use multiple hosts or via cross-fostering and choice tests (*sensu* Brooke and Davies 1991).

Data suggest that, ultimately, cowbirds should reduce the number of host species, given time for coevolutionary relationships to evolve (Rothstein et al. 2002). However, several field studies suggest that host use depends more on proximate features outside the context of those explicitly related to coevolutionary histories (Wiley 1985; Mason 1986a,b; Cruz and Wiley 1989) and that some specialists (more basal species) can benefit by adding hosts (Fraga 1998, Mermoz and Fernández 2003). Thus, if *rufoaxillaris* became a specialist through coevolution, some hosts have lost their defenses and are parasitized today, i.e. step 3 of Fig. 1.1 is reversible. Because this is unlikely, I suggest that host selectivity is not a unidirectionally evolving character that ultimately arrives at specialism, rather, more generalist use may reflect an evolutionarily stable state.

Thus, cowbirds are either at a more primitive state within a coevolutionary process (i.e. step 1, Fig 1.1), or host use by specialists may not be restricted by coevolution, i.e. alternative hosts can be used successfully. Generalists might be equally as selective of hosts as specialists, but use multiple hosts due to benefits associated with generalism (i.e. greater nest availability numerically and temporally). In essence, host use by generalist cowbirds may reflect strategies without genetic constraints of host or nest-site imprinting. This hypothesis would be supported if generalist cowbirds were capable of more specialized host use and could occur without step 2 (Fig. 1.1).

I tested the theoretical conditions for the sustainability of each strategy (Chapter 2). Specifically, I modeled the fitness gains made by specialists versus generalists. Next, I compared the theoretical success of generalists with empirical data and then determined

whether two sympatric, generalist cowbirds were capable of non-random and differential

host use at both the population and individual level, as revealed using molecular genetic

techniques (Chapters 2 and 3). The analyses also tested whether individual *aeneus* used

multiple host species. I also tested whether host use matched predictions from

estimations of host provisioning abilities (Chapter 3) and competition models among

sympatric populations of *ater* and *aeneus* (Chapter 4). Likewise, I tested whether the two

cowbirds selectively placed their offspring among host nests. Because cowbirds are

generally sexually size-dimorphic (Table 1.2), placement of eggs of each sex with hosts

of certain sizes may improve an individual's intrinsic reproductive success (Weatherhead

1989). Therefore, I tested whether eggs for either sex were differentially placed with

certain-sized hosts (Chapter 5). In Chapter 6, I summarize the implications of my

findings for hypotheses explaining host use by brood parasites.

CHAPTER 2. THEORETICAL ANALYSIS OF THE EVOLUTION OF HOST GENERALISM AMONG BROOD PARASITES

Host use by brood-parasitic cowbirds ranges from specialism on one primary host to the generalist use of more than 90 hosts (Lowther 1993, 1995; Lowther and Post 1999). Lanyon (1992) proposed that the positive correlation between host number and divergence time were causally related, with generalism the derived condition. By contrast, Rothstein et al. (2002) hypothesized that coevolution between parasites and hosts accounted for the decreasing trend in host diversity found in progressing from the more basal to the more specialized species. Because Rothstein et al. (2002) suggested that brood parasites tend to become host specialists over time, under their hypothesis, host generalism may be viewed ultimately as an evolutionarily unstable state in which populations of generalists could be invaded by specialists. However, at what point would generalism become disadvantageous?

Rothstein et al. (2002) predicted that cowbirds will be forced to coevolve with hosts given adequate time for host defenses to evolve. However, few potential cowbird hosts currently reject parasitism, although this may reflect an evolutionary equilibrium with costs of rejection (Spaw and Rohwer 1987; see reviews by Rothstein 1990, Hosoi and Rothstein 2000, Underwood 2003). Moreover, after some 2.8 million years, the most basal molothrine, *rufoaxillaris*, is reared by multiple alternative hosts (Mermoz and Fernández 2003) and its eggs are not discriminated against by its primary host (Mason 1980, 1986a; Fraga 1983, 1998). Thus, with respect to host use, cowbirds may be more similar to parasitoid insects, for which models and empirical data show prevailing

strategies are context-dependent such that either specialism, generalism, or mixed strategies may be selected (Hassell and May 1986, Bonsall et al. 2002).

Because of the fluctuating payoffs during parasite-host coevolutionary cycles and the availability of alternative hosts, the time required for specialization to evolve may be greater than suspected previously (Takasu 1998, Rothstein et al. 2002). Indeed, generalists can benefit from greater nest availability, both numerically and temporally, across host populations. Thus, any benefits to *rufoaxillaris* from coevolved mimicry (improved chick rearing by its primary host, *badius*) may be outweighed by the availability of equally capable hosts and the specialist may not be limited by constraints from coevolution (Fraga 1998, 2002; Mermoz and Fernández 2003). This raises questions for the ancestral state of molothrine host use. Specifically, would a generalist be derived from a more specialized ancestor, as proposed by some authors (Fig. 1.4a; Friedmann 1929, Hamilton and Orians 1965, Lanyon 1992)? Is specialism derived through coevolution (Rothstein et al. 2002) (Fig. 1.4b)? Likewise, is host use even evolutionarily labile? Or is host use a relatively inflexible trait limited by processes such as egg appearance or host imprinting (see Slagsvold and Hansen 2001)?

I have employed theoretical models to examine payoffs to different strategies to determine the contexts that favor each. Such information may elucidate whether either transition, specialism to generalism, or the reverse, is more probable. Theoretically, transition costs may vary such that host-parasite lag may be prolonged or interminable. Such analyses are equally tenable describing competing strategies between species or individuals. Thus, coexistence of parasitic strategies may also occur, as for insect

parasitoids (Hassell and May 1986) or conspecific brood parasites (Lyon 1997, Broom

and Ruxton 2002).

To test the factors contributing to strategy stability, I used empirical data to

compare the profitability of specialist versus generalist parasitic strategies. I contrasted

potential fitness gains from specialist and generalist strategies based upon data collected

on a host community exposed to two parasites, Brown-headed and Bronzed cowbirds. To

sample fitness gains for cowbirds, I tracked host use by individuals using variable genetic

markers. Thus, I determined whether both species were composed of generalists and

generated estimates for annual reproductive success of the observed strategies. I

reasoned that if specialism was to become favorable, potential gains must at least

approach those for generalist strategies.

METHODS

THEORETICAL ANALYSIS

Model

To determine the stability of generalist versus specialist strategies, I compared population

dynamics for each strategy based on the basic equations from May and Robinson (1985):

$$\textbf{Specialist: } S_{t+1} = (1-\mu_S)S_t + \lambda_S(1- \exp(-aS_t))H_t \qquad (1)$$

$$\textbf{Generalist: } G_{t+1} = (1-\mu_G)G_t + \lambda_G(1- \exp(-bG_t))H_t + AP \qquad (2)$$

$$\textbf{Host: } H_{t+1} = (1-\mu_H)H_t + \lambda_H\exp(-aS_t)H_t + \lambda_H\exp(-bG_t)H_t \qquad (3)$$

where $(1-\mu)$ represents proportional adult survival from t to t+1 and the terms $\exp(-aS_t)$

and $\exp(-bG_t)$ represent the probabilities that nests escape parasitism by specialists and

generalists, respectively. Encounter rates with hosts (searching efficiencies) are reflected

by 1-exp(-aSt) and 1-exp(-bGt), which depend proportionally upon population sizes for each group, hosts (H), specialists (S) and generalists (G).

When not parasitized, I assumed that hosts produced four host young and when parasitized, only one parasitic young. These values represent modal productivity levels for small hosts (see May and Robinson 1985, Pease and Grzybowski 1995). This assumption was varied when testing effects of coevolution. I also assumed the primary host population was limiting to the specialist parasite, whereas the host pool for generalists was supplemented via an alternative host pool term (AP). Potential gains from AP were held constant, ignoring effects of coevolved defenses or density-dependent changes in population sizes. This simulated a generalist's capability for switching hosts and maintaining relatively equal fitness (Mermoz and Fernández 2003, Mermoz and Reboreda 2003). Specialist payoffs (λ_S) were varied relative to those for generalists (λ_G) to represent periods of coevolution, i.e. host defenses and specialist counter-measures such as mimicry (Davies and Brooke 1989).

I assumed each parasite reproduced during discrete periods, with specialists acting prior to generalists within each time interval (*sensu* Hassell and May 1986). Whereas this misses a potentially important interaction, particularly where potential competition among offspring could occur, it is a more simple system to consider. Moreover, while the dynamics may differ using discrete intervals, the analysis provided a conservative test of whether a generalist strategy can invade a specialist one – the species acting second in time, in this case the generalist, is at a disadvantage.

Invasion Analysis

Coexistence can only occur provided each strategy can invade the other at some level and vice-versa. Individuals practicing a strategy can only invade if population growth can result when rare. Therefore, I examined the threshold conditions for which coexistence could occur. First, I assessed the conditions under which generalists could become established when specialists predominate and vice-versa. This would simulate a mutation of a specialist into a generalist using an alternative host at payoff of P equal to use of the primary host, because alternative hosts have not been exposed to parasitism and therefore the significance of host defenses should be diminished.

Next, I considered two likely stages during a continued, prolonged association between specialists and hosts (Fig. 1.1). Specifically, I considered the impacts of coevolution as 1) hosts could develop defenses, i.e. egg discrimination, which in turn alter payoffs to parasites, eventually resulting in a counter-defense by specialists, i.e. egg mimicry as part of a coevolutionary arms race (Rothstein 1990). Thus, the probability generalists would coevolve with specific hosts could be diminished, provided new and non-discriminatory hosts are continuously available. Such host-switching has been suggested to have occurred among cowbirds (Peer and Bollinger 1997, Rothstein 2001, Peer and Sealy 2004a) and has been observed among cuckoos (*Cuculus*: Nakamura et al. 1998, Gibbs et al. 2000, and possibly, *Clamator*: Soler et al. 2003 and *Chalcites*: Joseph et al. 2002).

STRATEGY COMPARISON WITH EMPIRICAL DATA

Study Site

I measured host use by cowbirds during four breeding seasons (1999-2002) at Ft. Clark

Springs, Brackettville, Kinney Co., Texas (29°18′N, 100°43′W). Both cowbirds have

co-occurred in the area for more than 50 years (Oberholser 1974). I measured host use in

two ways: I used microsatellite DNA loci to identify eggs laid by different individuals

and, to increase sampling of potential hosts, I monitored nests and host-fledgling groups

in areas surrounding the core where clutches were not manipulated. Because the genetic

study involved destruction of eggs to obtain DNA, the two methodologies were applied in

different plots (Fig. 2.1). All cowbird eggs were collected from nests located through

systematic searches within a 27-ha "core" area (Fig. 2.1). Specifically, searching was

focused by comparing areas without known nests and territories identified through

bi-weekly mapping of songbird locations.

The core consisted of a manicured golf course dominated by trees < 7 m tall

(honey mesquite (*Prosopis glandulosa*), huisache (*Acacia farnesiana*), and *Acacia* spp.).

Cowbird productivity was measured in surrounding areas within 2 km of the core area.

Because the genetic analysis involved switching cowbird eggs with model eggs (details

below), I did not manipulate cowbird eggs in any nests for one season (1999) as a control.

Thus, data collected on cowbird productivity in 1999 were for both the core and

surrounding areas.

The surrounding areas were a mixture of residential lots, riparian woodland of

Texas live oak (*Quercus virginiana*) and pecan (*Carya illinoensis*), and Trans-Pecos

brushland with mostly < 4-m honey mesquite and 1-m tall grass understory. All nest and
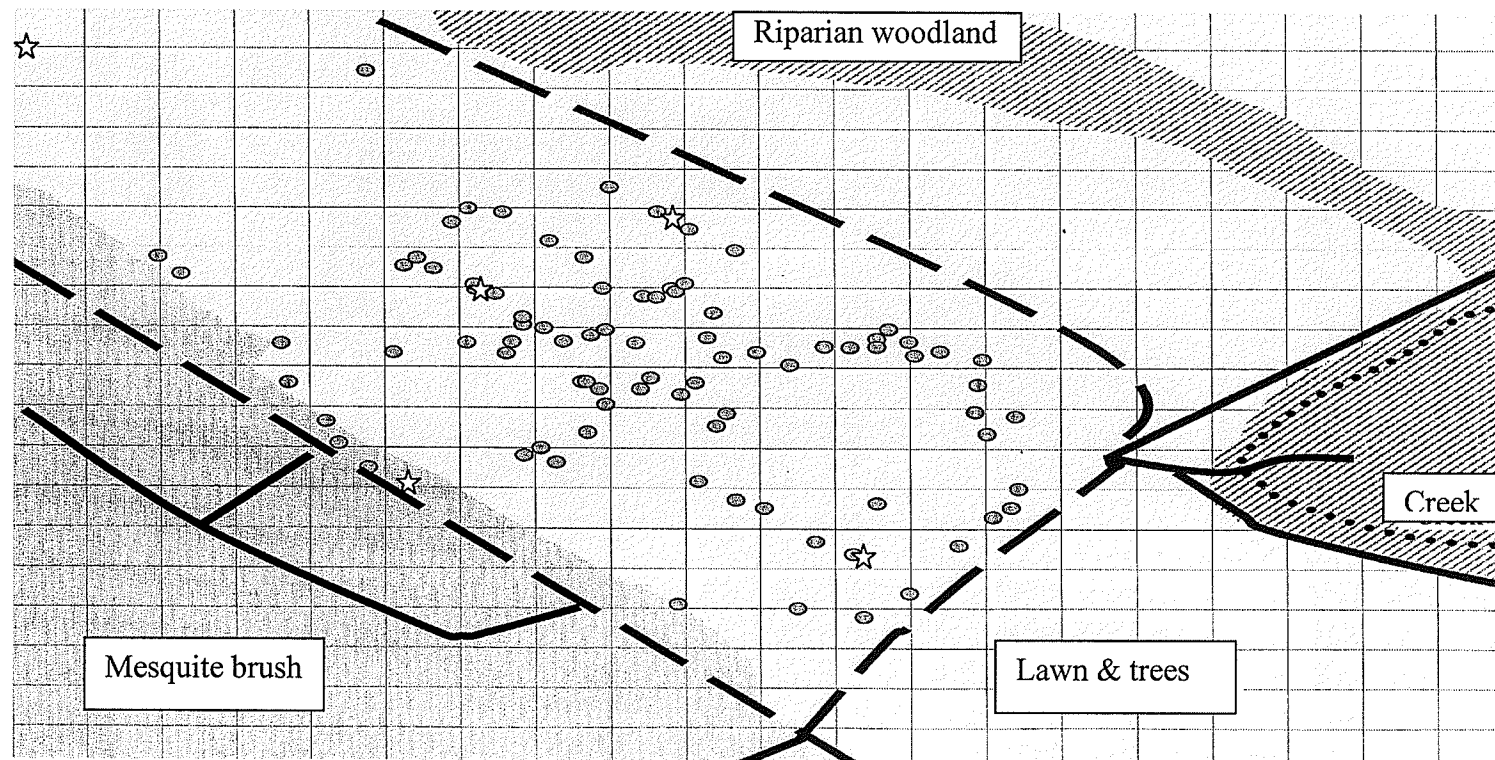
Figure 2.1. Core area (within broken lines) for cowbird egg collection 2000-2002, Ft. Clark Springs Golf Course, Brackettville, Texas. Brushy habitat (shaded areas) contrasted the manicured lawn and ornamental plantings (unshaded). Trees in the core are represented by circles, roads by solid lines and re-sighting locations by star symbols. Each portion of grid equals 50 m^2.

bird locations were mapped based on conspicuous golf course landmarks and Universal

Transverse Mercator coordinates recorded using a Garmin eTrex ® Global Positioning

System device.

Host Use

The number of cowbird eggs/young per nest was recorded among nests within the core

area. My primary objective was to collect all cowbird eggs laid within the core.

Therefore all songbird nests within the core were checked daily during 6-10 d periods

centered on the potential hosts' first egg day, i.e. from three days prior to egg day one

through two days beyond clutch completion. I monitored nests in the core intensively to

detect the use of species that may reject cowbird eggs. Therefore, I watched or video-

taped nests of potential hosts prior to sunrise, the time of day that cowbirds lay (Scott

1991, Neudorf and Sealy 1994, Peer and Sealy 1999a). I also checked the contents of

nests within 10-30 min of sunrise to further minimize chances of missing any cowbird

eggs that were laid (Scott 1977). I listed all common and scientific names for birds

mentioned from this point in Appendix 3.

IDENTIFICATION OF EGG-LAYING INDIVIDUALS

Cowbirds were captured in seed-baited walk-in traps and uniquely color-banded and

blood sampled. DNA was obtained from adult/young blood samples and eggs collected

from host nests. Cowbird eggs found on the rim of or directly below nests were included

in the genetic analysis as a representation of host use. Cowbird eggs were collected upon

detection as a hedge against destruction by predators or damage by cowbirds and were

substituted with painted wooden eggs of similar mass, dimensions and appearance (see

Peer et al. 2002). Model eggs were substituted for each cowbird egg to maintain volume

of host clutches and visual presence of egg(s). Host use in 1999 was monitored without

egg collection, hence, no egg models were placed in nests. This was necessary as model

eggs could affect cowbird behavior at nests, i.e. they cannot be punctured (Massoni and

Reboreda 2002) or their appearance may affect the probability of subsequent parasitism

(see Ortega et al. 1994, Strausberger and Ashley 1997). To test whether model cowbird

eggs affected multiple parasitism, I compared rates of multiple parasitism during the

control and treatment years. It is unlikely that the hatching success of host clutches was

affected when accompanied by model eggs versus real cowbird eggs (Ortega et al. 1994).

More so, because all host nests received the same type of model eggs, hatching success

among host nests is relative.

The number of cowbirds laying within the egg-collection plot was determined by

comparing adult and offspring microsatellite DNA loci (Alderson et al. 1999a,

Woolfenden et al. 2002). Collected eggs were artificially incubated 3-5 d and then stored

at -20°C. DNA was extracted from embryos and shells (*sensu* Sambrook et al. 1989) to

yield maternal (shell) genotypes and paternal haplotypes (non-maternal half of embryo

genotype) (Alderson et al. 1999a, Strausberger and Ashley 2001). Samples were PCR

amplified and genotyped at four to five microsatellite DNA loci using polyacrylamide gel

electrophoresis and autoradiography. Also, for one locus, Maµ.16, amplified DNA was

quantified by automated sequencing on an ABI 310 Genetic Analyzer® with

fluorescently labeled primers (Longmire et al. 2001, Strausberger and Ashley 2001).

Likelihood of parentage was determined using observational data, because each cowbird

can lay only one egg per day (Payne 1976, Sturkie 1976), therefore, simultaneous laying

dates represented eggs laid by more than one female. I also used the PARENTAGE and

KINSHIP (Goodnight and Queller 1999) programs (see Alderson et al. 1999a,b) to

statistically assign parentage based on genetic data. PARENTAGE excludes

non-matching candidate genotypes to yield high resolution parentage assignments (see

Chakrabroty et al. 1988, Alderson et al. 1999a). KINSHIP calculates relatedness

likelihood values (Goodnight and Queller 1999). I used KINSHIP to identify half- and

full-siblings and to determine the likelihood that eggs were laid by the same or different

females (*sensu* McLaren et al. 2003).

ESTIMATION OF PRODUCTIVITY

For estimation of cowbird productivity, I considered the frequencies of hatching, survival

and host rejection of cowbird eggs. Hatching and survival data were collected by

monitoring host nests, within the core area in 1999 and outside the core 2000-2002. I

estimated fledging success by reducing the total number of cowbird eggs laid per host by

the percentages of eggs not hatching and of nests not fledging due to predation or

abandonment. Thus, I reasoned the ratio of fledglings per eggs laid represented an

unbiased, relative estimator for comparisons of cowbird reproductive success among

hosts.

Few potential hosts at my site are known to reject cowbird eggs. Of those

commonly used, only the Bullock's Oriole is known to eject foreign eggs (Rothstein

1977, Rohwer et al. 1989, Sealy and Underwood 2004). Studies of host egg rejection

behavior were restricted to those involving responses to eggs of *ater*, however, I

considered responses to eggs of *aeneus* would be similar to those measured for eggs of

ater. I assumed this because species that lay spotted eggs reject immaculate eggs more readily than spotted ones (Peer et al. 2002). My 1999 data suggested that the Bullock's Oriole was the only host species to reject cowbird eggs (n = 2 cases, *aeneus* eggs). This conformed to the findings of Rohwer et al. (1989) who found that Bullock's Orioles reject foreign egg types as well as those of *ater* (see Sealy and Underwood 2004 for a review of egg rejection/acceptance by orioles). Moreover, I assumed any differences in egg acceptance would be detected through monitoring nests during the period for laying by cowbirds.

To assess cowbird productivity, within the surrounding area, I searched for nests and cowbird young with an emphasis on locating young cowbirds. Fledglings were watched until fed to identify their hosts. Although Sealy and Lorenzana (1997) cautioned against such a criterion for identifying hosts, the low frequency for feeding of cowbirds by non-fosterers suggests any effects of this error type would be negligible for a broad survey for fledglings. Furthermore, the relatively few records (2%, n = 519) for *Molothrus* fledglings fed by species other than their fosterers (Sealy and Lorenzana 1997) are greatly outnumbered by the usual case, in which cowbirds are fed by their fosterers (100%, n = 14; see also Eastzer et al. 1980, Woodward 1983, Smith and Arcese 1994).

Host Quality, Availability and Use

I estimated relative host quality to cowbirds on the basis of fledging success. Nest availability was estimated through daily systematic searches of the core area calibrated with bi-weekly spot-map censuses of songbirds (i.e., if a territory was delineated via census, then a nest was searched for in that area). Host use was determined through the

detection of cowbird eggs in nests. To minimize the potential bias of missing cowbird eggs in nests of species that often eject cowbird eggs, nests of these species were observed or video-taped during normal periods for cowbird laying. When cowbirds were detected near nests, the nests were observed continuously until their contents could be checked, in ≤ 10 minutes. Continuous observation allowed me to verify that any cowbird eggs laid were not removed by subsequent visits by any birds.

THEORETICAL STRATEGIES BASED ON EMPIRICAL DATA

I considered that historically, individual cowbirds may have employed one or more of the following strategies:

Specialist- use of one species' nests regardless of availability,

Generalist- random selection of nests during each time interval,

Restricted generalist- selection of nests within a restricted suite of hosts,

Optimal - selection of *one* host, the most profitable available each time interval. Therefore, I estimated the expected payoff for each host nest on the basis of availability of each species' nests and average fledging success. I then compared potential "paths" of host use during five-day periods. An optimal path yielded the highest possible reproductive success among nests available. Random paths were generated using a random number generator and were constructed across all available nests as well as among restricted pools of focal host species (Table 2.1). Focal species of hosts were those that received most cowbird eggs (see Table 2.1).

Table 2.1. Sample calculation of arbitrary payoffs for different strategies with three hypothetical hosts. Host A is the most profitable, yet least available, in contrast to the poorest host, C, that was always available.

5-d interval	Payoff per parasitized nest (in young)			Payoff obtained under each strategy			
	Host species			Specialist on host A	Random generalist	Restricted generalist [a]	Optimal generalist [b]
	A	B	C				
1	0.39	0.14	0.14	0.39	0.14	0.14	0.39
2	0	0.14	0.14	0	0.14	0.14	0.14
3	0.39	0	0.14	0.39	0.39	0.39	0.39
4	0	0	0.14	0	0.14	0	0.14
Total	0.78	0.28	0.56	0.78	0.81	0.67	1.06

[a] Determined as the average payoff obtained using only hosts A and B.

[b] Calculated as the use of the species with the highest payoff among those available each five-day interval.

RESULTS

THEORETICAL ANALYSIS

Assuming similar mortality and payoffs when hosts are parasitized, specialists can only

persist if their ability to find hosts exceeds a threshold near or above that for generalists.

Because equilibria occur when Eqn. 1 equals Eqn. 2, i.e.

$$S^* = (1-\mu_S)S_t + \lambda_S exp(-aS_t)H_t = (1-\mu_G)G_t + \lambda_G exp(-bG_t)H_t + AP = G^*,$$

the equilibrium can be abstracted as the searching efficiencies for each strategy (as α

and β replacing the $exp(-bx_t)H_t$ terms) and the alternative host pool, such that $\alpha = \beta + AP$.

Therefore, to be sustainable, the generalist strategy must yield enough benefits from the

alternative pool to offset the specialists' success with the primary host (Fig. 2.2).

Provided generalists used 15% of the primary hosts' nests, equilibria occurred when use

of AP was at 80% use of one alternative host species to 20% use of 2 species (Figs. 2.2,

2.3). The full range of equilibria obtained are presented in Figure 2.4.

The population model suggested either strategy was sustainable when alone or at

co-occurrence of certain levels. Host-parasite coexistence was maintained across a

relatively narrower range of parameter values for populations containing mixed strategies

relative to populations containing only a single strategy. Compared to specialism,

generalism was sustainable across a wider range of conditions. Specialists were more

sensitive to changes in primary host abundance, whereas generalists exhibited broader,

gentler cycles as the alternative hosts buffered them from changes in primary host

availability. Variation of parameters revealed specialists were most sensitive to changes

in payoffs with the primary host, and hence, conditions for coexistence depended on the

payoffs provided by the primary host and its use by generalists (Fig. 2.4). The specialists
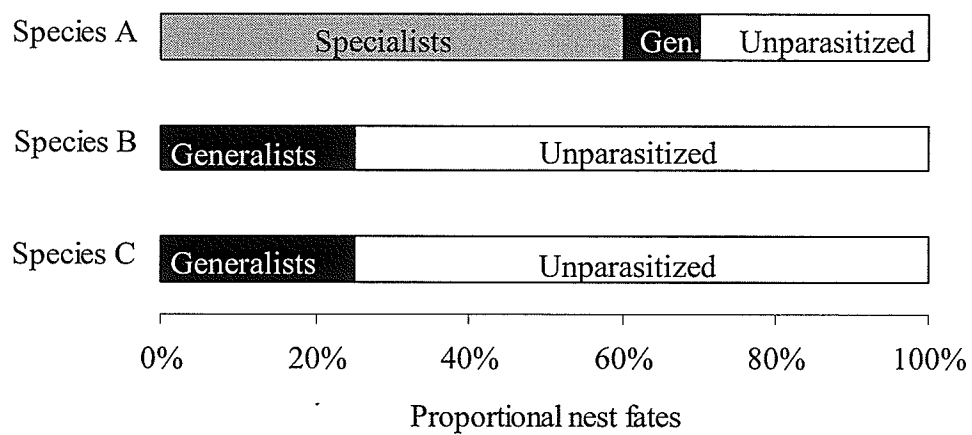
Figure 2.2. Theoretical representation of proportions of used and unused nests at equilibrium, assuming equal payoff for use of each host. Species A represents the primary host.
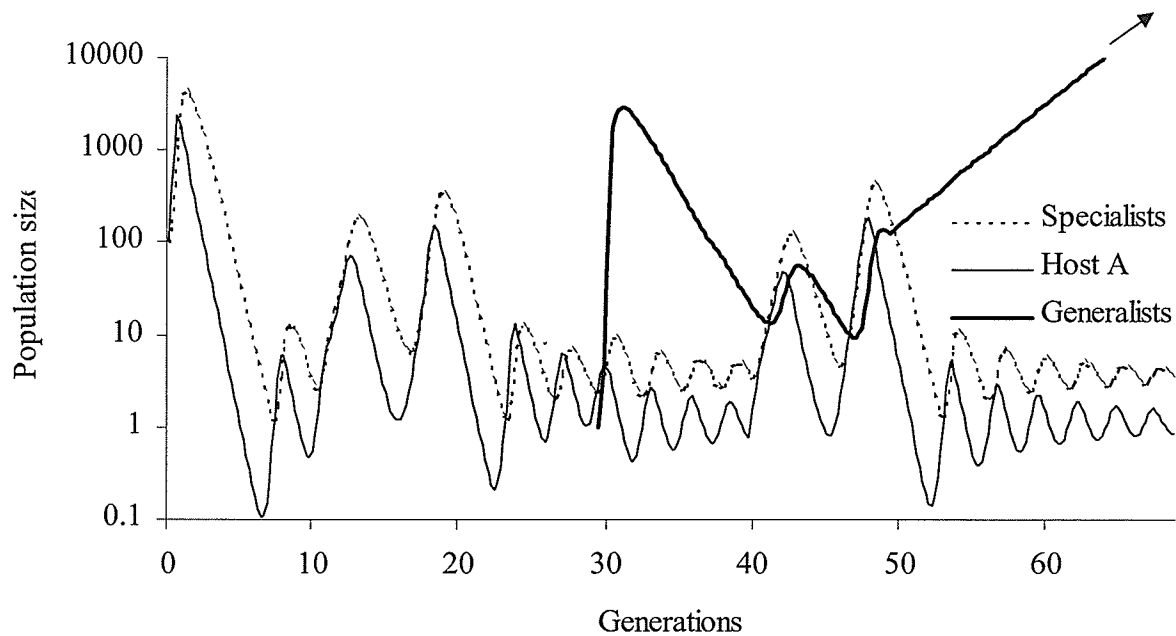
Figure 2.3. Population dynamics for each strategy assuming one host for specialists and a constant pool of alternative hosts available for generalists. The alternative hosts keep the generalist from extinction and experiencing density-dependence (exponential growth denoted by arrow), whereas specialists cycle at low levels with their only host.

A
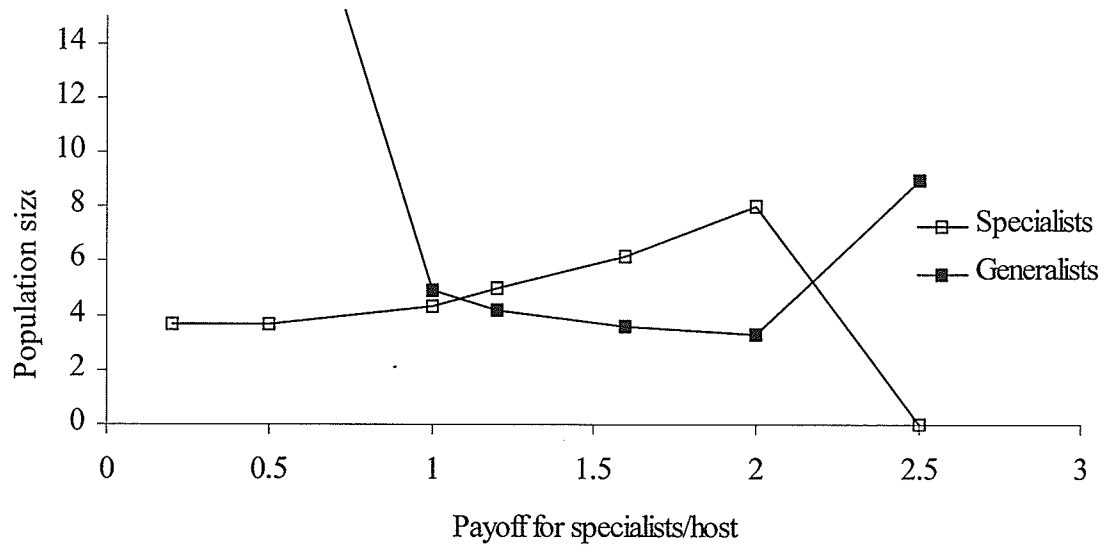
B
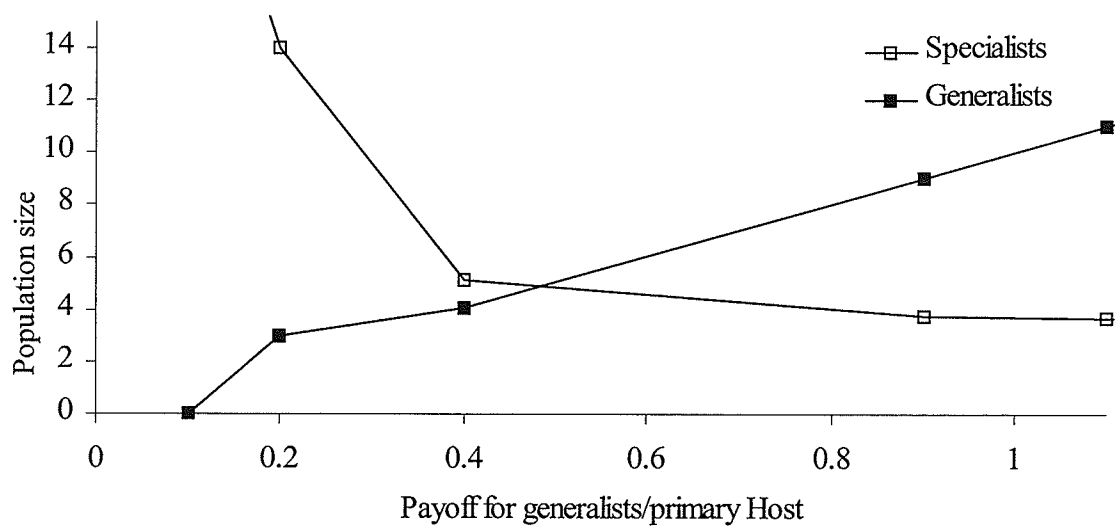
Figure 2.4. Equilibrium population sizes among competing strategies when varying the reproductive success for A) specialists or B) generalists with the primary host.

failed at levels of high and low success with hosts, whereas generalists persisted across all levels of payoff to specialists. Thus, generalists exhibited a wider range of stability and failed only at low levels (< 0.1) of success with the primary host.

Shifting Equilibria During Coevolution

Coevolution is initiated with hosts first gaining an advantage through a defense that counters the effect from another (Fig. 1.1, Step 2). Thus, when parameters were altered to reflect reduced reproductive payoffs for specialists and generalists with the primary host, both strategies were similarly affected and equilibria simply shifted to lower levels. However, once payoffs to specialists were modified to reflect counter-defenses (Fig. 1.1, Step 3) by the specialists, new equilibria resulted. During Step 3, specialists persisted at higher levels, however, generalists still dominated the system (Fig. 2.4).

STRATEGY COMPARISON WITH EMPIRICAL DATA

Host quality, availability and use

Icterus orioles were the most productive hosts of 28 species parasitized by cowbirds at the site. This reflected the high success for oriole nests, the ability of orioles to rear cowbirds and, to a lesser degree, their abundance (Table 2.2). Only two oriole nests were parasitized by *ater*, which mainly parasitized nests of Bell's Vireos and Blue-gray Gnatcatchers (Table 2.2). *Aeneus* parasitized mostly nests of Orchard Orioles and Hooded Orioles (Table 2.2). Host use reflected temporal changes in nest availability such that each cowbird parasitized nests of other host species when unparasitized nests of focal species were rare (Fig. 2.5).

Table 2.2. In phylogenetic order, abundance (mean males/count) and nest data for the core area during cowbird laying 2000-2002.

Species (mass, g)[a]	abundance ± SD[b]	Total eggs		% parasitism (n)	Number of cowbirds fledged[c]	
		ater	aeneus		ater	aeneus
Vermilion Flycatcher (16.0)	5.3 ± 2.4	9	0	6 (104)	7	0
Ash-throated Flycatcher (27.2)	0.8 ± 1.0	0	0	0 (7)	0	0
Western Kingbird (39.6)	2.2 ± 1.7	0	0	0 (21)	0	0
Scissor-tailed Flycatcher (43.2)	1.9 ± 1.8	0	0	0 (10)	0	0
Bell's Vireo (9.0)	8.1 ± 2.5	108	0	74 (118)	20	0
Cactus Wren (38.9)	1.1 (1.0)	0	0	0 (6)	0	0
Bewick's Wren (9.9)	1.3 (1.0)	0	0	0 (6)	1	0
Blue-gray Gnatcatcher (5.7)	1.5 (1.5)	12	0	82 (11)	53	0
Eastern Bluebird (31.6)	0.5 (0.7)	0	0	0 (6)	0	0

Northern Mockingbird (48.5)	9.6 (4.5)	0	0	0.(122)	0	0
Chipping Sparrow (12.3)	1.6 (1.3)	0	0	0 (21)	2	0
Lark Sparrow (29.0)	8.5 (3.3)	2	2	2 (200)	0	0
Northern Cardinal (44.3)	0.2 (0.5)	1	2	50 (3)	0	4
Blue Grosbeak (27.5)	0.4 (0.7)	2	2	67 (3)	2	0
Painted Bunting (11.8)	1.7 (1.1)	4	0	20 (21)	2	0
Great-tailed Grackle (107.0)	1.1 (1.7)	0	0	0 (6)	0	0
Orchard Oriole (19.6)	2.7 (2.1)	1	73	79 (34)	0	34
Hooded Oriole (24.3)	1.0 (1.0)	1	62	82 (30)	0	24
Bullock's Oriole (33.6)	1.6 (1.4)	0	15	33 (40)	0	6
House Finch (21.4)	1.5 (1.6)	0	1	0 (51)	0	0
Lesser Goldfinch (9.5)	0.4 (0.6)	0	0	0 (8)	0	0
Totals		155	157	n/a (828)	87	68

Species not detected on censuses

Couch's Kingbird (45.0)		0	0	0 (2)	0	0

Barn Swallow (15.8) [e]	0	0	0 (6)	0	0
Yellow-throated Vireo (18.0)	0	0	0 (2)	0	0
Black-tailed Gnatcatcher (5.1)	0	0	50 (2)	1	0
Yellow-breasted Chat (25.1)	0	0	25 (12)	1	0
Olive Sparrow (23.6)	0	0	0 (1)	0	0
Black-throated Sparrow (13.5)	0	0	0 (1)	0	0
Pyrrhuloxia (34.3)	0	0	66 (3)	0	2
Indigo Bunting (14.1)	0	0	100 (1)	0	0
Totals	0	0	n/a (62)	2	2

[a] Female mass data from Dunning (1993).

[b] Data from weekly morning censuses.

[c] From fledgling surveys outside core area (1999-2002).

[d] Dove species were not included in censuses, yet nests were located: Mourning Dove (15), White-winged Dove (19), Inca Dove (3), Common Ground Dove (4).

[e] Barn Swallows and Purple Martins were not counted during censuses.

ater
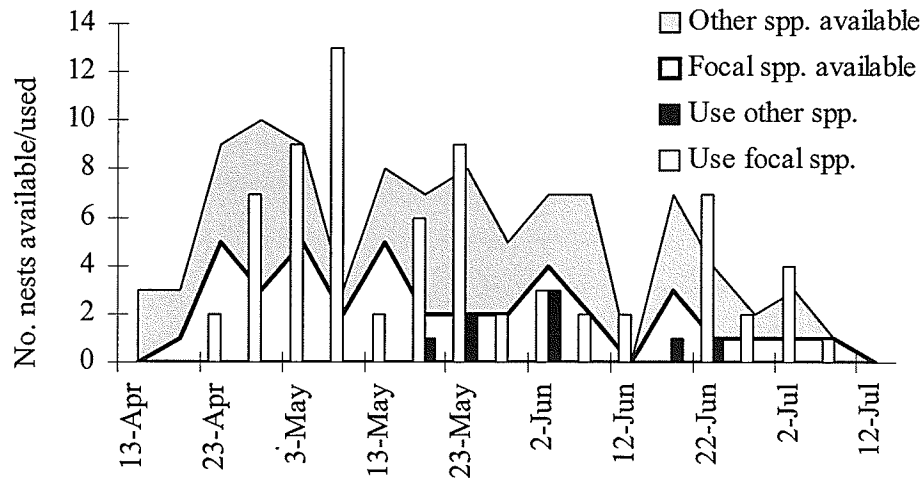
aeneus
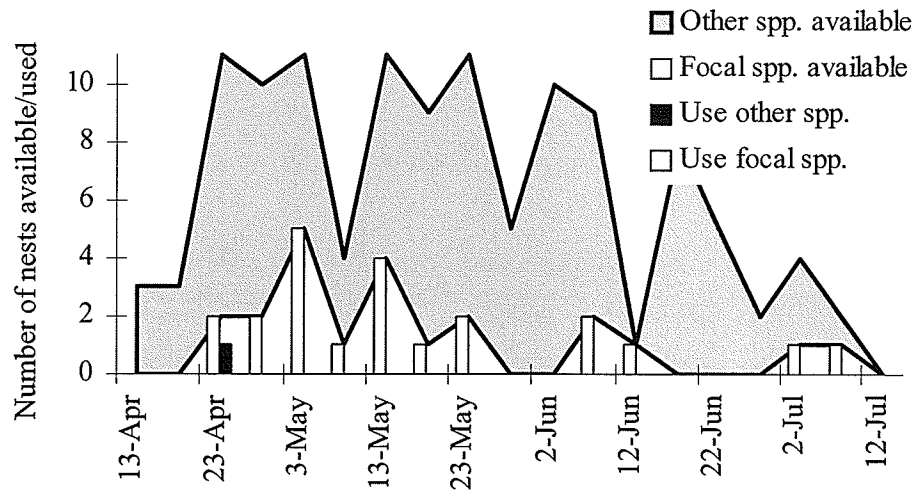
Figure 2.5. Host use relative to nest availability in 2002 for *ater* and *aeneus*. Each

cowbird laid >80% of eggs among nests of focal species, for *ater* and *aeneus*,

respectively: Bell's Vireo, Blue-gray Gnatcatcher, Orchard Oriole, Hooded Oriole.

Nests of other species (see Table 2.2) were used when unparasitized nests of focal

species were rare.

Host Use by Individuals

Overall, 163 and 233 samples from *ater* and *aeneus*, respectively, were genotyped at a minimum of four highly variable microsatellite loci (Table 2.3). This facilitated relatively high power of exclusion when assigning parentage (Table 2.3). In total, five and 11 females were assigned multiple eggs, for *ater* and *aeneus*, respectively. Individuals of both cowbird species regularly used up to three host species (Fig. 2.6).

STRATEGY SUCCESS

Reproductive success for *aeneus* was highest (0.43) with Orchard Orioles as hosts, followed by Hooded Orioles (0.14) and Bullock's Orioles (0.14). Only Bullock's Orioles removed cowbird eggs, puncturing four *aeneus* eggs before I could collect them. However, Bullock's Orioles occasionally accepted *aeneus* eggs (Table 2.2). Therefore, I estimated 80% of *aeneus* eggs would normally be ejected.

Optimal strategies delimited the maximum obtainable success among hosts available as 6.6 young. Specialization upon the most productive host, the Orchard Oriole, resulted in 6.2 young, whereas a purely random generalist strategy resulted in an average of 4.3 young (Fig. 2.7). Observed use produced on average an estimated 3.8 young, followed by an average of 2.8 young for the restricted generalist strategy.

Table 2.3. Measures of variability at microsatellite DNA loci.

Locus	Number of alleles (bp) n		% Heterozygosity observed (expected) PIC[a]		Exclusion probability 1st parent (2nd parent)	
	ater	aeneus	ater	aeneus	ater	aeneus
Maμ 1	23 (194-270) 160	25 (194-270) 222	89 (97) 97	78(94)94	0.879 (0.935)	0.784 (0.879)
Maμ 12	28 (179-269) 146	22 (169-233) 216	87 (97) 97	76(90)89	0.887 (0.940)	0.673 (0.803)
Maμ 15	23 (240-324) 96	8 (276-304) 187	76 (92) 91	78(79)76	0.708 (0.828)	0.419 (0.597)
Maμ 16	9 (327-788) 75	18 (368-824) 80	95 (98) 98	59(98)98	0.908 (0.952)	0.908 (0.952)
Maμ 25	24 (125-219) 93	15 (129-169) 136	86 (92) 90	71(80)80	0.698 (0.822)	0.439 (0.617)
Total	107 (125-788) 163	88 (129-824) 233	87 (95) 95	72(88)87	1.000 (1.000)	0.998 (1.000)

[a] Expected heterozygosity (Nei 1987) and PIC (point information criteria, a measure of the information related to heterozygosity across all loci; Hearne et al. 1992) calculated using Cervus 1.0 (Marshall et al. 1998).
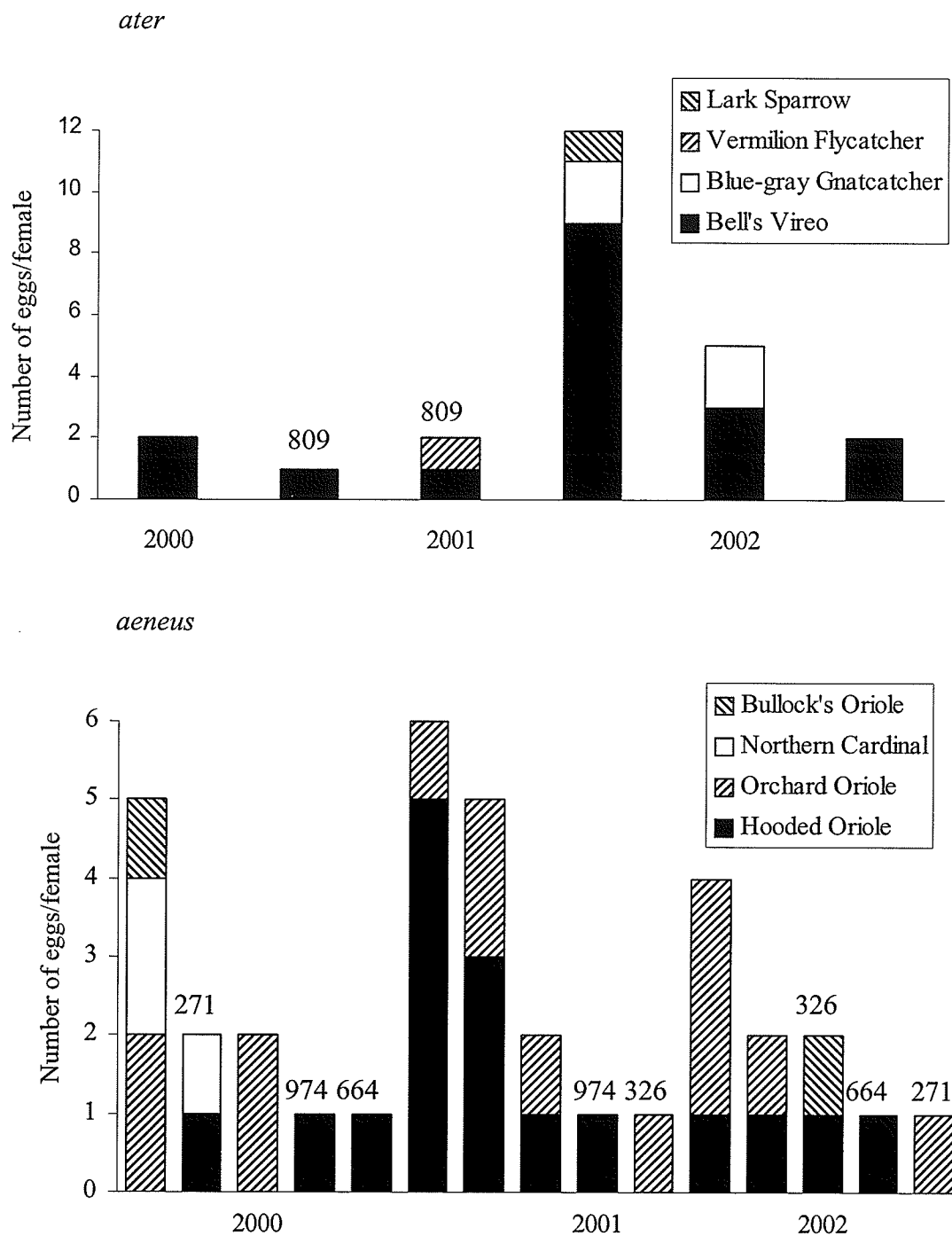
ater

aeneus

Figure 2.6. Host use by *ater* and *aeneus* for eggs genetically assigned to females at Fort

Clark Springs, Texas. Numbers above bars are the identification numbers for females

that laid in multiple years.
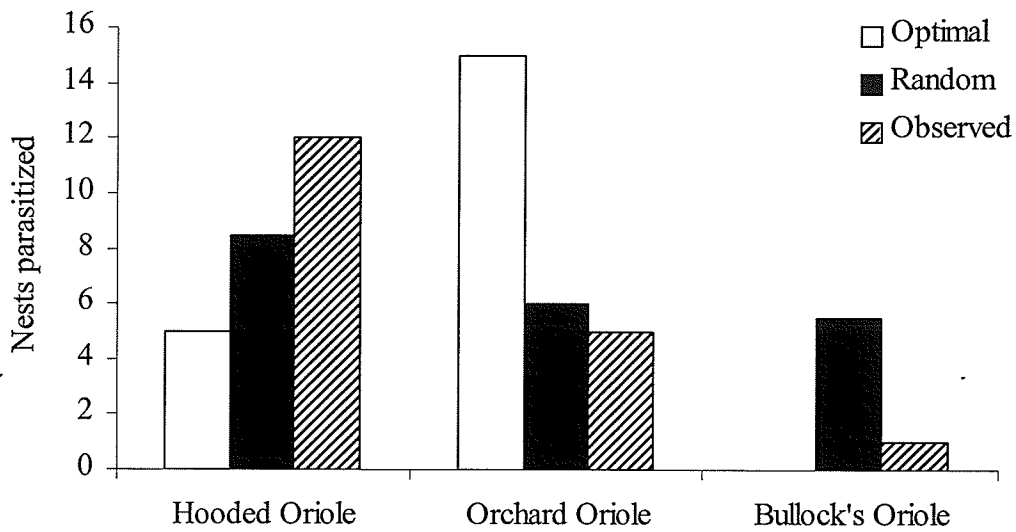
Figure 2.7. Comparison of expected and observed use by *aeneus* of the three focal hosts, those accounting for >80% of parasitism. Observed use fell between that expected under optimal or random strategies. The optimal strategy did not predict use of the Bullock's Oriole and observed use of this host was less than that under a random strategy.

DISCUSSION

THEORETICAL ANALYSIS

Theoretical analyses suggest that generalist strategies are sustainable and capable of invading systems dominated by specialists (Schoener 1974, Hassell and May 1986, Bonsall et al. 2002, Ney-Nifle et al. in press). These patterns remained consistent using models incorporating theoretical payoffs for coevolved specialism estimated for cowbirds. I found that generalists were favored under a variety of conditions (Figs. 2.3, 2.4) and thus transitions from specialism to generalism appear theoretically feasible. In the population model, specialism was favored only when payoffs (fledging success) far exceeded that for generalists. Such scenarios may have arisen historically as cowbird and host distributions would have varied during and following glaciation events (Peer and Bollinger 1997, Rothstein 2001, see also Avise and Walker 1998).

The only specialist cowbird, *rufoaxillaris*, parasitizes a primary host, *badius*, which exhibits two relatively unique traits that benefit *rufoaxillaris*: *badius* experiences low predation on its nests and it removes ectoparasites from young (Fraga 1998). However, it is difficult to see why *rufoaxillaris* would specialize on only one species when the potential for reproductive gains with other species remain (Table 1.3, Sick 1993, Mermoz and Fernández 2003). Indeed, several species appear capable of providing care benefits (and would have, historically, under the coevolution hypothesis) that far exceed those available with *badius*.

My results support the hypothesis that specialism may not be a derived state among *Molothrus*. Coevolution would explain specialism by *rufoaxillaris* but evidence of such processes are uncommon. For instance, most potential hosts, including *badius*,

do not discriminate foreign egg types (Mason 1986a, Sick 1993, Mermoz and Reboreda 1996, Fraga 1998). Likewise, specialists such as Common Cuckoos continue to parasitize nests other than their primary host species' (Moksnes and Røskaft 1995, Edvardsen et al. 2001, Vogl et al. 2002). Therefore, as in Common Cuckoos and other brood parasites, I suggest some form of imprinting constrains host diversity for *rufoaxillaris* (Teuschl et al. 1998, Vogl et al 2002, Payne and Sorenson 2004).

EMPIRICAL ANALYSIS

Consistent with the predictions of my model, field data demonstrated that individual *ater* and *aeneus* were host generalists. Individuals used multiple host species largely associated with the variation in nest availability. For instance, when few vireo or gnatcatcher nests were available, *ater* used flycatcher nests (Fig. 2.6a). Likewise, for *aeneus*, Orchard Oriole nests were not available after early June, whereas use of cardinal nests peaked shortly thereafter (Fig. 2.6b). Other authors have found host use by *ater* reflects host availability (Briskie et al. 1990, Woolfenden et al. 2004). My data exemplify the benefits of host generalism and associated lack of genetic cohesion in terms of host use; individuals using multiple species face no shortage of hosts and as such experience little opportunity for formation of host-based races (Gibbs et al. 1997, 2000).

The analysis using my field data further demonstrated that a specialist strategy can only be favored when payoffs exceed those for more generalist use. While specialism would result in high reproductive success (6.8 young), use of the more continuous supply of all three hosts' nests provided greater success (7.1 young). At my site, generalists had more reproductive opportunities than would any specialist.

Assuming generalism was ancestral, it is difficult to imagine scenarios other than intense coevolution or imprinting on host attributes (Lack 1968, Wyllie 1981) that could result in the derivation of sustainable specialism.

Overall, selection for specialism by *Molothrus* appears to be weak and host use may reflect constraints other than those inherently linked to coevolution. Indeed, generalists are more widespread and numerous due to their ability to use alternative resources (Fig. 1.5, Nakamura et al. 1998). By contrast, specialists face relatively reduced resource availability as coevolution often effectively winnows host availability (Fig. 1.1). Theoretically, specialist brood parasites should achieve greater reproductive gains, relative to generalists (Fig. 2.7), from their primary hosts. However, despite exhibiting traits attributed to coevolution, *rufoaxillaris* achieved gains of 1.8-2.4% proportional fledging success beyond that for *bonariensis* (Fig. 2.8, Fraga 1998, Mermoz and Fernández 2003). Likewise, specialism among hosts in Texas would not allow greater seasonal fecundity than that for generalists. Thus, the questions: "why is *rufoaxillaris* a specialist?" and "have cowbirds and their hosts coevolved?" remain.

GENETIC COHESION

Cowbirds are distinct from most brood parasites as they lack within-species genetic cohesion associated with using a certain host or group of hosts (Gibbs et al. 1997, Joseph et al. 2002). This is related to life-history differences among these parasites. *Cuculus* cuckoos appear to imprint upon their nest, fosterers, and/or natal habitats (Teuschl et al. 1998). This explains how separate gentes laid their eggs (44%, n = 11,870) in nests where their eggs did not match those of the hosts' yet 76% matched the type of nest site
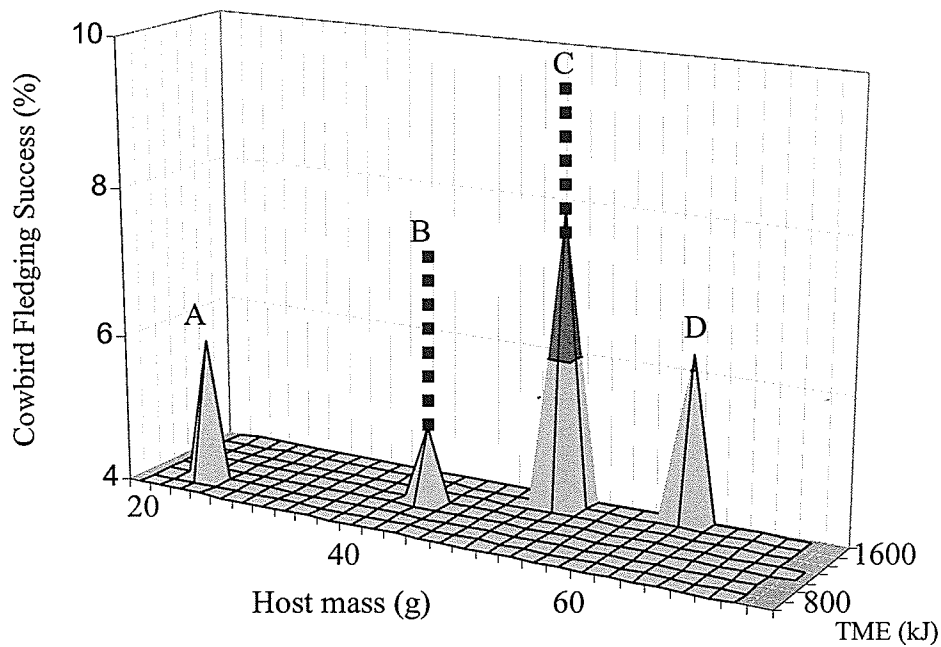
Figure 2.8. Heuristic adaptive landscape for cowbirds. Axes approximate features

analyzed as potential determinants of cowbird fledging success. Total metabolized

energy (TME) on the Y-axis represents estimated energy provided per normal host chick

and is associated with ability to provision cowbirds (Weathers 1992, Kilpatrick 2002).

Each letter represents cowbird success with a hypothetical host. A-D represent success of

bonariensis with *Zonotrichia capensis*, *Agelaioides badius*, *Pseudoleistes virescens*, and

Mimus saturninus, respectively (Fraga 1978, 1985, 1998; Mermoz and Fernández 2003).

Success for *rufoaxillaris* with B and C is represented by dashed lines, thus comparing the

potential gains obtainable to generalists or specialists.

for that gens (Moksnes and Røskaft 1995). Thus, cuckoos lay in nests similar to those in which they were reared (Teuschl et al. 1998). Furthermore, genes for egg appearance occur on the female W chromosome, facilitating gente formation through differential success with hosts based on egg appearance (Davies and Brooke 1989, Gibbs et al. 2000).

Similarly, viduine finches exhibit genetic cohesion because they learn the songs of their hosts (Payne et al. 1998, 2000). Males sing their host's song and females raised by the same hosts mate assortatively with them (Payne et al. 1998, 2000; Payne and Sorenson 2004). New hosts are acquired through "accidental" laying in nests of different hosts or "mis-imprinting" by either sex on the song of another potential host species (Payne et al. 2000, Payne and Sorenson 2004).

Cowbirds lack such a mechanism that promotes genetic cohesion related to host use. Among *ater*, females may preferentially mate with males from similar dialects (O'Loghlen and Rothstein 1995), yet this does not assort individuals raised by the same hosts directly, as occurs among other brood parasites. Thus, *ater* does not exhibit host-based genetic structure (Gibbs et al. 1997). Horsfield's Bronze-cuckoo also does not exhibit host-based genetic structure (Joseph et al. 2002) despite exhibiting apparent host-specific races (Payne and Payne 1998a). However, the lack of genetic structure likely reflects a recent (16,000 my) population range expansion following a bottleneck (Joseph et al. 2002). Thus, evolutionary stable host-specific races have either evolved recently or they may not exist. Because less genetic divergence was found than expected assuming current or past host races, it appears that despite the cuckoo's more historic appearance, strong host specificity has not resulted parallel to the case for *Molothrus*.

The Most Basal Specialist, the Screaming Cowbird

Fraga (1998) summarized the *badius-rufoaxillaris* system as stable and possibly in an

evolutionary equilibrium. He noted the major coevolutionary pressures on *badius* were

avoidance of parasitism, yet *rufoaxillaris* is winning because *badius* does not eject

rufoaxillaris eggs (Fraga 1998). I agree with his reasoning, that because the costs of

rearing *rufoaxillaris* and cross-fostered *bonariensis* were comparable, there is no

evidence for "coevolutionary amelioration" in the older and more specialized parasite.

This view was further supported by natural use of Brown-and-yellow Marshbirds by

rufoaxillaris, for which parasitism did not differ from random and parasite success was

similar (Mermoz and Fernández 2003). Likewise, Mason (1986a) tested several hosts

sympatric with *bonariensis* and *rufoaxillaris* with eggs of each. He found that most of

the 16 songbirds accepted both egg types. Thus, for *rufoaxillaris*, host availability does

not appear constrained by egg appearance (Fraga 1998).

Jaramillo (1993) found *rufoaxillaris* eggs closely matched those of *badius* in

shape and size at one site but not another. He suggested that *rufoaxillaris* eggs have

undergone selection for mimetic shape and size from *badius* that use the darkened nests

of Rufous Horneros similar to Shiny Cowbird use of the same species' nests (Mason and

Rothstein 1986). However, no rejection of eggs dissimilar in shape or size has been

recorded elsewhere. It is unclear why *badius* would favor tactile discrimination of eggs

in one nest type over another, particularly when eggs must receive comparable time in

contact with the brood patch regardless of nesting structure. Therefore, Jaramillo (1993)

concluded selection for similarity in host and parasite egg dimensions was from removal

by other *rufoaxillaris*. Conspecific egg removal appears frequent at parasitized *badius*

nests, where as many as five eggs may be removed and replaced by others' eggs (Rothstein and Robinson 1998, Fraga 1998).

Both the coevolutionary and phylogenetic hypotheses invoke coevolution when describing the *rufoaxillaris*-host system (Lanyon 1992, Rothstein et al. 2002). However, because the *rufoaxillaris*-host system lacks clearly coevolved traits restricting host diversity, I suggest that *rufoaxillaris* individuals imprint upon aspects of their natal rearing conditions as cuckoos do (Moksnes and Røskaft 1995, Teuschl et al. 1998, Vogl et al. 2002), i.e. a mixture of cues associated with host and/or nest type. This would explain why *rufoaxillaris* rarely uses alternative hosts, especially despite the use of a variety of nest types by *badius*. Likewise, the high degree of chick mimicry would be facilitated through genetic cohesion associated with imprinting. Under the imprinting hypothesis, coevolution would have acted secondarily and, thus, better explain the current lack of egg discrimination/mimicry among hosts and potential hosts for *rufoaxillaris* (Mason 1986a, Fraga 1998, Mermoz and Fernández 2003).

Despite the apparent elements of mimicry, chick appearance does not affect success with hosts for *Molothrus* (Fraga 1978, Manolis 1982, Fleischer and Rothstein 1988, Appendix 2) or *Vidua* (Payne et al. 2001). Indeed, rejection by hosts has not selected for egg mimicry (but see Jaramillo 1993) and *rufoaxillaris* is not coevolutionarily restricted to a certain host as in *Cuculus* cuckoos. The variable color, spotting, volume, and shape of *rufoaxillaris* eggs further suggests little coevolution has occurred (Fraga 1998).

Other than chick mimicry, paired nest searching by *rufoaxillaris* has been suggested as a coevolved behavior selected for by heightened host nest defense to counter

parasitism (Rothstein 1990). However, *badius* may display equal nest defense from other enemies (Sealy et al. 1998). Paired activities cannot be discerned easily from other processes, such as mate-guarding (see Strausberger and Ashley 2003). Likewise, females of *aeneus* and *bonariensis* may search for nests in groups but this is not viewed as an adaptation (Carter 1986, Wiley 1988).

Therefore, *rufoaxillaris* does not exhibit relatively more coevolved traits than more recent *Molothrus* species. The coevolution of chick mimicry is better explained as a result of imprinting followed by modification to improve success rather than a winnowing of success with hosts down only to *badius*. This could be tested by cross-fostering eggs/young of *rufoaxillaris* and non-specialists among host nests (Fraga 1998) or through detection of genetic structure based on hosts (see Gibbs et al. 1997, 2000).

Hypothetically, provided natal imprinting explains host use and chick mimicry by *rufoaxillaris*, further questions about such a process must be considered. For instance, why would *rufoaxillaris* have so few hosts, i.e. why more 'laying mistakes' have not resulted in more host-based lines? One explanation is that natal imprinting is strong enough that mistakes have been few relative to *Vidua*. This is reasonable as hosts for *Vidua* nest in mixed colonies where more mistakes can be expected. Likewise, *Vidua* and their hosts breed in sharp temporal peaks following relatively erratic rains and near-random losses to predators and fire (Morel 1973). Finally, observer effort has been focused at describing and not manipulating the *rufoaxillaris- badius* system. Thus, Rothstein et al. (2002) noted that more hosts for *rufoaxillaris* will probably be found, as Pereya (*in* Friedmann 1963) listed additional hosts that were not acceptable to Friedmann who believed misidentified eggs of *bonariensis* were more likely.

COWBIRD-HOST COEVOLUTION?

Coevolution is defined by reciprocal genetic changes induced between organisms

(Futuyma 1998). Among cowbird hosts, discrimination of cowbird eggs appears to exist

for >50 species (Rothstein 1990, Underwood 2003, Peer and Sealy 2004b). Despite this

behavior, induced almost exclusively by brood parasitism (see Peer and Sealy 2004b),

cowbirds exhibit few potentially coevolved traits. Of these, only thicker eggshells

represent a possible adaptation to counteract ejection attempts (Picman 1997, Mermoz

and Ornelas 2004). However, all cowbirds frequently puncture eggs (see Mermoz and

Ornelas 2004) and some lay eggs from above host clutches (Appendix 4). Thus, eggshell

thickness may have evolved to protect cowbird eggs from damage either during laying or

puncture attempts by conspecifics, rather than to resist host rejection attempts (Rohwer

and Spaw 1988).

My analyses suggest that host generalism, under current host egg acceptance

rates, is more profitable than specialism. Thus, it is unclear why *rufoaxillaris* does not

use more hosts. Perhaps imprinting limits the establishment of new hosts. Indeed, the

unexpected results from recent studies of cowbird mating systems (Alderson et al.

1999a,b; Strausberger and Ashley 2003; Woolfenden et al. 2003), social development

(Hauber et al. 2000), and demography (Woolfenden et al. 2001) underline the need for

further cowbird research, particularly of the more basal species. Furthermore, despite the

costs of parasitism, host populations often are not strongly regulated by cowbirds

(Stutchbury 1997, De Groot and Smith 2001). Indeed, mortality from predation and

migration may often swamp parasitism effects on host population productivity (Nolan

1978, Finch 1983, Mermoz and Reboreda 1994, Pease and Grzybowski 1995,

Grzybowski and Pease 2000). Likewise, seasonal productivity is often determined by food availability in some ecosystems (Grant 1999, Sillett et al. 2000, Morrison and Bolger 2002) and thereby would diminish potential impacts of parasites. Competition between cowbirds is also greater than that measured for most brood parasites and may favor a more dynamic equilibrium than that which exists for cuckoos (Nakamura et al. 1998). These forces combine to result in poor conditions for coevolution and, hence, may explain the current lack of coevolution found among cowbirds and their hosts.

CHAPTER 3. MULTIPLE PARASITISM BY TWO GENERALIST COWBIRDS: HOW MANY EGGS ARE TOO MANY?

Breeding cowbirds commonly occur at high densities and often parasitize more than 50% of host nests (Friedmann 1929, Johnsgard 1997, Table 3.1), whereas most brood parasites are less common and parasitize 5-20% of host nests (Johnsgard 1997, Rothstein and Robinson 1998, Davies 2000). Because they occur at high densities, cowbirds are expected to parasitize some nests more than once. Such multiple parasitism (hereafter, MP) of a host can result from either one cowbird laying more than one egg or two (or more) cowbirds laying in the same nest (McLaren et al. 2003). Thus, each female often faces trade-offs of reducing nest searching costs by laying more than one egg per nest, or risking a wasted egg if hosts cannot rear more than one cowbird (Hahn et al. 1999, Trine 2000, Carter 1986).

MP often has been portrayed as a wasteful result of population-level laying patterns that do not differ from random series (reviews by Lowther 1984, Lea and Kattan 1998). However, cowbirds appear capable of at least coarse levels of discrimination among hosts, using more appropriate hosts over those with which success is poor (Table 1.5). Thus, akin to discrimination displayed between potential host species, recognition and differential use of species that are likely to rear more than one cowbird per brood would be adaptive. Previous studies have focused on four hypotheses for why cowbirds parasitize hosts multiply: (1) extraordinary egg production by cowbirds (Kattan 1997, Goguen 1999), (2) host nest limitation (Ortega 1998, Strausberger 1998), (3) loss of preferred nests to predation – essentially, a best-of-a-bad-job strategy, and (4) inability to detect whether nests are already parasitized (McLaren et al. 2003).

Table 3.1. Aspects of MP by some brood parasites.

Species	Birds /100 ha	Mean eggs per nest	Maximum eggs per nest	Fit to Poisson[a]	MP by >1 female (n)[b]	Source
Rufoaxillaris	Fairly common	1.3 – 4.3	20	Mixed	Yes [b,d]	Stotz et al. (1996), Fraga (1998), Mermoz and Fernández (2003)
Aeneus	96	2.1 – 2.3	14	Mixed	92% (36)[e]	Friedmann et al. (1977)
Ater	20 – 40	1.0 – 2.5	13	Mixed	53% (58)[f], 87% (23)[e]	Johnsgard (1997)
Bonariensis	15 – 32	1.8-2.6	37	Mixed	Yes[b,g]	Johnsgard (1997), Lea and Kattan (1998)
Clamator glandarius	1.3	1.5 – 3.7	6	Yes	32% (28)[c]	Martínez et al. (1998)
Cuculus canorus	Low	1.0	4	No	< 1% [b,d]	Johnsgard (1997), Nakamura et al. (1998)
Vidua species	High	1.4 – 1.5	4	Mixed	Yes [b,d]	Morel (1973), Payne (1977a), Mines (1999)

[a] Fit tested with Kolmogorov-Smirnov tests (see Appendix 5).

[b-g] Determined using: [b] simultaneous laying dates, [c] DNA fingerprinting (Martinez et al. 1998), [d] egg dimensions and/or appearance, [e-f] microsatellite DNA ([e] Chapter 2, [f] McLaren et al. 2003), [g] egg morphs where two distinct morphs co-occur (Lyon 1997).

Several studies have concluded that high egg production was the most likely explanation (Goguen 1999, Lea and Kattan 1998). This has since been countered by genetic findings that cowbirds successfully lay fewer eggs, annually, than previously determined or expected (Hahn et al. 1999; Strausberger and Ashley 2003; Woolfenden et al. 2003, 2004). I measured MP by *ater* and *aeneus* among an array of potential hosts to identify why cowbirds parasitize hosts multiply. I used molecular genetics to determine the number of females laying at each nest, which facilitated testing the hypotheses of extraordinary egg production (1) and inability to detect previous parasitism (4). Essentially, if individual cowbirds did not parasitize the same nest twice, this would suggest that MP by different cowbirds may reflect a lack of recognition when nests will be parasitized by another. I tested the nest limitation (2) and best-of- a-bad-job (3) hypotheses by recording cowbird eggs among all potential host nests to determine the relative availability of nests suitable for parasitism. My analyses consider the constraints cowbirds may face when laying decisions are made, whereas previous workers relied upon comparison with Poisson series to characterize host use by cowbirds as a random or near-random process (Preston 1948, Mayfield 1965, Lowther 1984, Lea and Kattan 1998).

If some hosts can rear two cowbird young, MP of these nests by the same female should be common and the reverse is expected if competition between cowbirds is costly (Goguen 1999). Therefore, I estimated the hatching rates and provisioning abilities of hosts to determine the number of cowbird eggs per nest to maximize cowbird success. If MP is related to these factors, cowbird host use would appear less random than previously characterized (Lea and Kattan 1998, but see Woolfenden et al. 2003).

Alternatively, if MP reduces cowbird reproductive success, then does MP decrease when more nests are available? To test these hypotheses, I measured aspects of host use by sympatric *ater* and *aeneus* in south Texas where MP was common (Carter 1986). I also compared host abundance and nest failures to test which affected MP.

METHODS

STUDY SITE

To determine the frequency of MP, I monitored potential host nests within the core area as described in Chapter 2 (Fig. 2.1). The year without manipulation of eggs (1999) served as a control for subsequent years when egg models were placed in nests. This was necessary as model eggs could affect cowbird behavior, i.e. they cannot be punctured (Massoni and Reboreda 2002) and/or their appearance may affect the probability of subsequent parasitism (see Ortega et al. 1994, Strausberger and Ashley 1997). To test whether model eggs affected MP, I compared the occurrence of MP during control and treatment years.

COSTS ASSOCIATED WITH MULTIPLE PARASITISM

I quantified costs of MP to cowbirds at the egg and nestling stages. I estimated hatching failure for cowbird eggs as the number of eggs left in nests four days after a chick had hatched in the nest, whether host or cowbird. This controlled for late-hatching eggs. Most nests used for this analysis were checked for eggs that had not hatched once the young were ready to fledge. As eggs that do not hatch are rarely removed from nests

(Mayfield 1960, Rothstein 2001), my data provide minimal estimates of hatching failure, i.e. eggs or young could have been removed during the 10-14 d nestling periods.

Because most deleterious effects of MP should occur only when multiple cowbird eggs hatch, I calculated the expected number of cowbird eggs hatching per multiply parasitized nest (*sensu* Mayfield 1960:174). The distribution of eggs not hatching was assumed to be randomly distributed within the sample. Therefore, according to a Poisson series, the probability that a cowbird egg would hatch was used to determine the number of cowbirds hatching per multiply parasitized nest. These data were then used to predict the clutch sizes that would optimize the chance of hatching one cowbird (probability of hatching^{-1}).

From the nests and fledgling broods in surrounding areas, captured young cowbirds were weighed, color-banded, and blood-sampled. I also recorded numbers of accompanying host or cowbird young. I assumed it was unlikely that the hatching success of host clutches was affected when accompanied by models versus real cowbird eggs (Ortega et al. 1994). More so, because all host nests received the same type of model eggs, hatching success among host nests should be relative, except for potential differences associated with host egg/body size (see Strausberger 1998).

I compared the variation for masses of cowbirds of fledging age (10 and 12 d for *ater* and *aeneus*, respectively) that were reared with and without nestmates. When not known from hatch dates, age was estimated based on plumage and physical development (*sensu* Scott 1979). Because adult cowbirds are sexually size-dimorphic, size differences may appear among young (Scott and Lemon 1996). I determined offspring sex through PCR amplification of chromo-helicase-DNA binding (CHD1) genes from avian W and Z

sex chromosomes (Griffiths et al. 1998). PCR products were viewed through

electrophoresis on 2% agarose gels (see Kasumovic et al. 2002). CHD-analysis resulted

in two distinct bands for females, one for males, and none if amplification failed. I

verified the accuracy of this technique for each species with DNA from 10 adults of

known sex (five of each sex).

CORRELATES OF MULTIPLE PARASITISM

Identification of females practicing Multiple Parasitism

To determine whether MP was most often due to laying by the same or different females,

I identified the cowbirds laying within the egg-collection plot by comparing adult and

offspring microsatellite DNA loci (Alderson et al. 1999a, Woolfenden et al. 2002).

Genetic analysis was conducted as described in Chapter 2. I used output from the

PARENTAGE and KINSHIP (Goodnight and Queller 1999) programs to determine the

likelihood that eggs were laid by the same or different females (*sensu* McLaren et al.

2003). I also deduced the number of females laying at a nest using observational data, as

each cowbird lays only one egg per day (Payne 1976) and, therefore, same-day laying

represented eggs laid by more than one female. Thus, this method of exclusion differed

from that used for parental assignment in Chapter 2.

Because cowbirds may avoid laying in a nest containing another cowbird egg (see

Ortega et al. 1994) and some cowbird eggs are found below nests, I sought to determine

whether these eggs were ejected from nests or were laid there (see Budnik et al. 2001).

To determine whether hosts or other cowbirds ejected eggs, I watched nests prior to

sunrise, the time which cowbirds normally lay their eggs (Scott 1991, Neudorf and Sealy

1994). Nest watches also allowed me to determine whether cowbirds interact at nests or if laying resulting in MP occurred later than for initial eggs. The latter scenario would be expected if nests were depredated before the morning a cowbird would arrive to lay and, hence, the female was forced to lay in another nest (Carter 1986). Time lost to arriving at and/or locating a secondary nest would result in cowbird laying times later than for initial eggs during the normally restricted window for parasitism prior to sunrise (Scott 1991, Neudorf and Sealy 1994, Peer and Sealy 1999a).

Spatial and Temporal Patterns of Multiple Parasitism

To assess whether distances between nests affected cowbird egg dispersion, I calculated mean distances between nests that were simultaneously available to cowbirds, hereafter referred to as "inter-nest" distances. I assessed nest availability during five-day periods, counting nests as available if they were within two days of the hosts' first egg day, e.g. first egg day $\pm$ 2 d. I used this criterion as most cowbird eggs are laid in nests during this period (Sealy 1992, Pease and Grzybowski 1995). For this analysis, I again considered only nests of the focal host species (see Chapter 2), however, I excluded Vermilion Flycatcher nests as they were extremely common and were used relatively infrequently (Table 2.2).

To test whether MP is more likely during periods when fewer nests are available, I compared the dates of MP relative to the number of alternative nests available on those days. To do this, I used binomial logistic regression with 1) the same or different females laying in nests and 2) females with one or more eggs per nest coded as zero and one, respectively, as the dependent variables (Martínez et al. 1998). These were compared

with the total number of nests simultaneously available and the number of unparasitized nests available on the date MP occurred, as independent variables.

Host Quality Indices

To determine whether cowbirds simply parasitize any species, I compared parasitism and measures of host abundance. Assuming that all hosts are equally suitable, cowbird parasitism would be expected to occur in a direct relationship with number of host adults (see Barber and Martin 1997) or nests available (Wiley 1988). Proportions of host nests parasitized should reflect their availability. Therefore, I compared species' use by the number of nests simultaneously available during the five-day periods of susceptibility to parasitism. If any species were differentially used despite availability of others, then a "preference" of that host would be demonstrated.

To predict the number of cowbird young hosts could rear, I estimated the relative costs of rearing a cowbird versus a host young using Weathers' (1992, 2001) nestling energetic formulae (see below). I divided the total energetic expenditure per host brood by the hatching probability for the cowbird that used the host. Estimates were then compared to the measured number of cowbirds fledged by each host. This technique ignores the effects of host nestmates, which is reasonable as cowbirds often hatch before hosts (Briskie and Sealy 1990) and cowbird fledgling mass varies little with respect to host species (Kilpatrick 2002).

Host fostering abilities were also estimated using Weathers' (1992) formulae. The formulae are based on the linear relationships between time, energy metabolized and chick mass across 30 avian species. These estimates were based on asymptotic fledging

mass, which is correlated with survival to independence (Linden et al. 1992) and represents a meaningful point in offspring growth. Specifically, I defined fledging age as the point at which asymptotic mass is attained (Weathers 1992, Kilpatrick 2002). For hosts, I used adult body masses from Dunning (1993) and cowbird fledgling age and mass data from this study and Carter's (1984) to estimate energy requirements (Table 2.2). Total energy metabolized by a nestling from hatching through fledging (TME, in kJ), peak daily energy metabolized (pDME, kJ· d^{-1}), and metabolic conversion of food to chick tissue (R_C, kJ· g^{-1}) were estimated. Associations between estimates and host use were tested using regression.

These estimates have comparative value because all estimates are relative (Weathers 1992, Kilpatrick 2002). The estimates for parental provisioning represent minimal estimates of potential energy available to parasitic young as cowbirds often receive food at higher rates than host young at unparasitized nests (Carter 1986, Dearborn 1998, Lichtenstein and Sealy 1998). Based on fledging mass and time to fledging, estimates represent cumulative food assimilation rate, which is nearly constant among avian young fed insects (69.2%, n = 10 species) (Bryant and Bryant 1988). I present all three variables when analyzing cowbird host use because each variable quantifies different physiological constraints that affect host and parasite growth.

RESULTS

HOST USE

Cowbirds used nests of 15 of the 18 species available as potential hosts (Table 2.2), however, 90% of cowbird eggs were distributed among the nests of six species (Tables

2.6 and 3.2). The two cowbirds rarely used the same host species and host use was not closely associated with host abundance for 25 species measured by counting adults (ρ = 0.16, P = 0.44) or nests (ρ = 0.24, P = 0.24). Each cowbird commonly parasitized three hosts, hereafter referred to as "focal" hosts. *Ater* used Bell's Vireo (81 % of 126 eggs), Blue-gray Gnatcatcher (11 %) and Vermilion Flycatcher (8 %) nests, whereas, *aeneus* used nests of Hooded Orioles (46 % of 136 eggs), Orchard Orioles (44 %), and Bullock's Orioles (7 %) (Table 3.2). Nests of the focal hosts were available across an average of 73 d (range: 61-81 d) and 83 d (73-94 d) for *ater* and *aeneus*, respectively (Figs. 2.5 and 3.1). During these periods, the modal number of nests active per day ranged from 1-3 and 0-1 nests per season, peaking at eight and 10 nests for *ater* and *aeneus*, respectively.

Cowbirds regularly parasitized nests multiply, 36% (n = 99) and 63% (n = 76) of nests for *ater* and *aeneus*, respectively (Table 3.2). However, most nests received two or fewer eggs (*ater*: 97%, n = 96 nests; *aeneus*: 72%, n = 55 nests) with an average of 1.2 and 2.1 eggs per nest for *ater* and *aeneus*, respectively (Table 3.2). Host use was not affected by the substitution of models for cowbird eggs. MP during control and treatment years varied significantly, yet all significant differences were from increased MP (Table 3.3). Therefore, cowbird parasitism did not decrease due to the presence of model eggs.

Costs Associated with Multiple Parasitism

At unmanipulated nests where at least one host or cowbird egg hatched, 23% of 13 *ater* eggs did not hatch, whereas 34% of 32 *aeneus* eggs did not hatch. These values closely matched those found elsewhere (Table 3.4). The probability of cowbird eggs hatching was lower than that for four hosts: Bell's Vireo, Lark Sparrow, Orchard Oriole, and

Table 3.2. Cowbird egg distribution among the nests of the focal hosts for each cowbird.[a]

| | Cowbird eggs per nest | | | | | | Mean eggs |
	1	2	3	4	5	6	per nest
Ater							
Vermilion Flycatcher	9	0	0	0	0	0	1.00
Bell's Vireo	56	16	2	0	0	0	1.27
Blue-gray Gnatcatcher	7	3	0	0	0	0	1.30
Total	72	19	2	0	0	0	1.25
aeneus							
Orchard Oriole	7	10	4	2	3	0	2.38
Hooded Oriole	9	9	6	1	1	1	3.56
Bullock's Oriole	8	3	0	0	0	0	1.27
Total	24	22	10	3	4	1	2.13

[a] Eleven additional nests of seven species were parasitized singly by *ater*. Likewise, four and two nests of three more species were singly and doubly parasitized by *aeneus*, respectively (see Table 2.2).
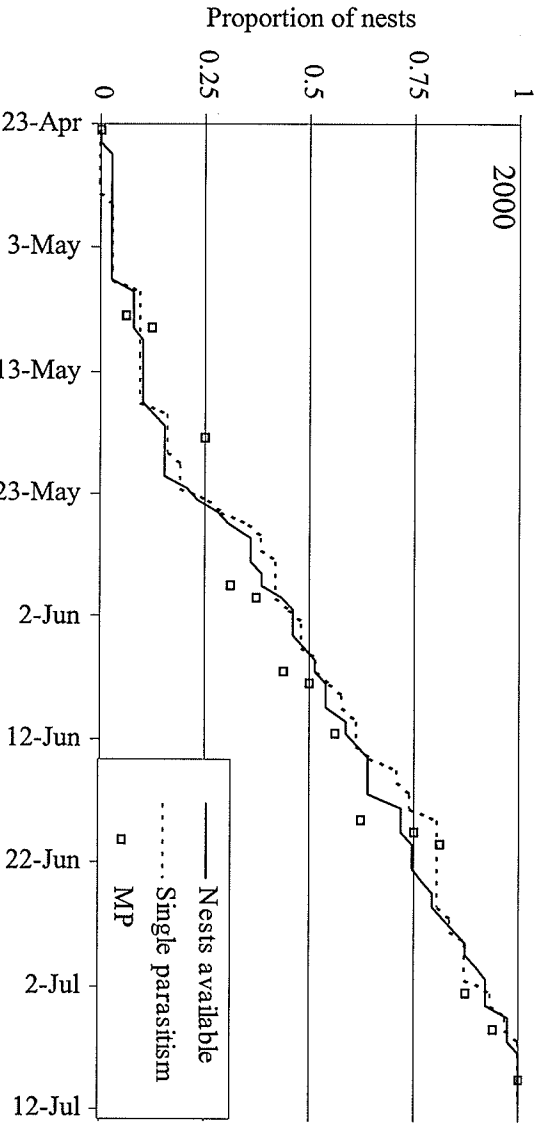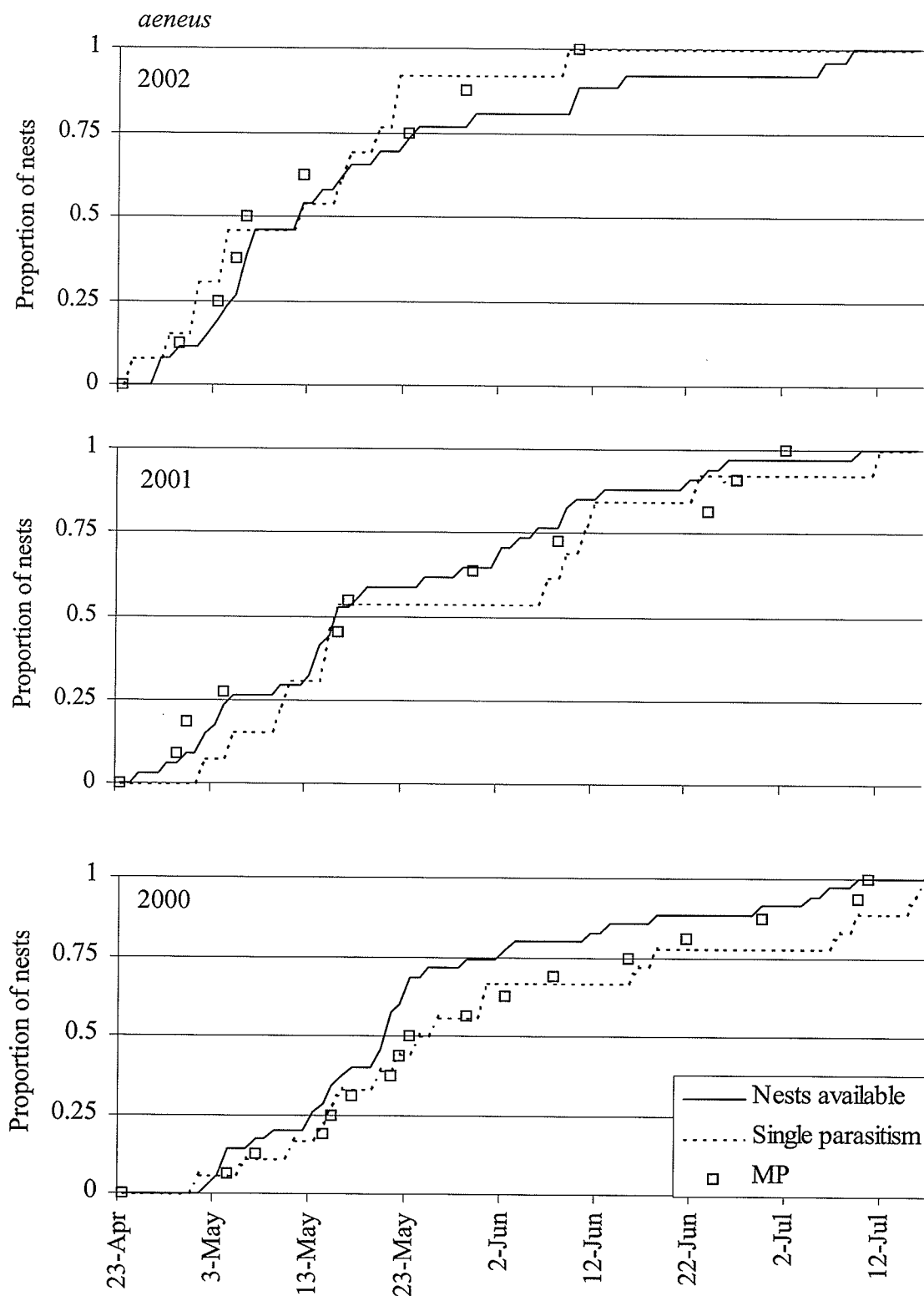
Figure 3.1. Timing of MP by *ater* and *aeneus* relative to the number of available nests of focal hosts and the proportion already parasitized with one cowbird egg.

Table 3.3. The frequencies of MP during seasons with (2000-2002) or without

substitution of models for cowbird eggs (1999). The only significant differences from the

control season occurred during two and one seasons for *ater* and *aeneus*, respectively.

	ater (n)	*aeneus* (n)
1999	15.6% (32)	46.5% (43)
2000	48.0% (25)**	71.4% (28)*
2001	40.6% (32)**	66.7% (24)
2002	18.5% (27)	40.0% (15)

*= P <0.05, **= P <0.001.

Table 3.4. Proportion of cowbird eggs hatching in nests of different host species.

	1	2	> 3	Source
ater				
Bell's Vireo (24) [a]	0.87	[b]	[b]	This study
Plumbeous Vireo (37)	0.55	0.57	0.44	Goguen (1999)
Blue-gray Gnatcatcher (55)	0.34	0.64	0.22	Goguen (1999)
Blue-gray Gnatcatcher (6)	0.75	0.67	[b]	This study
Northern Cardinal (29)	0.45[c,d]	[e]	[e]	Scott & Lemon (1996)
Song Sparrow (335)	0.64[c,d]			Smith & Arcese (1994)
Indigo Bunting (6)	[e]	[e]	0.67	Payne & Payne (1998b)
Common Yellowthroat (24)	[e]	0.71[c]	[e]	Hofslund (1957)
Yellow Warbler (33)	0.49			Weatherhead (1989)
Prothonotary Warbler (121)	0.52	0.66	0.49	Hoover (2003)
Red-winged Blackbird (69)	0.59			Weatherhead (1989)
aeneus				
Orchard Oriole (31)	0.75	0.60	0.54	This study
Hooded Oriole (21)	0.75	0.63		This study
Bullock's Oriole (6)	1.00	1.00		This study

[a] Number of eggs.

[b] No hatching data due to predation and/or abandonment.

[c] Most nests with given number of eggs, however, clutch-specific data were unavailable.

[d] Includes nest predation.

[e] Data not provided.

Hooded Oriole ($G_{87} = 15.6$, $P < 0.001$). Thus, for at least one egg to hatch, *ater* and

aeneus should have laid 1.3 and 1.5 eggs per nest, respectively. Taking hatching

probabilities into account, the conformity of cowbird egg dispersion to Poisson series

became diminished (Fig. 3.2).

Because few nests parasitized by *ater* survived to hatching, I analyzed costs of

MP to young for only *aeneus*. Chick masses were only slightly more variable among

those without nestmates (coefficients of variation: 0.19 for lone chicks and 0.14 for those

with a nestmate, $Z=0.02$, $P=0.53$). However, the mean mass for chicks reared alone was

significantly greater than that among chicks reared with a cowbird nestmate ($F_{1,29} = 10.6$,

$P = 0.03$). More males (larger sex) than females were present in multiply parasitized

broods (10 versus six) (Fig. 3.3).

Energetic estimates suggested that hosts can rear more than one cowbird per nest

(Fig. 3.4) and several did so (Tables 3.5 and 3.6). For unparasitized broods, the smallest

hosts for each cowbird, Blue-gray Gnatcatcher and Orchard Oriole, provided 756 and

1959 kJ TME, respectively. Thus, gnatcatchers normally provide unparasitized broods

with TME equal to that for rearing 1.6 *ater* young. Likewise, Orchard Orioles provide

TME equivalent to the needs of 2.2 *aeneus* young. Estimates based on pDME were

similar, suggesting gnatcatchers and orioles could rear 1.1 and 2.2 *ater* and *aeneus*

young, respectively. Thus, incorporating hatching probabilities, *ater* and *aeneus* should

have laid 1.4 - 2.1 and 3.3 eggs per nest, respectively, to produce the maximum number

of young per nest.

In contrast to my predictions, only hosts of *aeneus* regularly fledged more than

one cowbird per nest (25%, $n = 55$; Fig. 3.4 and Table 3.5). Hosts for *aeneus* sometimes
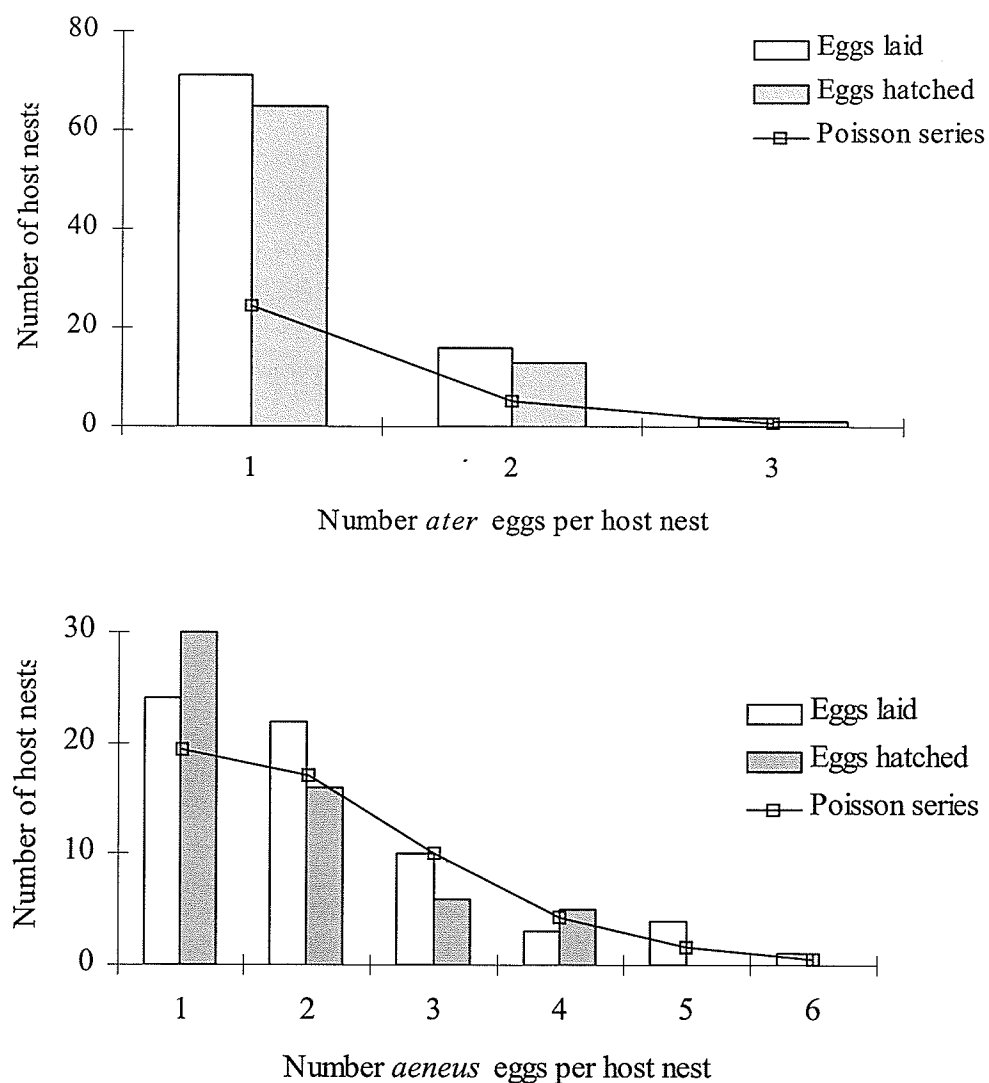
Figure 3.2. Parasitized nests observed (bars) and predicted using Poisson series (lines) for

ater and *aeneus* (2000-2002). For both species, egg dispersion was less random than

predicted, as more nests received 1-2 eggs and fewer had >3 eggs than predicted.

However, the difference was significant only for *ater* ($D = 0.63$, $P < 0.001$). Taking

hatching probabilities (shaded bars) into account, parasitism remained non-random for

ater and became significantly so ($D = 0.17$, $P = 0.04$) for *aeneus* (see Mayfield 1960).
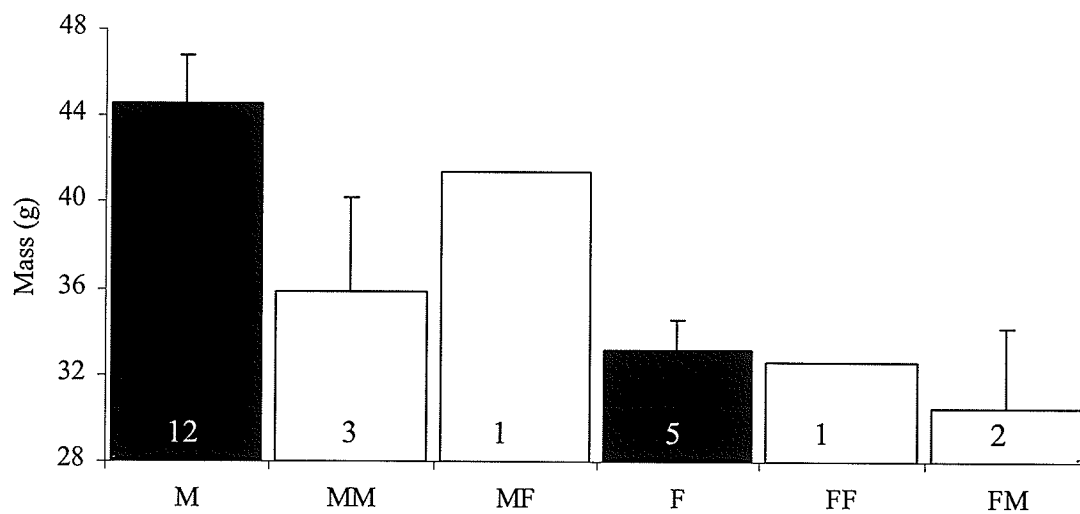
Figure 3.3. Mean fledgling masses ($\pm$ SE) for *aeneus* reared with (empty bars) and without conspecifics (solid bars), categorized by nestmate sex, male (M) or female (F). Data for only the heaviest chicks in pairs presented, sample sizes are inside respective bars.
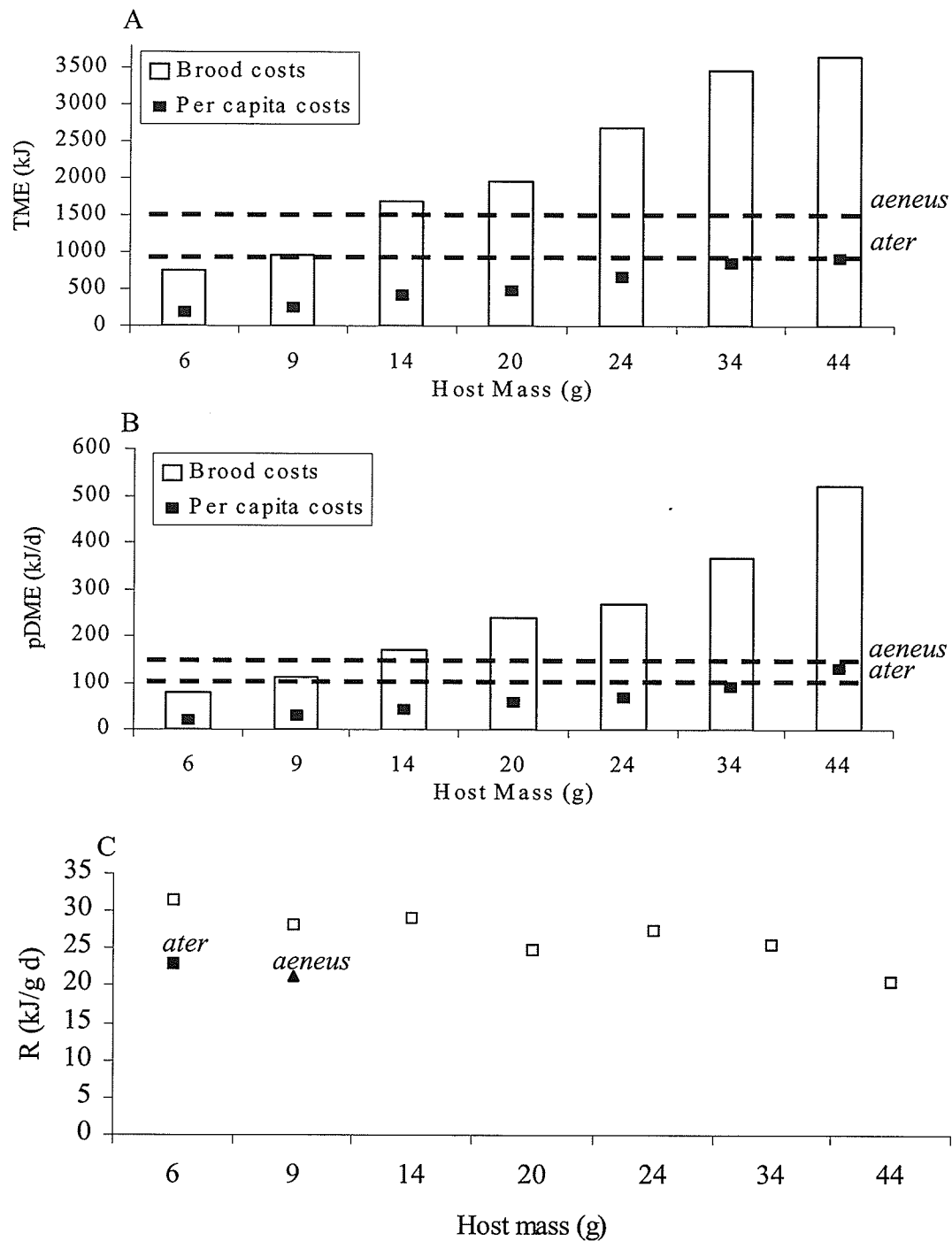
Figure 3.4. Rearing costs for hosts and cowbirds estimated for (A) total metabolized

energy (TME), (B) peak daily metabolized energy (pDME), and (C) energy density (R)

sensu Weathers (1992). Brood costs estimated using modal size of four young. Cowbird

costs represented as dashed lines in (A-B) and symbols in (C).

Table 3.5. Proportions of cowbird fledglings and eggs per nest (in %) compared across host species.

Hosts of [a]	1	2	3	> 3	Source
ater					
Vermilion Flycatcher (28, 179)	100 (100)				This study
Bell's Vireo (21, 75)	100 (64)	0 (28)	0 (8)	.	This study
Plumbeous Vireo (122, 153) [b]	43 (56)	25[c] (28)	32 (9)	(7)	Goguen (1999)
Blue-gray Gnatcatcher (55, 9)	96 (67)	4 (33)			This study
Blue-gray Gnatcatcher (85, 147)	21 (68)	* (23)	* (7)	(2)	Goguen (1999)
Wood Thrush (51, 163)[b]	60 (13)	* (25)	5 (26)	0 (38)	Trine (2000)
Yellow Warbler (2, 310)[bd]	(88)	(10)	0 (2)		Weatherhead (1989)
Prothonotary Warbler (370, 551)	51 (46)	26 (28)	13 (13)	12 (13)	Hoover (2003)
Indigo Bunting (33, 132) [be]	91 (61)	9 (25)	(12)	(2)	Payne and Payne (1998b)
Lazuli Bunting (38,*) [b]	74	16			Greene (1999)
Western Tanager (60 [f], 54) [b]	28 (70)	7 (20)	12 (6)	(7)	Goguen (1999)
Red-winged Blackbird (26, 382)[bd]	(70)	(21)	(5)	(3)	Weatherhead (1989)
Northern Cardinal (74, 88)	70 (40)	30 (26)	0 (15)	0 (13)	Scott and Lemon (1996)

aeneus[g]

Northern Mockingbird (5, 25)[h]	40 (19)	20 (14)	40 (31)		Carter (1984)
Long-billed Thrasher (56, 25)[h]	59 (18)	39 (51)	2 (31)		Carter (1984)
Green Jay (26, 12)[h]	42 (33)	50 (17)	4 (17)	4 (8)	Carter (1984)
Summer Tanager (6, 6)	67 (67)	33 (33)			This study
Olive Sparrow (15, 11)[h]	60 (36)	40 (27)	0 (9)	0 (18)	Carter (1984)
Pyrrhuloxia (1, 3)	0 (67)	100 (33)			This study
Northern Cardinal (6, 18)	67 (67)	33 (33)			This study
Yellow-breasted Chat (4, 1)	0 (0)	100 (100)			This study
Red-winged Blackbird (1, 3)[h]	0 (66)	100 (33)			Carter (1984)
Orchard Oriole (28, 26)	71 (27)	29 (23)	0 (23)	0 (23)	This study
Hooded Oriole (22, 27)	86 (33)	14 (30)	0 (26)	0 (4)	This study
Bullock's Oriole (3, 12)	67 (75)	33 (25)			This study

[a] Broods and nests.

[b] Differences between nests and broods represent losses to predation, abandonment, etc.

[c] Nests with > 2 cowbirds pooled.

[d] Nests manipulated, fledgling data not reported here.

[e] Egg data (Burhans et al. 2000).

[f] Reported only nests in which both species survived and pooled nests with ≥ 3 cowbird eggs.

[g] Sealy et al. (1997) reviewed fledgling records for small samples on 19 species not reported here.

[h] Reported ranges, I fit data with the lowest possible brood sizes.

* Not provided.

Table 3.6. The fledgling composition of parasitized broods based on surveys. Host species listed in order of increasing mass (see Table 3.5 for data on the incidence of MP).

	Single cowbird	At least one cowbird and one host	At least two cowbirds
Hosts to *ater*			
Blue-gray Gnatcatcher	51	1	2
Bell's Vireo	21	0	0
Painted Bunting	1	0	1
White-eyed Vireo	1	1	0
Total	74	2	3
Hosts to *aeneus*			
Orchard Oriole	20	2	8
Hooded Oriole	13	2	6
Bullock's Oriole	1	1	1
Yellow-breasted Chat	0	1[a]	1
Summer Tanager	2	2	2
Pyrrhuloxia	0	0	1
Northern Cardinal	4	0	1
Long-billed Thrasher[b]	1	5	3
Total	40	13	23

[a] One nest parasitized by *ater* fledged young.

[b] Data from Carter (1984), maximum brood size fledged was one Long-billed Thrasher with three *aeneus*.

fledged multiple cowbirds or host young plus one cowbird (40%, n = 67 broods), whereas most hosts of *ater* did not fledge young in addition to a cowbird (96%, n = 103 broods). The greatest estimated expenditures for observed broods were 959 and 2109 kJ by Blue-gray Gnatcatchers and Orchard Orioles, respectively.

CORRELATES OF MULTIPLE PARASITISM

Genetic Identification of Egg-laying Individwuals

Both cowbirds were relatively equal in abundance and laid similar numbers of eggs (Table 3.7). Most eggs in multiply parasitized nests were laid by different females as determined through the exclusion analysis. However, not all eggs at nests parasitized multiply yielded DNA (*ater*: 51%, n = 39 nests; *aeneus*: 48%, n = 50 nests), therefore, sampling may have been biased toward MP by different individuals due to the number of female assignments made by laying day (26% and 44% of assignments for *ater* and *aeneus*, respectively; Table 3.8). Nonetheless, only 15% (n = 20) and 12% (n = 25) of multiply parasitized nests contained eggs laid by one female for *ater* and *aeneus*, respectively. Thus, MP was largely due to laying by more than one female.

Overall, I found 20 and 14 eggs beneath nests that were laid by *ater* and *aeneus*, respectively. Observations during cowbird laying attempts (*ater*: 23; *aeneus*: 41) revealed that cowbirds sometimes failed to lay eggs into nests as four eggs missed nests (two of each species), two *ater* laid eggs atop hosts, and one laid on the ground. For all seven cases, laying failure was associated with host nest defense. Furthermore, although cowbirds removed host eggs (n = 3 observations), none removed cowbird eggs or models.

Table 3.7. Annual proportion of cowbird eggs laid by each species and minimum

estimated number of females laying in the core area.

	ater (n eggs)	Number of females	*aeneus* (n eggs)	Number of females	G (P-value)
2000	42.9% (51)	16	57.1% (68)	12	2.02 (0.10)
2001	33.3% (30)	5	66.7% (60)	8	11.37 (0.005)
2002	67.9% (57)	17	32.1% (27)	5	13.11 (0.003)

Table 3.8. The number of female *ater* and *aeneus* that laid at multiply parasitized nests, by number of cowbird eggs per nest. Subset of cases for which different individuals were identified by same-day laying in parentheses.

ater

Number of females	2 eggs	3 eggs
1	3	0
2	17 (4)	0
$\geq^a 2$	--	4 (2)

aeneus

Number of females	2 eggs	3 eggs	4 eggs	5 eggs	6 eggs	7 eggs
1	3	0	0	0	0	0
≥ 1	1	3	0	0	0	0
2	11 (4)	3	0	0	0	0
≥ 2	0	5 (4)	1	0	0	0
3	0	1 (1)	3 (1)	0	0	0
≥ 3	0	0	1 (1)	0	0	2 (1)
4	0	0	0	2 (1)	0	0
≥ 4	0	0	0	1 (1)	0	0
5	0	0	0	1 (1)	1 (1)	0

[a] Inequalities ($\geq$) represent minimal estimates for nests where the number of laying females could not be determined.

Thus, defense by hosts appeared to be the cause for most cowbird eggs found beneath nests.

Most host nests that failed during the five-day period of susceptibility to parasitism bore evidence that cowbirds were associated with their failure. Bell's Vireo nests received 69% of *ater* eggs (n = 274) and 35% of the 99 Bell's Vireo nests that failed during 2000-02, did so during the five-day window to parasitism. Vireo eggs were often removed or punctured (48%, n = 58), presumably by cowbirds. This was confirmed through nest watches during which *ater* removed or punctured an egg (n = 3). Likewise, oriole nests often lost host eggs, yet remained active longer than vireo nests: 15 d (n = 93) for orioles versus 10 d (n = 118) for vireos. Oriole nests remained active even when they contained up to seven cowbird eggs (mean = 2.4, n = 71 eggs). Because both cowbirds usually laid before the second host egg (*ater*: 77 %, n = 142; *aeneus*: 92 %, n = 99; Fig. 3.5), nests were infrequently depredated by the time nests were multiply parasitized (Table 3.9). Indeed, nest predation usually lagged MP, thus, MP occurred at more nests than could be attributed to predation of other nests prior to laying. Furthermore, laying times did not differ between the categories of initial egg or MP (U = 180.0, P = 0.81).

Spatial and Temporal Patterns of Multiple Parasitism

Inter-nest distances ranged from nine to 803 m and were inconsistent among years. For both species, MP was not closely associated with inter-nest distance (linear regression R^2 values for 2000-2002, respectively for *ater*: 0.01, 0.13, 0.27 and *aeneus*: 0.05, 0.06, 0.17). Despite declining nest availability across each season (Fig. 3.1), MP was not significantly associated with nest availability for *ater* (ρ: -0.08, -0.01, 0.16; 2000-2002,
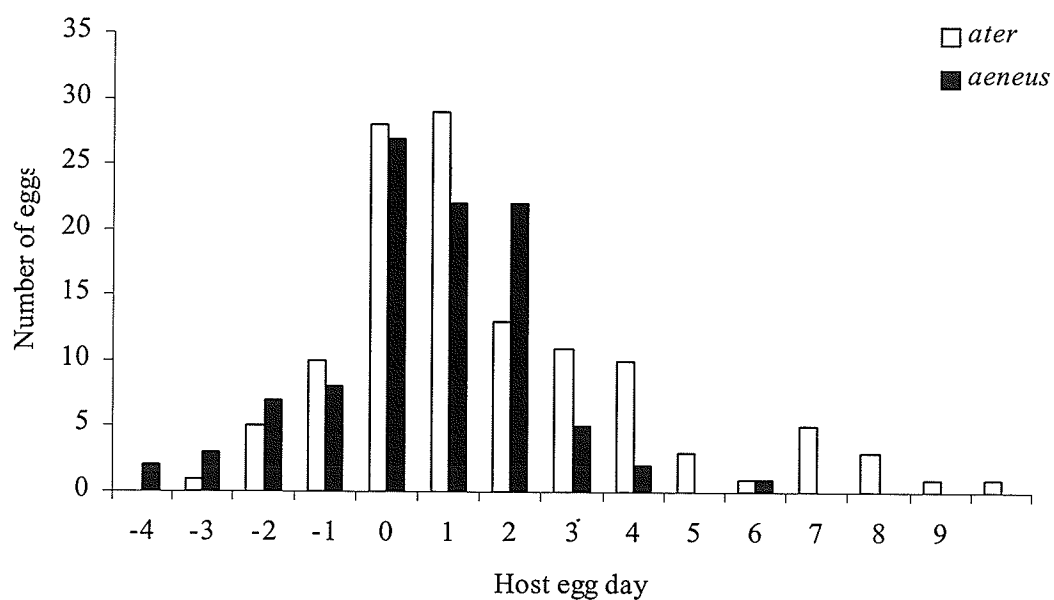
Figure 3.5. Cowbird laying relative to host laying for 121 eggs of *ater* and 99 of *aeneus*.

Most eggs were laid by day two of the host's laying.

Table 3.9 Timing for MP relative to nest predation. The frequency of MP generally exceeded that for predation.

	10-d periods when MP > predation (n)	Cases when MP > predation (cases MP)
ater		
2000	2 (8)	47% (17)
2001	1 (5)	0% (1)
2002	3 (7)	94% (16)
aeneus		
2000	5 (7)	79% (14)
2001	4 (6)	64% (11)
2002	3 (5)	75% (8)

respectively) or *aeneus* during 2001 (ρ: 0.50, 0.11, 0.51; 2000-2002, respectively). MP tracked nest availability only during 2000; by contrast, in 2002 MP peaked ahead of seasonal declines in nest availability. MP was most frequent during the first half of each season except for *ater* in 2001, during which only three multiply parasitized nests were found (Fig. 3.1).

In all years *ater* parasitized nests multiply less frequently than *aeneus* (*ater*: 15% (20), *aeneus*: 55% (40); G_{64} = 15.6 , P < 0.05, Table 3.2, Fig. 3.2). For both cowbirds, host nest availability peaked in mid-May (Figs. 2.5, 3.1). Each season, MP by *ater* tended to occur earlier than MP by *aeneus* (Figs. 3.1 and 3.6). Eggs laid inappropriately due to excessive prior parasitism were more likely during the peak and early host laying periods, for *ater* and *aeneus*, respectively (Fig. 3.6). However, differences in timing were significant only for MP by *aeneus* ($Z_{75,75}$ = 2.1, P < 0.001). MP by *ater* occurred on different mornings (74%, n = 19 nests), whereas female *aeneus* parasitized the same nests on the same mornings (86%, n = 21 nests). Of these, 19 involved different females and nests already containing a cowbird egg were more than three times as likely to receive an egg of another rather than the same female (seven versus two cases).

For *aeneus*, there were 24 dates on which MP occurred and for which laying females could be identified. Of these dates, 23 involved laying by different females. Likewise, nests already containing a cowbird egg(s) were more than three times as likely to be subsequently parasitized by a different female than by a returning female(s) (19 versus 5 cases). Exclusion of MP occurring on same mornings from the analysis improved model fit, but did not significantly affect the fit for the relationship between nest availability and MP (change in log likelihood = 2.19, P = 0.14).
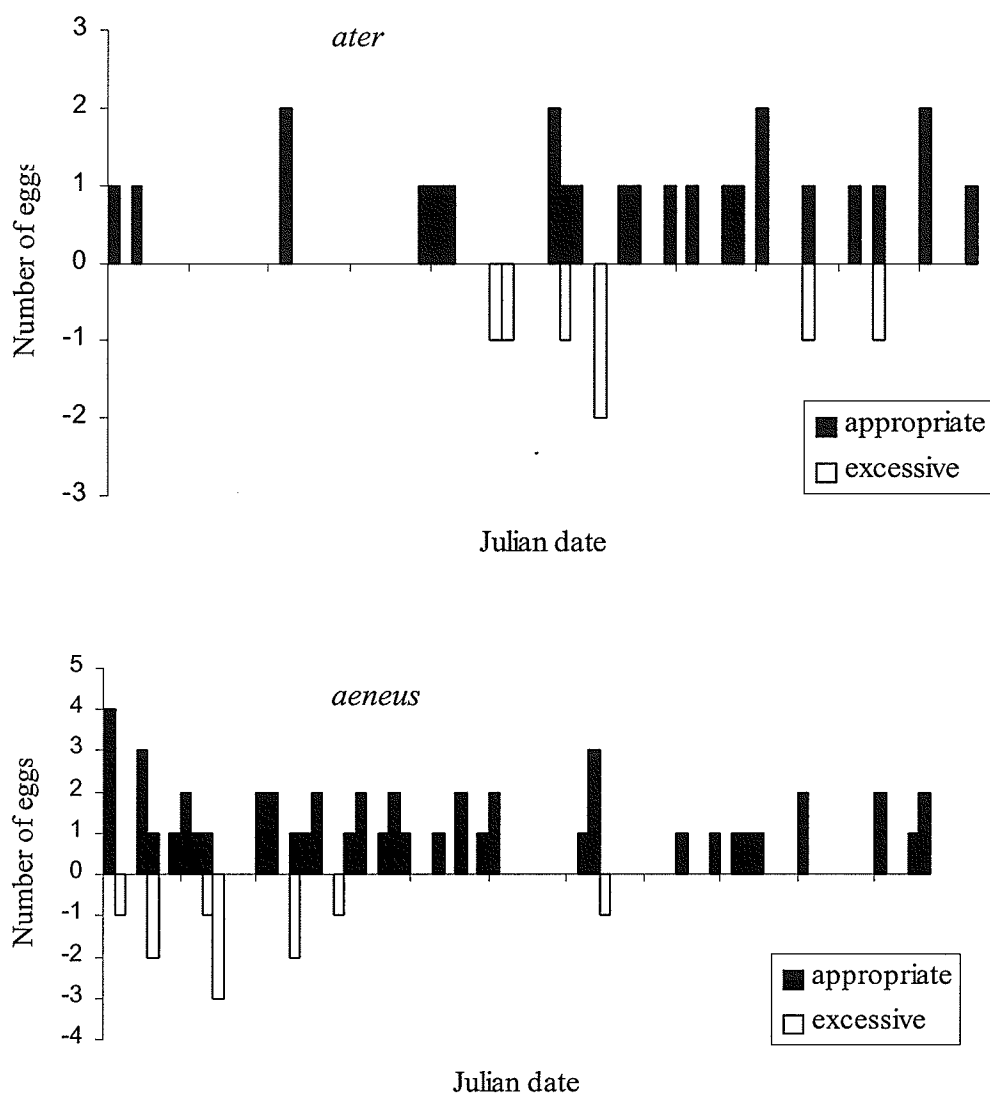
Figure 3.6. The timing of MP by *ater* and *aeneus*. The frequency of same-day MP (solid bars) compared to eggs laid after parasitic clutches exceeded sizes that could be conceivably cared for (open bars), i.e. all eggs beyond two and three per nest, *ater* and *aeneus*, respectively, were classified as excessive. Same-day laying was classified as appropriate because cowbirds were presumably committed, physiologically, to laying at these nests. The initial Julian date is 27 April.

Host Quality Indices

Cowbirds infrequently used the most abundant potential hosts. Species used by *ater* were moderately abundant, whereas *aeneus* focused on the relatively rare orioles and larger hosts (Tables 3.2 and 3.4). Despite seasonal reductions in the availability of these hosts, cowbirds still parasitized their nests (Figs. 3.1 and 3.2). For instance, *ater* parasitized 80% of Bell's Vireo nests and 8% of Vermilion Flycatcher nests, despite the greater abundance of and fledging success with flycatchers (Table 3.2). However, it is noteworthy that overall nest success reflects losses inflicted by cowbirds. Comparing success with parasitized nests, only unparasitized nests of Blue-gray Gnatcatchers and Bell's Vireos fledged young significantly more often, 0% (n = 3, 4) versus 20 (5) and 50% (38), respectively. By contrast, hosts of *aeneus* exhibited the highest success (Tables 3.5 and 3.6). Indeed, despite the partial rejection by Bullock's Orioles, *aeneus* continued to parasitize this species but with low success (Table 2.2, six young fledged).

At fledging, *aeneus* averaged 18.2 g more than *ater* (*ater*: 20.2 $\pm$ 1.1 g, n = 10; *aeneus*: 38.4 $\pm$ 1.3 g, n = 26). Thus, the larger *aeneus* chicks require greater TME than *ater*. However, *aeneus* chicks grow more slowly and, hence, exhibited lower pDME and R_c. R_c and TME were significantly associated with host use by cowbirds (linear regression R_c: β = -0.14, t = -1.95, P = 0.05; TME: β = -0.16, t = -2.52, P = 0.03). Overall, host use differed significantly from rank abundance (Kruskal-Wallis H = 13.95, df = 1, P < 0.001) and was not associated significantly with ranked R_c values (r_s = 0.50, n = 10, P = 0.14). Likewise, use among hosts separated for each cowbird, was associated with R_c, however, significantly so only for *aeneus* (*ater*: ρ = 0.20, P = 0.75; *aeneus*: ρ = 0.90, P = 0.04). Based on energetic estimates and fledging success, cowbirds

consistently parasitized nests of the most capable hosts and infrequently used hosts of

lesser quality. However, during the periods when focal species' nests were not available,

80 % (15) and 100% (13) of these periods, alternative hosts' nests were used by *ater* and

aeneus, respectively (Fig. 2.5).

DISCUSSION

I found that most multiple parasitism was a result of laying by different females rather

than repeated laying by individuals. Moreover, costs of multiple parasitism were diffused

by poor hatching, predation and the rearing of multiple cowbirds by hosts. Of the four

general hypotheses that explain the occurrence of MP, I consider those centering on

constraints to appear most tenable.

The hypothesis that MP is associated with high fecundity among cowbirds

(Kattan 1997, Goguen 1999) posits that because cowbird eggs are relatively cheap to

produce, costs associated with MP are reduced and, hence, cowbird MP of hosts is

common. However, this view has since been countered by the finding that cowbird eggs

are not less costly, energetically, to produce than those of non-parasitic relatives

(Mermoz and Ornelas 2004). Likewise, extraordinary estimates of annual egg

production, up to 40-100 eggs/female/year (Scott and Ankney 1983, Holford and Roby

1993, Kattan 1993) have been countered by genetic findings that cowbirds lay only up to

17 eggs annually (Hahn et al. 1999, Shonk 2001, Strausberger and Ashley 2003,

Woolfenden et al. 2003, this study). Indeed, through dissection, I found no difference in

the frequencies at which *aeneus* and two congeners, *bonariensis* and *ater*, produced

ovarian follicles (Appendix 1).

The hypothesis of host nest limitation (Strausberger 1998), appears unlikely as a large number of unparasitized nests were available when MP occurred (Fig. 3.1). Therefore, best-of-a-bad-job hypotheses attributing MP to predation and poor recognition of prior parasitism at nests, appear to best explain the persistence of MP. However, cowbirds still incur costs of MP that could be avoided through more coordinated egg dispersion. Thus, the central question remains, why do cowbirds lay eggs in nests already parasitized?

COSTS OF MULTIPLE PARASITISM

Because most MP involved laying by different females (Fleischer 1985, Strausberger and Ashley 2003, this study; but see McLaren et al. 2003) the costs of MP are not uniformly distributed among individuals. Ultimately, costs of MP are diminished or nullified when hosts raise all the cowbirds that hatch in their nests (see Goguen 1999, Tables 3.5 and 3.6). However, competition among nestlings can remain costly in terms of mass (Fig. 3.2, Goguen 1999), a correlate of survival (Krementz et al. 1989, Linden et al. 1992). This did not occur for *aeneus*; mass did not differ significantly between chicks reared alone and the largest chicks with conspecific nestmates. Thus, in terms of fledgling mass, competition created a winner and one or two losers. My analysis using energetic estimates ignored competition from host young; however, such competition was reduced as few host eggs remained in nests parasitized by *aeneus* and cowbirds often hatched before hosts (see also Carter 1986). This may reflect characters of orioles (the main hosts of *aeneus*) such as 14 d nestling periods, whereas cowbirds and many potential hosts require 8-12 d (Carter 1986, Kilpatrick 2002). Also, because I measured chicks at

fledging, I may have missed differences present among younger nestlings that did not survive (see Goguen 1999).

Goguen (1999) and Trine (2000) also found that cowbird fledging success declined relative to the number of *ater* eggs in a nest. Trine (2000) focused on the overall linear trend of fledging success, whereas Goguen (1999) more appropriately assessed trends by categories of the number of *ater* eggs/nest. He found that cowbird survival was directly related to the number of cowbird young/nest when effects of nest predation were removed; however, inclusion of losses to predation resulted in nonlinear trends (Goguen 1999). For instance, the proportion of cowbird eggs that produced fledglings was highest among nests with two eggs for three hosts (Blue-gray Gnatcatcher, Song Sparrow, Orchard Oriole) and did not differ for nests with one or three eggs for Plumbeous Vireos (Fig. 3.7). Likewise, for one to two cowbird young per nest, some studies have shown no significant differences in cowbird mass or the proportion of cowbird eggs producing fledglings (Trine 2000, Hoover 2003). However, other studies have suggested one cowbird may seriously challenge adult brood rearing capability (Dearborn et al. 1998, Burhans et al. 2000).

These patterns reflect the poor evolutionary feedback cowbirds must receive with regards to natural selection acting upon the number of eggs laid per nest; in effect other processes produce "noise" that diffuses selection against MP. A major source of noise was nest predation, which is often both frequent and uncorrelated with readily discernable features at nest sites (Martin 1992, Misenhelter and Rotenberry 2000), therefore, cowbirds cannot gauge which nests will fail or succeed. Only slight gains from lowered risk of losses to nest predation were available under more even egg dispersion
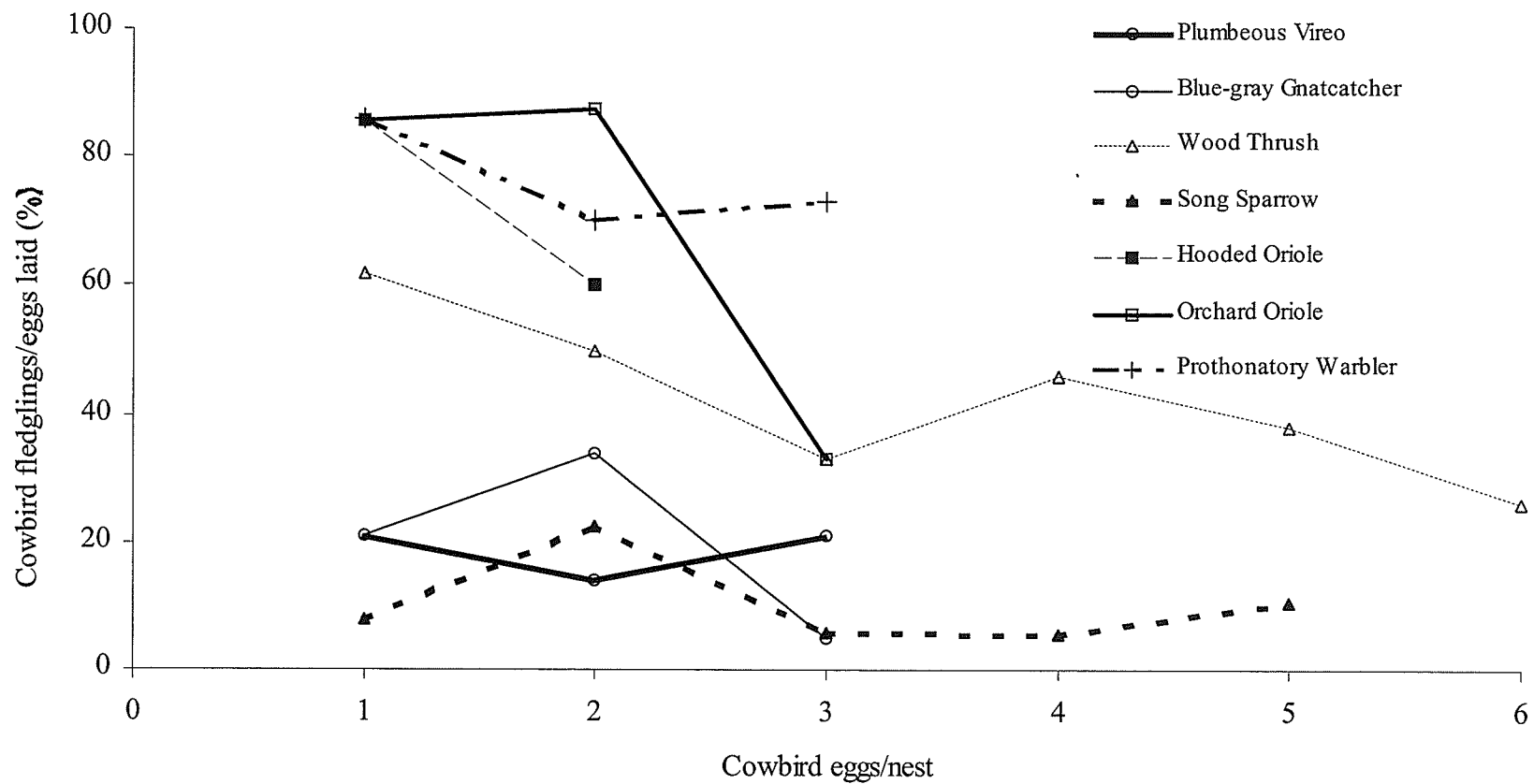
Figure 3.7. The proportion of eggs producing fledgling cowbirds at varying levels of MP (sources listed in Table 3.5).

(Payne 1977b). Moreover, hosts are plastic with the amounts of care they provide and this likely diffuses selection against MP.

Numerous studies involving brood enlargement or handicapping parents (e.g. tail weighting, mate removal) have demonstrated high variation in brood care (reviewed by Gowaty 1996, Eckerle and Breitwisch 1997). Likewise, host chicks from unparasitized nests were not significantly heavier than those from parasitized nests (Smith and Arcese 1994, but see Dearborn and Thompson 1994). These studies suggest parents can provide the extra care necessary to rear more than one cowbird and indeed many hosts do so (Fig. 3.3 and Tables 3.5 and 3.6). Kilpatrick (2002) showed that Blue-gray Gnatcatchers may provide 1.4 times more energy (peak daily metabolizable energy) when rearing two *ater* chicks versus a brood of four of its own young, as found by Goguen (1999) and this study, including other hosts as well (Tables 3.5 and 3.6).

Counter-intuitively, theoretical and empirical data suggest minimal reproductive losses would have occurred due to MP, as I found most parasitism involved one or two cowbird eggs per nest. Incorporating host rearing capabilities, nests with two and three cowbird eggs may be viewed as appropriate for *ater* and *aeneus* hosts, respectively. Using these criteria, fewer than 5% of *ater* and 20% of *aeneus* eggs would have been laid in nests inappropriately. Thus, MP by cowbirds may be less costly than commonly portrayed in analyses of egg dispersion that rely solely upon comparison with Poisson series. Indeed, many hosts rear multiple cowbirds (Tables 3.5 and 3.6, Fig. 3.7).

CONSTRAINTS PROMOTING MULTIPLE PARASITISM

Other authors have favored best-of-a-bad job hypotheses, primarily focusing on the unpredictable nature of nest predation (Carter 1986). I suggest that in addition to predation, low hatching frequencies, variable care and competition from hosts, and phylogenetic constraints may further diffuse selection against MP.

Cowbird hatching success is poor when compared to that of host species (Young 1963, Koenig 1982, Johnsgard 1997, Ortega 1998, Table 3.4). Elevated hatching failure of cowbirds resulted from poorly timed laying (Fig. 3.4, Scott and Lemon 1996, Goguen 1999), damage/removal by hosts or other cowbirds (Smith and Arcese 1994, Massoni and Reboreda 2002), or infertility (21%, n = 57 eggs; Weatherhead 1989). Thus, my estimates for guaranteeing that at least one egg would hatch (1.3 and 1.5 eggs for *ater* and *aeneus*, respectively) appear realistic. MP may also provide fluctuating benefits from more than a single nestling cowbird begging (Kilner 2003) in the nests of hosts whose young may never hatch or be outcompeted early in the nestling period. However, the comparative data needed to test this hypothesis are lacking.

Nestling competition should reflect cowbird-to-host ratios. This is of particular interest because such ratios are particularly dynamic as cowbirds and other blackbird species have undergone extensive range and habitat expansions in the past 100 years (Robbins and Easterla 1981, Cruz et al. 1985, Post et al. 1993, Rothstein 1994, Whetje 2003). Thus, cowbird egg dispersion may not be highly refined due to a lack of time for such use to evolve under steady cowbird-to-host ratios and counter-selection from intraspecific competition among nestlings would be diffused by the factors discussed above. A similar process has been hypothesized to describe the relatively less refined use

of hosts by the Common Cuckoo in Japan (Nakamura et al. 1998) where clearing of land

has made more hosts accessible to the cuckoos. Thus, in Japan, the cuckoo frequently

lays poorly mimetic eggs, sometimes multiply in more recently acquired host species'

nests. Similar to the common case among cowbirds, these cuckoos are reared alongside

host young (Nakamura et al. 1998).

Egg Production by Brood Parasites

Among brood parasites, potential fecundity has been best studied among Common

Cuckoos and Great-spotted Cuckoos, and *ater* (Chance 1940, Wyllie 1981, Nakamura

and Miyazawa 1997, Martínez et al. 1998, Table 1.4). Likewise, *aeneus* does not appear

grossly more fecund than *ater* or *bonariensis* (Niles 1970, Kostecke et al. 2004,

Appendix 1). Thus, estimates of egg production bouts among free-living brood parasites

are relatively equal (Table 1.4) and realized fecundity estimates based on molecular

genetics (Table 1.4) suggest these species lay at maximum, 17 eggs per year.

Error in these estimates is unlikely great enough to account for differences

between those obtained by other means (Table 1.4). Instead, it appears that not all

ovarian follicles produced become eggs, i.e. potential fecundity is constrained and grossly

over-represents primary fecundity. Follicular atresia, due to chronic or acute shortages of

energy (Curson and Matthews 2003), calcium (Holford and Roby 1993), water (Coe and

Rotenberry 2003), or even host nests (Scott and Ankney 1983), may best explain the

disparate estimates of egg production obtained by different methods (Table 1.4).

Recognition of parasitism by conspecifics

For *aeneus*, MP was frequently (>80%) due to same-day laying (Fig. 3.6; Carter 1986, n

= 12 nests), thus, cowbirds appear to lack recognition of which nests other cowbirds have

laid or will lay at. Multiple individuals were present at and near nests while nest

searching and laying. Because individuals laid eggs at nests despite observing others,

even pecking them, while at the same nest (*aeneus*: n = 3 nests, Appendix 6), a lack of

recognition of MP as the mechanism appears unlikely. Indeed, even seeing another

cowbird at a nest should serve as a probable cue that parasitism by another has occurred

or may occur. However, whether recognition was possibly overridden by a lack of

alternatives cannot be known, although for *aeneus*, nest loss prior to clutch completion

was low (20%) relative to frequencies of MP (Table 3.2). Regardless, MP was frequent

and occurred despite the presence of conspecific eggs laid on different days. Conspecific

eggs were not damaged or removed more often than host eggs (10% versus 70%). Thus,

conspecific egg recognition by cowbirds appeared unlikely (see also Nolan 1978).

MP is common throughout *Molothrus* and hosts can rear multiple cowbird young

(Table 3.10). Greater MP by the more tropical species (*aeneus* and *bonariensis*) may

reflect a greater number of cowbirds per host or social interactions among cowbirds.

Alternatively, non-territorial cowbirds may be responsible for most MP (Friedmann 1929,

Friedmann et al. 1977; Hahn et al. 1999). I observed groups of *aeneus* during typical

hours of nest searching and I saw females enter the same nest shortly after observing

another do so (n = 3), whereas *ater* never searched in groups (see also Darley 1982).

This conforms to the stable egg laying ranges that are reported for *ater* (Darley 1982,

Yokel 1989, Hahn et al. 1999, Shonk 2001) but not among radio-tracked *aeneus* (Carter

Table 3.10. Maximum number of cowbirds hosts have reared, single accounts unless noted otherwise in parentheses.

Cowbird and host species

Rufoaxillaris- **Fledged three:** Chopi Blackbird, Baywinged Cowbird.[a]

Aeneus- **Fledged two:** Olive Sparrow, Red-winged Blackbird [b]; Summer Tanager (2), Pyrrhuloxia, Northern Cardinal, Yellow-breasted Chat, Orchard Oriole (8), Hooded Oriole (6), Bullock's Oriole [c]; White-throated Towhee (2).[d] **Three:** Northern Mockingbird, Long-billed Thrasher.[b] **Four:** Green Jay.[b]

Ater- **Fledged two:** Eastern Phoebe [e]; Acadian Flycatcher (5) [f]; Hutton's Vireo [g], Plumbeous Vireo (12), Blue-gray Gnatcatcher (2) [c,h]; Lark Bunting [i]; Eastern Towhee (2), Worm-eating Warbler (3), Ovenbird (2), Louisiana Waterthrush (2), Kentucky Warbler (18) [f]; Western Tanager (4) [h]; Northern Cardinal (3,) [f]; Indigo Bunting (3) [j]; Painted Bunting.[c] **Three:** Red-eyed Vireo (2) [k]; Wood Thrush (2) [l]; Brown Thrasher [m]; Prothonotary Warbler (9) [n]; Le Conte's Sparrow [o]; Song Sparrow.[p] **Five:** Western Meadowlark.[q]

Bonariensis- **Fledged two:** Chalk-browed Mockingbird.[r] **Three:** Short-tailed Field Tyrant [s], Diuca Finch (2) [t], White-edged Oriole[s], Yellow-shouldered Blackbird.[u] **Four:** Chopi Blackbird (4) [a]; Brown-and-Yellow Marshbird [v], Black-cowled Oriole.[w]

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[a] Sick (1993), [b] Carter (1986), [c] This study, [d] Forcey (2002), [e] Woodward (1983), [f] Trine et al. (1998), [g] Chace (2001), [h] Goguen (1999), [i] Sealy (1999), [j] Payne & Payne (1998b), [k] Southern (1958), [l] Trine (2000), [m] Moore (1956), [n] Hoover (2003), [o] Murray (1969), [p] Friedmann (1929), [q] Davis in Davies (2000), [r] Fraga (1985), [s] Marchant (1960), [t] Fraga (2002), [u] Post & Wiley (1977), [v] Mermoz & Reboreda (1994), [w] Wiley (1985).

1984; 1986). Both *aeneus* and *bonariensis* appear to lack female territoriality as groups of two to six females have been observed nest searching together (Friedmann et al. 1977, Carter 1986, Wiley 1988). Also, because MP was concentrated before the peak in nest availability (Fig. 3.2), I suggest that cowbirds may misjudge the timing for peak nest availability and produce more eggs per nest early in each season.

I also suggest that multiple cowbirds may be physiologically committed to lay at the same nest on the same day (Fig. 3.5). This would explain the persistence of excessive MP (more eggs than hosts can hatch and care for) as a best-of-a-bad-job scenario. Therefore, *aeneus* may compete in more of a scramble for nests than *ater* does. Under scramble competition, selection for non-random laying among appropriate hosts' nests by individuals would be diminished (Davies 2000). Alternatively, cowbirds may not be able to exclude other cowbirds from their laying ranges (Fleischer 1985, Hahn et al. 1999, Strausberger and Ashley 2003) and scramble competition may result beyond threshold cowbird-host ratios.

SUMMARY

MP was primarily the result of different females laying in the same nests, MP persists due to constraints and diffused counter-selection. Moreover, because hosts can rear more than one cowbird, MP is not inherently wasteful. Indeed, selection against MP is diminished by nest abandonment (Parker 1999), predation (see Goguen 1999), poor hatchability (Table 3.4), and variation in the amount of care (Fig. 3.7, Table 3.5). The variation added by competition at nests, primarily for one's eggs to hatch first, further diminishes selection against MP. As the probability of a cowbird fledging was

maximized when more than one egg was laid per nest, moderate MP may be profitable.

Therefore, conformity of MP to random Poisson series cannot be used to infer that

cowbirds use hosts at random. Host use by both cowbirds was not random with respect

to species used and those used multiply. Instead, host use was more closely related with

host rearing capability rather than abundance. Models for cowbird-host coevolution can

be improved by incorporating non-random elements of host use. Likewise, conservation

efforts may be better focused through recognition that cowbirds do not randomly

distribute their eggs among nests. For instance, potentially threatened hosts may be

prioritized for study or protection as cowbirds colonize areas (see Cruz et al. 1998,

Kostecke et al. 2004).

CHAPTER 4. DIFFERENTIAL HOST USE BY SYMPATRIC COWBIRDS. I. INTERSPECIFIC COMPETITION BETWEEN BROWN-HEADED AND BRONZED COWBIRDS

Niche differentiation, involving species partitioning of niche parameters such as food and space, may reduce competition and permit coexistence (Gause 1934, Kotler and Brown 1999). Niche partitioning is a common result of competition (Dickman et al. 1983, Price 1986, Rosenzwig 1987, Kotler and Brown 1999, Grant 1999). Competitive exclusion has been demonstrated most directly through removal of potential competitors (Schoener 1974, Connell 1983), with resultant shifts in resource use in the predicted direction, e.g. a greater diversity of seed sizes were consumed when competitors were excluded (Brown 1989). Likewise, broad geographic studies may reveal trends in resource use that match predictions for competitive exclusion (Kotler and Brown 1999). For instance, a species' success in areas with and without a competitor may be compared to infer competition.

Friedmann (1967) and Higuchi (1998) considered host nests as limiting resources for species of brood-parasitic cuckoos (*Cuculus* spp.) and favored the competition hypothesis to explain the lack of overlap in host species used by cuckoos in sympatry. By contrast, three of the five brood-parasitic cowbirds (*aeneus*, *ater* and *bonariensis*) have been considered incapable of partitioning hosts as they employ little to no selectivity in their use of songbirds as hosts (Friedmann 1929, et al. 1977; Rothstein 1975, 1990; Kattan 1997). These cowbirds are host generalists, as individuals parasitize multiple species (Gibbs et al. 1997, Chapter 2) such that each cowbird species collectively has parasitized the nests of more than 95 species of hosts (Table 1.2). The hypothesized lack of selectivity has been supported by studies of *ater* demonstrating

extraordinary annual egg production, 40-77 eggs (Table 1.1), parasitism on unsuitable

hosts (Rothstein et al. 1986, Rothstein and Robinson 1998) and conformity of egg

dispersion to random Poisson series (Orians et al. 1989, Lea and Kattan 1998, Mermoz

and Fernández 2003). However, all three areas of evidence remain in dispute.

Recent genetic-based studies have determined that for *ater*, the number of eggs

laid in nests as opposed to number produced is far lower (1-17 eggs) than that measured

in captivity (Hahn et al. 1999, Shonk 2001, Woolfenden et al. 2002, Strausberger and

Ashley 2003). Secondly, *ater* reduced the use of unsuitable hosts over time (Kozlovic

1998) and do not use some rejecter species (Table 1.5). Moreover, comparison between

egg dispersion and Poisson series has essentially been applied as a litmus-test for random

egg dispersion (Lowther 1984, Lea and Kattan 1998, Chapter 3). Host use has rarely

been analyzed at the level of the community relative to nest availability or host quality,

which potentially obfuscates non-random patterns within songbird communities.

The correct measure of host use requires the comparison of parasitized nests with

those that were simultaneously available, yet not used. Several community-based studies

have suggested that cowbirds differentially use certain species' nests (Briskie et al. 1990,

Barber and Martin 1997, Woolfenden et al. 2004), nest substrates (Hahn and Hatfield

1995) and habitat features (F. R. Thompson 1994, Curson and Matthews 2003).

Nevertheless, no study has clearly demonstrated that host use reflects adaptive features,

relative to community composition. Therefore, areas where two cowbirds breed in

sympatry should be ideal for determining how cowbirds use their hosts. For instance,

does the presumably heightened competition for host nests affect host use, as suggested

by Friedmann (1928, 1929, 1967)? If sympatric cowbirds partition hosts, then the suite

of species commonly parasitized by each may be predicted to differ in some general characteristics, such as body size or egg appearance. Also, cowbirds may modify their use of hosts, geographically, relative to the presence or absence of competitors. Thus, determination of the processes affecting host use by sympatric cowbirds can yield insights into the evolution of host use and potential character displacements promoting speciation, i.e. isolation via geographic or behavioral/physical divergence.

To test whether sympatric *ater* and *aeneus* use different hosts, I examined whether the hosts favored by each reflected greater suitability due to abundance, body size, and response to parasitic eggs. Alternatively, cowbirds may randomly distribute their eggs among nests of small-bodied songbirds and/or resulting patterns of host use may reflect differential nest defense (Briskie et al. 1990) or rejection of eggs by hosts (Fraga 1985). Likewise, cowbirds may use different habitats (Chace 2004) and/or exhibit interspecific territoriality (Brooker and Brooker 1990). Assuming random use, hosts would be used in proportion to their abundance and no differential host use should be observed (Wiley 1988). Differentially directed host behaviors or interspecific territoriality would be detected through patterns of egg dispersion and/or behavioral observations, such as interspecific antagonism (i.e., physical and vocal interactions). Differences in habitat use may also be reflected among the host species used by sympatric cowbirds.

THE HYPOTHESES

Ideally, competition is detected through manipulative or descriptive studies where competitors are excluded physically (Alatalo et al. 1985, Abramsky et al. 1991, Bonsall

and Hassell 1997) or geographically (Bowers and Brown 1982). Manipulation was logistically impractical and descriptive geographic data were incomplete. Therefore, I relied upon detailed measurement of host use at a site with sympatric cowbirds to facilitate comparison with available data for each cowbird in allopatry.

Prediction 1: If competition among cowbirds for host nests is high, variance in reproductive success will reflect cowbird density. This prediction follows Gause's (1934) theory that competition reduces reproductive success. Authors commonly assume cowbirds compete for host nests, yet this has not been tested directly (see Hahn et al. 1999). Frettwell (1977) hypothesized that parasitism frequencies on hosts should be inversely related to their densities. This can be extended to consider cowbird reproductive success: as cowbird-to-host ratios increase, losses associated with multiple parasitism will increase, e.g. egg puncturing or removal (Massoni and Reboreda 2002) and nestling competition (Goguen 1999, Trine 2000, Chapter 3). Therefore, cowbird reproductive success should decline once cowbirds reach some threshold density (McGeen 1972). Such patterns should be similar across different host communities and nest predation rates.

Prediction 2: Where two cowbirds breed in sympatry, host use will be less variable with respect to host quality. If cowbird species competed for hosts historically, current host use by sympatric cowbirds will be nonrandom with respect to host qualities. Specifically, because body size is generally correlated with nestling provisioning rates (Weathers 1992, Kilpatrick 2002), the larger *aeneus* (57 g) is predicted to use larger hosts than *ater* (32 g) (Lowther 1993, 1995). Thus, because the two cowbirds differ in size, which largely determines nestling growth rates (Weathers 1992, Starck and Ricklefs

2000), each should use hosts nearer their respective optima for host care more frequently than where allopatric.

Prediction 3: If the two cowbirds do not share hosts locally, then host use should be similarly affected elsewhere relative to densities of each species of cowbird. Each species of cowbird should use a greater proportion of the host species available at sites when in allopatry versus sympatry. Differences should be reflected in number of species used as well as the breadth of host body sizes and host species availability.

Because I did not test for competition among cowbirds directly, I could only infer competition from measurement of host use. I reasoned that if the preceding predictions were supported and no alternatives were, then competition most likely explained host use among cowbirds in Texas.

METHODS

DETECTING THE RESULTS OF COMPETITION

Data for cowbirds in allopatry

Recent genetic studies have measured host use for *ater* (Hahn et al. 1999, Strausberger and Ashley 2003, Woolfenden et al. 2003), however, these studies also frequently involved collection of cowbird eggs and/or radio-tracked female cowbirds and, therefore, only provide estimates for realized fecundity and not reproductive success *per se* (see Hahn et al. 1999). Hence, I tested for a relationship between cowbird densities and estimates for reproductive success (percent fledging success) from observational studies of *ater* and *aeneus* in allopatry.

To test for density-dependence, I used regression to test for a relationship between cowbird density or reproductive success and parasitism frequency. Because few studies recorded female cowbird density, I assumed cowbird parasitism frequencies reflected cowbird densities. Since cowbirds may differentially parasitize certain species (McGeen 1972, Sedgwick and Knopf 1988, Wiley 1988, Briskie et al. 1990), it was important to weight cowbird density relative to host abundance *and* differential parasitism patterns by cowbirds. To do this, I used McGeen's (1972) cowbird "pressure" statistic,

$$C = (p + mp) / 2 ,$$

where *p* represents the percent of nests parasitized and *mp* the percent of parasitized nests with more than one cowbird egg. I tested the assumption that cowbird reproductive success reflects cowbird abundance (or "pressure") and compared the incidence of multiple cowbird eggs using regression. I also compared the reported densities and rates at which cowbirds punctured or removed each other's eggs (Mayfield 1960, Trine 2000, Massoni and Reboreda 2002).

Data for cowbirds in sympatry

I previously described cowbird reproductive success and host densities in Texas (Chapter 2). Here, I describe in greater detail methods employed to measure the densities for each cowbird at the site. I determined bird densities by spot-mapping all species within the 27-ha core area every 3 - 4 d between 0650 and 0836 CDT (Koskimies and Vaisanen 1991). I recorded the location of each bird encountered within 50 m of four parallel transects such that the entire core area was surveyed. This was crucial for measuring host/cowbird abundance and calibrating success at locating all nests on the site. Host

abundance was determined for each species as the number of males per spot-map count

(Koskimies and Vaisanen 1991). Nest availability was recorded by two to three trained

nest searchers who searched for all nests within the area each day. Nest densities were

then calculated based on the average number of nests per ha of the core.

Accurate estimation of cowbird abundance is difficult because cowbird

populations often are male-biased (Ortega 1998) and cowbirds may commute up to 14

km from feeding to breeding areas (Curson et al. 2000). To minimize error, cowbird

abundance was measured as the number of female cowbirds detected during

spot-mapping. Because most cowbirds have moved to feeding grounds by 1100 h (F. R.

Thompson 1994, Curson et al. 2000), abundance counts were completed prior to 0830

CDT. The number of females laying in the core was also determined using microsatellite

DNA markers to assign maternity to cowbird eggs, as in Chapter 3.

PATTERNS OF HOST USE BY SYMPATRIC COWBIRDS

Nests were located at the site as described above and in Chapter 3. Data were collected

following the methods in Chapter 3, although here, I outline further methods applied to

analyses of host use. Nests susceptible to cowbirds were those of species recorded as

hosts that were within ± 3 d of the host's first egg during cowbird laying (see Sealy 1992,

Pease and Grzybowski 1995). During host laying, nests were monitored daily for

cowbird eggs. After laying, nests were checked every 1-3 d. The 1999 control season

established egg ejection and multiple parasitism (≥ 1 cowbird egg per nest) frequencies at

unmanipulated nests. In 1999, songbird nests were monitored across a wider range of

habitat types (Fig. 2.1) to measure cowbird habitat use.

Cowbird eggs found beneath nests (n = 20 *ater*, 13 *aeneus*) or on the nest rim (one

egg of each species) were counted as parasitism. Video-analysis revealed cowbirds may

miss nests while laying (n = 5, Chapter 3). I included these eggs in my analysis of host

use as they reflected a cowbird's behavioral commitment to visit and presumably lay in

these nests.

Because spatial structure and interference may affect the magnitude of

competition (Nilsson and Ruxton 2004), I analyzed whether female cowbirds were

territorial (i.e. physical and vocal displays *sensu* Darley 1982) or were spatially restricted

by the distribution of males. To determine the dispersion of individuals, I recorded the

locations, associations (sex and species of birds within groups) and categorized behaviors

(foraging, territoriality and courtship) for all cowbirds sighted. These data were collected

through opportunistic encounters as well as during frequent systematic resighting periods.

Systematic resighting took place with a spotting scope at designated locations from which

approximately one-quarter of the study area was visible (Fig. 2.1).

Behaviors categorized as territoriality included attempts to displace and chase

members of the same sex. For males, this meant overt icterine displays such as head-up

and chest swelling displays (Skutch 1996). For females, chasing and chatter

vocalizations were recorded as territoriality (Darley 1982). Male song could convey

elements of territoriality and/or courtship and was therefore not considered in the

analysis. For courtship, I included only observations of courtship displays or copulations.

I recorded birds as foraging if they probed a substrate more than four times per minute.

Resighting periods allowed me to detect banded birds that had moved from the

study site as well as record the behavior (foraging versus courtship) of birds away from

the breeding area. Observational data were then compared with respect to the amounts of time cowbirds spent in the core areas involved in laying, courtship and/or foraging. Territoriality by females has been described for *ater* (Darley 1982, Yokel 1989, Hahn et al. 1999), but not *aeneus* (Carter 1984). However male *aeneus* exhibit a distinct aerial hover display in exploded leks (Carter 1984, 1986). Therefore, to test the stability and effects of male dispersion on host use by females, I quantified male daily activities. I recorded the frequency and daily timing of male displays. The display is a pre-requisite for courtship culminating in a copulation (Friedmann 1929, Clotfelter 1995).

TESTING FOR GEOGRAPHIC DIFFERENCES IN HOST USE BY COWBIRDS

I consulted the literature to assess host use by cowbirds in areas of allopatry. I summarized use data from studies of host communities that demonstrated use among several species because studies of one focal species may have missed use of alternative hosts (Table 4.4, Appendix 7). I quantified the diversity of hosts used at each site using the Shannon-Weaver diversity index, H and associated Evenness statistic, E (*sensu* Mason 1986b). For this analysis, I considered as hosts only species that were parasitized and known to have reared cowbirds. I compared average host diversity between sites where cowbirds bred in allopatry and sympatry. For comparison, I calculated H values for the same sites using host use by host mass categories of: ≤ 14, 15-19, 20-24, 25-29, 30-34, 35-39, and ≥ 40g. Such analysis may reveal patterns obscured by phylogeographic trends present among species. For instance, a size class of hosts may be over-represented in a species-based analysis due to radiation and speciation without differences in body size. Likewise, cowbirds may not discriminate between species by

details of appearance and instead may only discern gross differences in host body (or nest) size. I categorized host adult female masses from Dunning (1993) and for more recently recognized species (Solitary Vireo complex and the Eastern Towhee) I used masses from the appropriate monographs from the *Birds of North America Series*.

I considered that Carter's (1986) study involved only *aeneus* as he observed a total of seven eggs and one fledgling of *ater* during his three-year study, which surveyed 212 nests, 153 adult-fledgling broods, and included 6700 h of mist-netting. I also did not include studies of *aeneus* that focused on the use of one or a few species and were not community surveys, i.e. Peer and Sealy (1999b), McGaha (2000), Hathcock (2001).

All statistical tests were performed using SPSS statistical software. All comparisons were two-tailed unless otherwise noted. Only critical values resulting in P ≤ 0.05 were considered significant.

RESULTS

DETECTING THE RESULTS OF COMPETITION

Data for cowbirds in allopatry

Cowbirds competed for host nests in a density-dependent fashion. Although the trends were not significant, they indicated that cowbird reproductive success decreased at higher densities across a variety of habitat types (Figs. 4.1-2). The trend was apparent where only parasitism data were available (Fig. 4.2) and persisted across years during long-term studies (Fig. 4.3). The substitution of cowbird pressure for cowbird density was supported by the inverse relationship between cowbird pressure and density (Fig. 4.2). Likewise, the frequency of parasitism was directly related to cowbird density (Fig.

ater
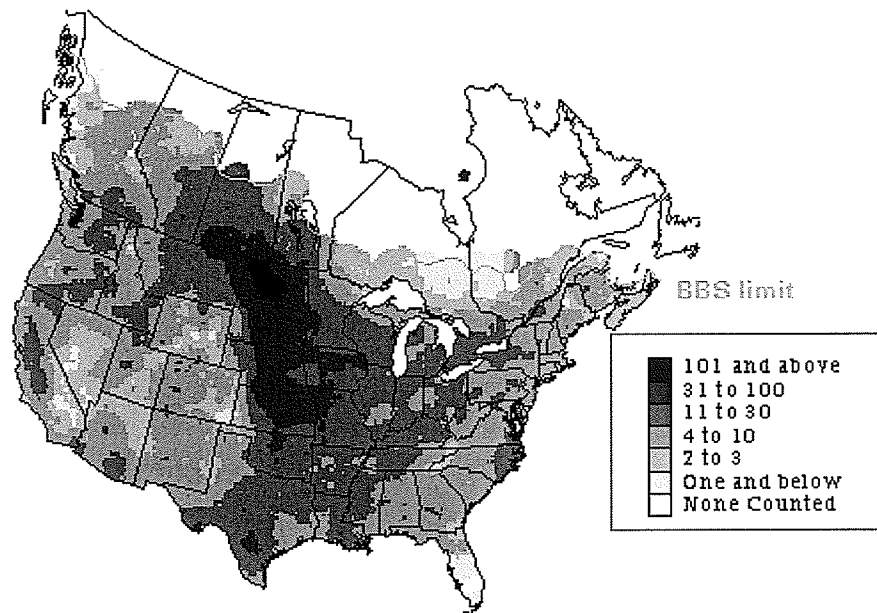
aeneus
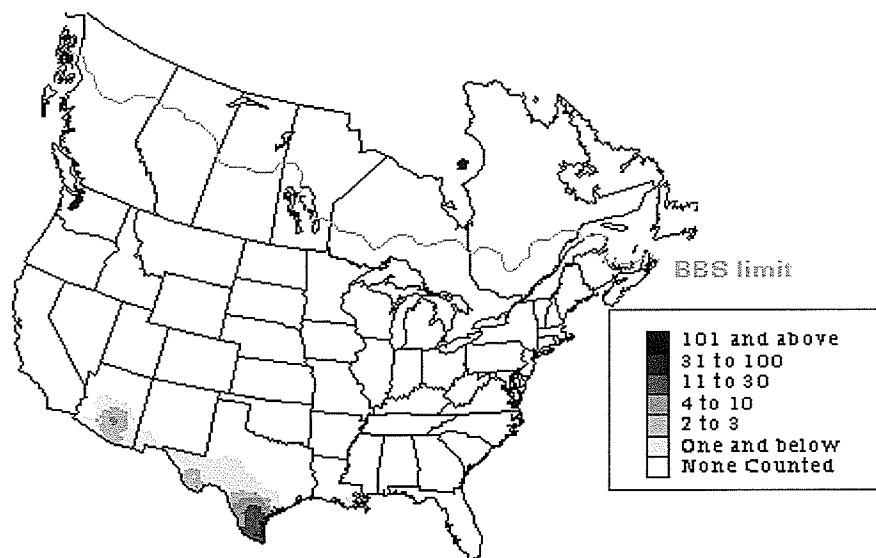
Figure 4.1. Regional estimates for cowbird density derived from Breeding Bird Survey

(BBS) counts of males and females along established roadway routes (Sauer et al. 2003).

Populations of *ater* and *aeneus* are male-biased (Ortega 1998), thus density values are

higher than those I estimated for females alone. BBS limits represent the northern limit

for data collection.

A

B
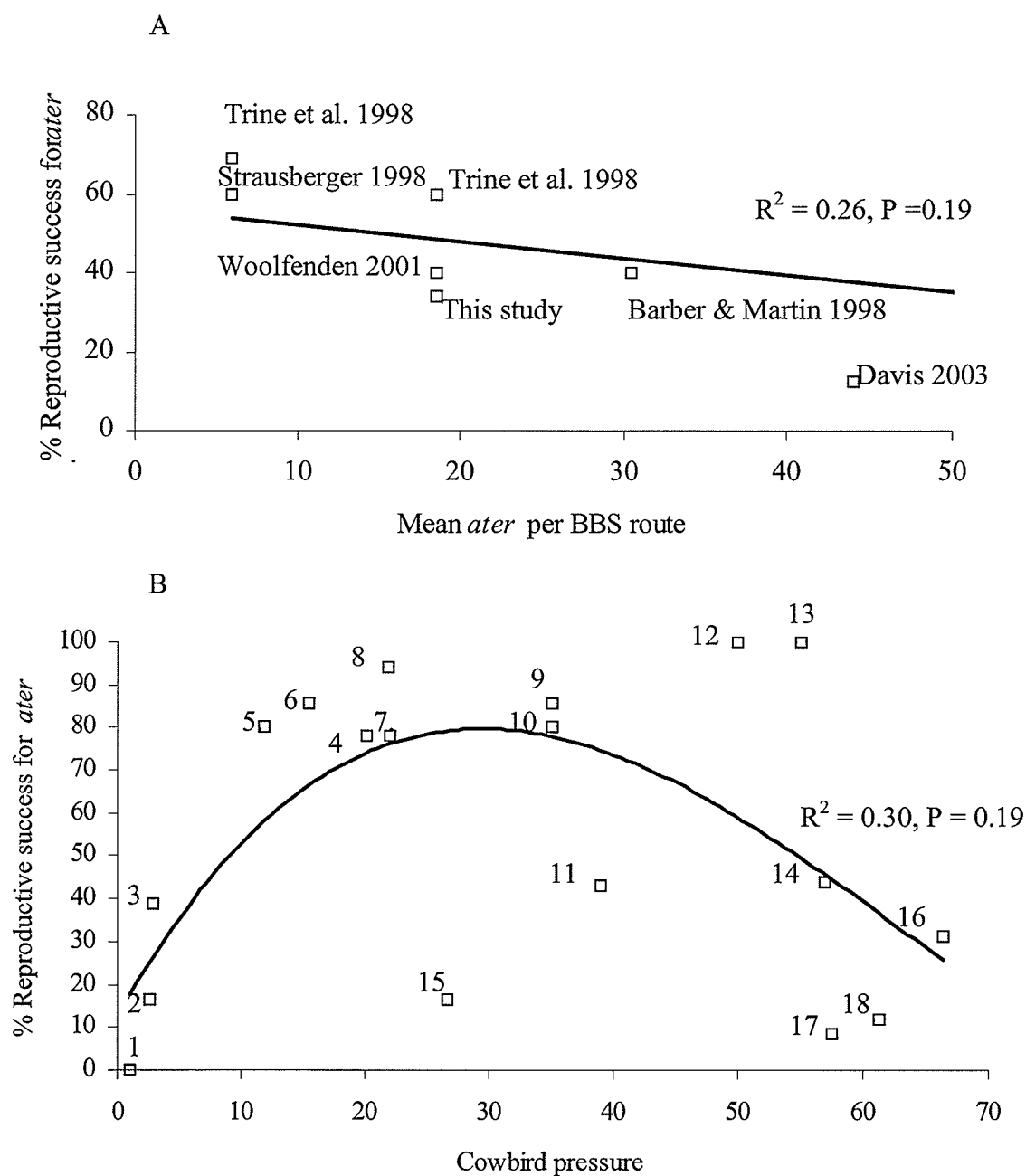
Figure 4.2. Cowbird success as function of (A) cowbird density and (B) relative cowbird

pressure (*sensu* McGeen 1972). Cowbird productivity decreased at high cowbird

densities; conforming to predictions if cowbirds compete for host nests. Sources in (B):

1. Ellison (1999), 2. Vander Hagen and Matthews (1999), 4. Nolan (1978), 5-14. Trine et

al. 1998, 15-16. McGeen (1972), and 3, 17-18. this study.

ater

aeneus
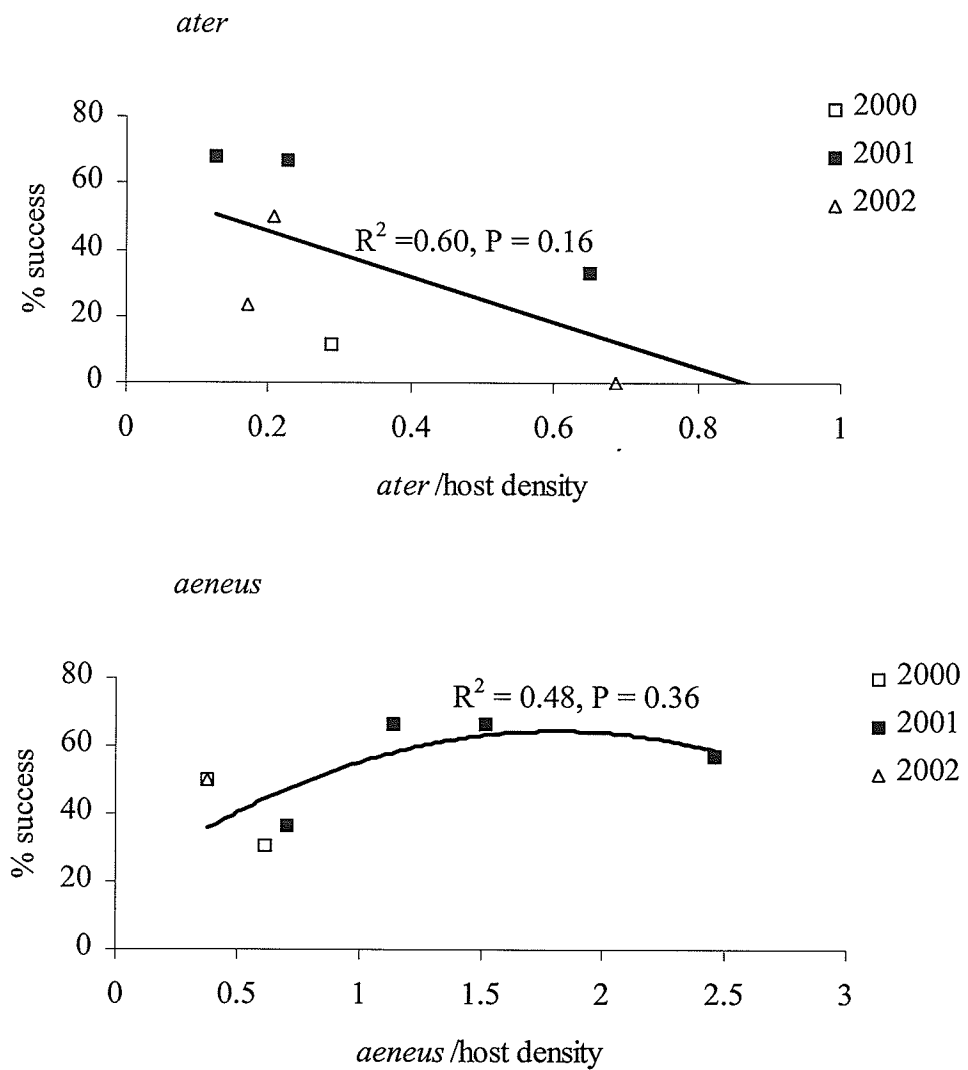
Figure 4.3. Variation in cowbird success relative to intraspecific density at Ft. Clark Springs, Texas.

4.4). This relationship was demonstrated when cowbird densities were reduced through trapping (Fig. 4.5). The reduction in cowbird productivity at high densities was associated with more multiple parasitism and more pierced eggs (Fig. 4.6).

Data for cowbirds in sympatry

Overall, 1,447 potential host nests suitable for cowbird parasitism were monitored (1999-2002), among which 393 cowbird eggs/young were found (Table 2.2). Within the core area (2000-02) 686 nests were monitored, of which 170 (24.8%) were parasitized (Table 2.2). Annually, host abundance did not vary significantly among the most abundant 10 species during 60 censuses (Friedman χ^2 = 5.0, df = 2, P = 0.08). The two cowbird species were nearly equally abundant, with female *ater* and *aeneus* ranked 14[th] and 15[th] among species detected, respectively. Females did not differ in annual abundance (Kruskal-Wallis H= 5.60, df = 5, P = 0.35) or overall detection rate (*ater*: 90 detections, 1.50 $\pm$ 2.01 females per count; *aeneus*: 86 detections, 1.43 $\pm$ 1.51 females per count). Based on genetic maternity, 17 *ater* and 12 *aeneus* laid eggs in the core area. The number of laying females, determined through genetic analysis (Chapters 2 and 3), did not differ between the cowbird species. Among years, there was no consistent pattern in the number of eggs laid by each species; in 2002 more eggs were laid by *ater* than *aeneus* and vice versa in 2000 and 2001, however the differences were significant in only 2001 and 2002 (Table 3.7). Genetic tracking of host use by individuals revealed use of multiple host species (Chapter 2).

Each species used a few hosts in a density-dependent fashion, however, all potential hosts were not parasitized in this manner (Table 2.2). Indeed, each species
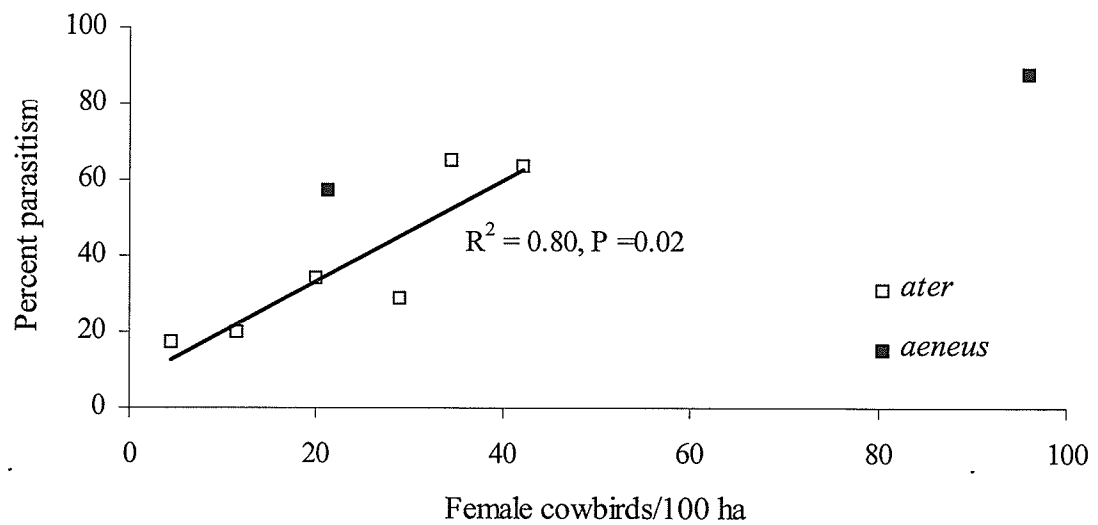
Figure 4.4. Cowbird parasitism levels as a function of cowbird density (data from Hahn et

al. 1999, Davis and Sealy 2000, Strausberger and Ashley 2003, this study). Regression

line calculated for only *ater*, as data for *aeneus* were available from only two sites.
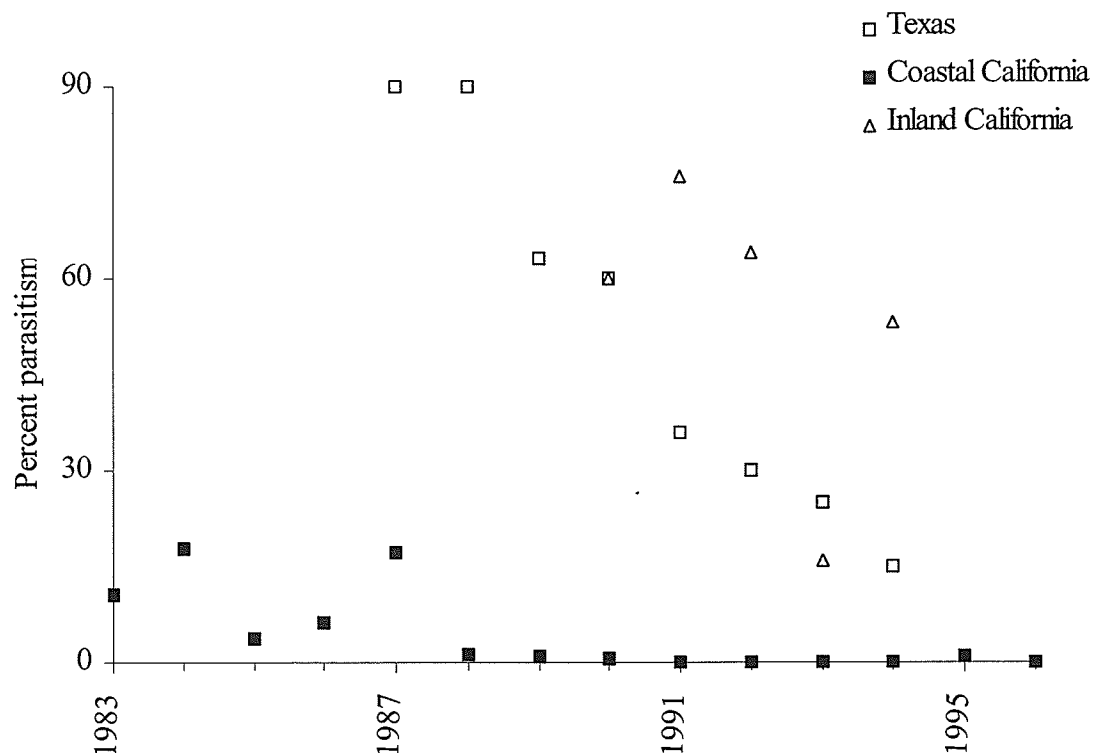
Figure 4.5. *Ater* parasitism levels on single hosts during annual cowbird removal programs in Texas (Black-capped Vireo: Hayden et al. 2000) and coastal and inland California (Bell's Vireo: Griffith and Griffith 2000; Willow Flycatcher: Whitfield 2000). Annually, averages of 1,265, 173, and 190 females were removed during the studies in Texas and coastal and inland California, respectively. The studies in California also involved variable levels of cowbird egg removal or addling, see studies for details. All studies demonstrate declines in parasitism frequency associated with reduced cowbird numbers.

A

B
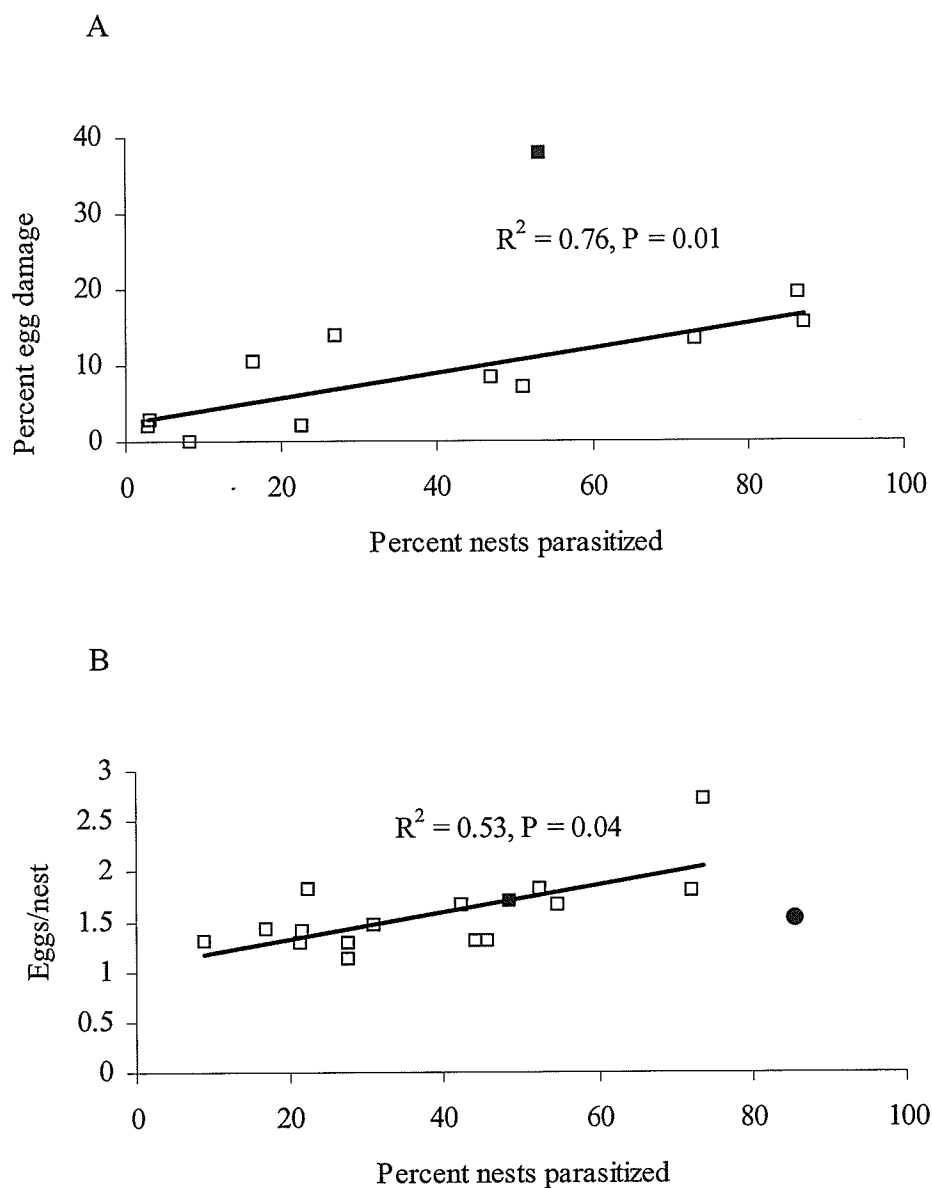
Figure 4.6. The incidence of (A) egg damage and (B) multiple parasitism relative to the

frequencies of cowbird parasitism. In (A), data from Blankespoor et al. (1982) (solid

square) was considered an outlier as their analysis using microscopy was far more

sensitive than other workers. In (B), data from this study indicated by solid square and

circle for *ater* and *aeneus*, respectively.

parasitized primarily only two hosts; 85% of *ater* eggs were laid in Bell's Vireo and Blue-gray Gnatcatcher nests, whereas 87% of *aeneus* eggs were laid in Orchard Oriole and Hooded Oriole nests (Tables 2.2, 3.3). Nests of these hosts were often parasitized (> 70%), whereas other hosts were used less frequently (Table 2.2). The lack of host overlap found among nests within the core area was also found among nests and host-cowbird fledgling pairs in adjacent areas (Table 2.2). Because the cowbird species infrequently parasitized the same host species, interspecific competition for hosts appeared to be minimal (Figs. 4.2 and 4.5), particularly relative to the intraspecific competition (multiple parasitism and egg damage) measured at my site and elsewhere (Fig. 4.3).

PATTERNS OF HOST USE BY SYMPATRIC COWBIRDS

Cowbirds used relatively restricted host suites among 1,442 nests of 36 potential host species available during cowbird laying. Only 10 instances of overlap in host use occurred, three of which were first records of parasitism by *aeneus* (Table 2.2). The pattern of host use did not result from differential habitat use as nests parasitized by each species overlapped extensively both spatially (Fig. 4.7) and in habitat types. The clustering tendency for *aeneus* hosts was due to orioles nesting in clusters or "loose colonies" (Williams 1988) and nesting higher in larger trees than were available on the east side of the site (mean nest height = 5.2 m, n = 36). Likewise, the dates and duration of breeding for both *ater* and *aeneus* overlapped extensively, therefore, the cowbirds laid their eggs when sympatric in space and time (Table 4.1). Overall, host nest availability did not vary among years (Friedman χ^2 = 1.1, df = 2, P = 0.58) and host abundance and
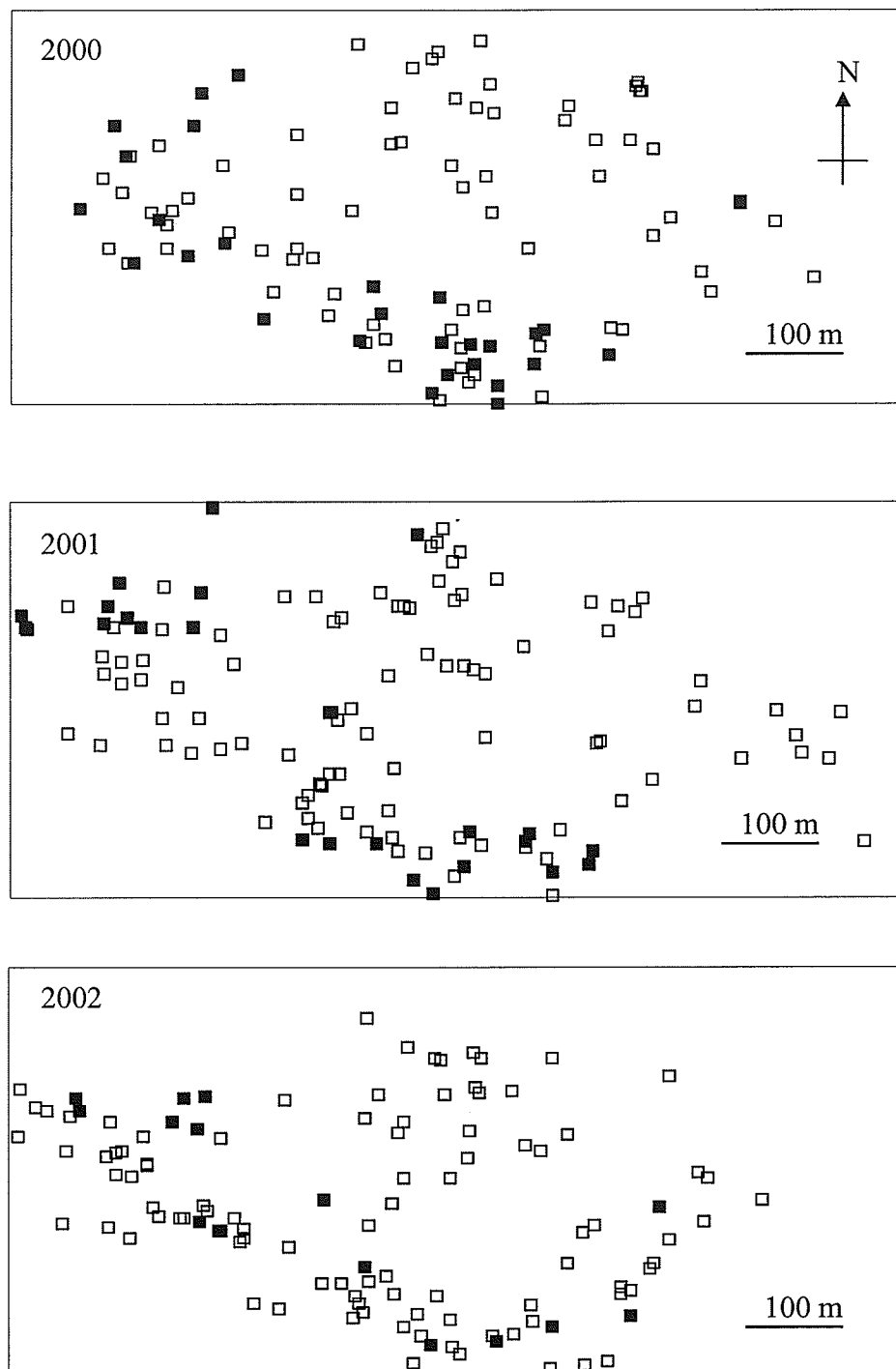
Figure 4.7. Locations of nests of focal hosts for *ater* (open squares) and *aeneus* (solid

squares), during 2000-2002. Nest and cowbird egg dispersion overlapped extensively for

potential hosts of *ater* and *aeneus*.

nest availability were correlated (2000: ρ = 0.70, P = 0.02; 2001: ρ =0.76, P = 0.01; 2002: ρ = 0.62, P = 0.05).

Parasitism by cowbirds was not strongly associated with any measure of host abundance (Chapter 3). Nest abundance and nesting dates differed among species. However, dates of nest availability were correlated among species used as hosts and those not parasitized by each cowbird (Chapter 3, Figs. 2.5 and 3.1). Each year, the duration of cowbird laying did not differ (Table 4.1), however, initiation and laying dates differed among years (Table 4.1). The lack of overlap in host use sharply contrasts with numerous studies of host use by *ater* in allopatry where a greater diversity of hosts were used (Figs. 4.2 and 4.4). The pattern was not a result of sampling host use for one or two females, as multiple individuals of each species regularly parasitized up to four host species each with virtually no overlap (2%, n = 10) (Fig. 2.6). The lack of overlap in host use I measured was not due to any species rejecting the eggs of either cowbird. During 70 of 458 nest watches when cowbird laying was recorded, I did not detect evidence that any species commonly ejected cowbird eggs that I may have subsequently missed. Bullock's Orioles were the only species known to eject cowbird eggs during the study, however, by checking nests shortly after cowbird nest visits, I collected fourteen *aeneus* eggs from Bullock's Oriole nests. Five of those cowbird eggs were punctured.

Cowbirds did not use hosts randomly with respect to characters of host quality as host mass most clearly predicted host use for each (stepwise multiple regression: $F_{1,9}$ = 5.20, P = 0.049). The smaller *ater* (32 g) used hosts ranging from 5 to 30 g, whereas *aeneus* (57 g) primarily used hosts > 25 g (Fig. 4.8, Table 2.2). Mean masses for the two groups of hosts differed significantly (Mann-Whitney U_{24} = 3.00, P = 0.047). Host mass

Table 4.1. Breeding season initiation and cessation dates. Breeding dates represent first egg date for each host nest.

| | Breeding dates (duration in days) | | | |
	1999	2000	2001	2002
Vermilion Flycatcher	14 Apr.-22 July (99)	4 Apr.-7 July (94)	1 Apr.-6 July (96)	1 Apr.-25 June (85)
Bell's Vireo	18 Apr.-11 July (84)	13 Apr.-7 July (85)	13 Apr.-18 June (66)	22 Apr.-11 July (80)
Blue-gray Gnatcatcher	23 Apr.-27 May (31)	--[a]	1 May-21 June (51)	3 May-25 June (53)
Focal hosts	14 Apr.-22 July (99)	4 Apr.-7 July (94)	1 Apr.-6 July (96)	1 Apr.- 11 July (101)
ater	23 Apr.-16 July (84)	29 Apr.-9 July (71)	25 Apr.-28 Jun. (64)	23 Apr.-11 July (79)
Orchard Oriole	17 May-26 June (40)	4 May-3 June (30)	28 Apr.-9 June (42)	29 Apr.-24 May (25)
Hooded Oriole	20 May- 21 July (62)	1 May-16 July (76)	20 Apr.-10 July (81)	27 Apr.-9 July (73)
Bullock's Oriole	17 May-6 July (50)	2 May-13 June (42)	4 May-26 June (53)	12 May-10 June (29)
Focal hosts	17 May-21 July (65)	1 May-16 July (76)	20 Apr.-10 July (81)	27 Apr.-9 July (73)
aeneus	30 Apr.-21 July (82)	1 May-16 July (76)	21 Apr.-12 July (82)	24 Apr.-7 July (74)

[a] No nests found in study area that year.
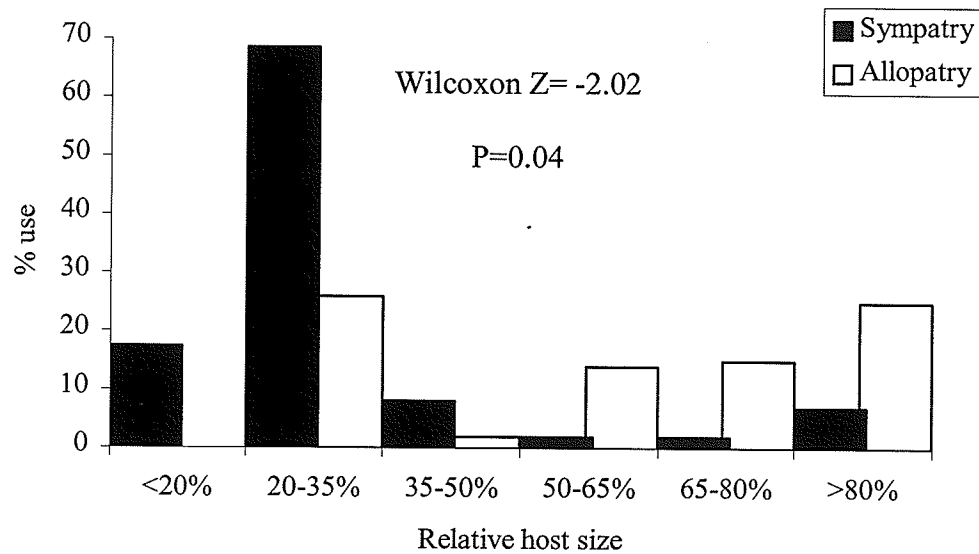
Figure 4.8. Percent parasitism according to host size (mass ratio: female *ater*/host) for

ater in allopatry and sympatry with *aeneus*. Data for host use by *ater* in allopatry are

from Strausberger (1998) and Hahn et al. (1999).

was correlated closely with egg volume ($\rho = 0.93$, n = 11 hosts, P = 0.06) and measures of nestling provisioning rates (Table 3.5). Host use was not related to host abundance as measured by bird or nest abundance (Chapter 3).

Host use did not reflect avoidance of species that detect cowbirds at nests. Both cowbirds frequently encountered and were attacked by some hosts (Table 4.2). Some potential hosts caused parasitism attempts to fail (Chapter 3). However, this was relatively rare and did not affect overall patterns of host use. Host use patterns did not differ across habitat types in the greater area studied in 1999. However, host use differed with respect to distance inside riparian forest edge among the limited sample of parasitized nests in this habitat. Indeed, *aeneus* did not parasitize nests more than 16 m into riparian forest. By contrast, *ater* laid eggs up to 56 m from the forest edge. However, riparian forest was limited in extent and the primary study site for 2000-2002 did not consist of riparian forest.

I recorded 4,255 and 3,441 observations of *ater* and *aeneus*, respectively. Within the core area, *aeneus* displayed more courtship behavior than *ater*. I observed two and eight copulations for *ater* and *aeneus*, respectively. Male *aeneus* exhibited a bi-modal pattern for aerial hover displays that was inversely associated with daily temperatures (Fig. 4.9), as was overall activity. Male *aeneus* were more territorial than females (Table 4.3), whereas among *ater*, females were more territorial than males. *Aeneus* used the core area for courtship significantly more often than *ater* did (G=119.5, P<0.001). The frequency of hover displays by male *aeneus* was greatest during the two hours following normal laying time. Displaying then decreased throughout the day until

Table 4.2. Cowbird-host encounters and outcomes. A laying attempt was considered successful if an egg was laid in the nest cup during that visit.

Species	Host-cowbird encounters (visits)		% successful (n)	
	ater	aeneus	ater	aeneus
Bell's Vireo	74% (23)	0%	83 (23)	--
Blue-gray Gnatcatcher	43% (7)	0%	86 (7)	--
Painted Bunting	100% (2)	0%	50 (2)	--
Orchard Oriole	100% (1)	68% (38)	100 (1)	95 (38)
Hooded Oriole	100% (1)	73% (30)	100 (1)	100 (30)
Bullock's Oriole	0%	50% (6)	--	100 (6)
Northern Cardinal	0%	0% (2)	--	100 (2)
Total	71% (34)	68% (76)	82 (34)	97 (76)
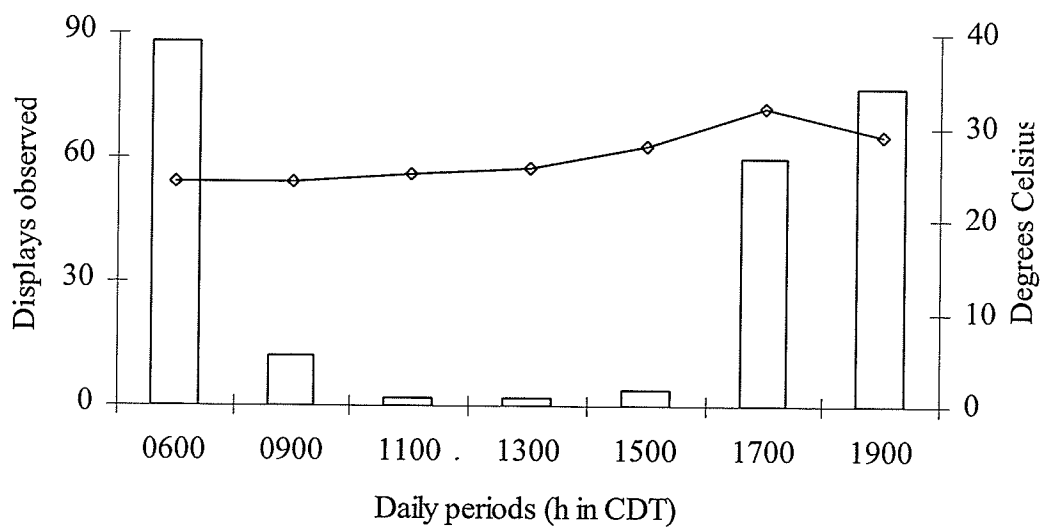
Figure 4.9. Daily timing of aerial hover displays by male *aeneus* (bars). Crepuscular

peaks reflect typical daily temperatures (line: 1 July, 2002) and possible insemination

window.

Table 4.3. Categorized behaviors within the core area.

		Foraging	Territoriality	Courtship	Total observations
ater					
	Female	95.2%	4.4%	0.4%	794
	Male	99.0%	0.6%	0.3%	2,032
aeneus		77.9%	2.7%	19.4%	962
	Female				
	Male	66.2%	12.6%	21.2%	1,260

again peaking in the evening (> 1700 h) tailing to a lower rate at pre-roosting areas. Few displays and no copulations were observed outside the core area.

TESTING FOR GEOGRAPHIC DIFFERENCES IN HOST USE BY COWBIRDS

Comparison of Host Use in Sympatry and Allopatry

Host use by sympatric cowbirds differed dramatically from that in allopatry (Fig. 4.8, Tables 4.4, 4.5 and 4.6). For both cowbirds, the average number (*ater*: -1.7; *aeneus*: +2.0) and diversity (Shannon-Weaver H: *ater*: -0.2; *aeneus*: -0.6) of hosts generally declined among sympatric populations (Tables 4.4 and 4.5). Moreover, host use was less even (E) for both species (*ater*: -0.8; *aeneus*: -0.1) in sympatry, emphasizing the restricted use that occurred (Table 4.5). Likewise, the diversity measures based on host masses confirmed the analysis based on species diversity, as mass diversity generally decreased when cowbirds were in sympatry (average differences, ΔH: *ater*: -0.8; *aeneus*: -0.1 ; ΔE: *ater*: -0.8; *aeneus*: -0.1) (Table 4.6). Cowbirds restricted host use with respect to body size in the predicted manner, *ater* used species $\leq$ 18g and *aeneus* used larger species (t = -7.15, *df* = 24, P < 0.001). While the differences in allopatric and sympatric host use were often not statistically significant, the overall trend suggests interspecific competition affects host use. The only exceptions to the trend predicted by the resource partitioning hypothesis were the host mass diversity and evenness scores for *aeneus* (Table 4.4).

Table 4.4. Summary of comparisons for host use characteristics of *ater* and *aeneus* in allopatry versus sympatry. Shannon-Weaver indices for Diversity (H) and Evenness (E) based on number of cowbird eggs laid per host species'[a] nest. * = P-value < 0.05 using Mann-Whitney U test.

	Number of studies compared	N (# p_i)[a]	Diversity, H[b]	Evenness, E[c]
By host species				
ater	11	>	>	>
aeneus	1	<	>	>
By host mass				
ater	11	> (>)	>*	>
aeneus	1	> (<)	<	<

[a] For comparisons by host mass, hosts were categorized by mass, therefore, I used average mass score (N) and number of species per mass category (# p_i) to calculate H and E.

Table 4.5. Characteristics of host use by *ater* and *aeneus* when in allopatry and sympatry. Diversity (H) and Evenness (E) based on number of cowbird eggs laid per host species' [a] nest.

Site	Species used (available) [b]	H [c]	E [d]	Source
Allopatry				
ater				
New York	13 (25)	2.32	0.91	Hahn et al. (1999)
Illinois	18 (19)	2.18	0.76	Strausberger & Ashley (1997)
Illinois	10-16 (10-16)	1.43-2.29	0.43-0.82	Trine et al. (1998), 3 sites
Manitoba	9 (12)	1.58	0.72	Hill & Sealy (1994), Woolfenden (2000), Underwood et al. (2004)
Saskatchewan	6 (6)	1.48	0.92	Davis (2003)
Kansas	4 (4)	1.05	0.76	Fleischer (1985)
Texas	5 (5)	1.26	0.78	Barber & Martin (1997).
Arizona	8 (9)	2.01	0.97	Brown (1994)
California	6 (23)	1.62	0.90	Purcell & Verner (1999)

Washington	3 (6)	0.90	0.82	Vander Hagen & Walker (1999)
average	9.5	1.63	0.76	

aeneus

Texas	6 (10)	1.62	0.91	Carter (1986)

Sympatry

ater

Texas	10 (18)	0.98	0.71	This study
Arizona	4 (7)	1.01	0.73	Chace (2001)
Average	7	1.00	0.72	

aeneus

Texas	11 (18)	1.37	0.76	This study
Arizona	5 (7)	1.35	0.84	Chace (2001)
Average	8	1.36	0.80	

[a] Host species from each site listed in Appendix 7. [b] Species considered available were known hosts with ≥ 4 nests found per study.

[c-d] Shannon-Weaver Index, $H = \sum -p_i \ln (p_i)$, where p_i = percent of cowbird eggs in nests of each species, s and [c] Evenness, $E = H/\ln(s)$.

Table 4.6. Mass-based host use Diversity (H) and Evenness (E) calculated for *ater* and *aeneus* when in allopatry and sympatry.

Parasitism frequencies were summed within host species' mass categories[a], using formulae and data sources as in Table 4.4

Site	Species used	Mean size score (n used, available)[b]	H^c	E^d	Source
In allopatry					
ater					
New York	13	3.7 (7,7)	1.63	0.84	Hahn et al. (1999)
Illinois	18	4.1 (6,6)	1.32	0.74	Strausberger & Ashley (1997)
Illinois	10-16	2.9-3.0 (4-6,6)	0.91-1.07	0.56-0.66	Trine et al. (1998), 3 sites
Manitoba	9	2.9 (5,6)	1.27	0.79	Woolfenden (2000)
Saskatchewan	6	3.0 (4,4)	0.989	0.71	Davis (2003)
Kansas	4	6 (2,2)	0.65	0.93	Fleischer (1985)
Texas	5	2.8 (4,4)	1.05	0.76	Barber & Martin (1997)
Arizona	8	1.6 (3,3)	0.62	0.56	Brown (1994)
California	6	1.8 (3,4)	0.89	0.81	Purcell & Verner (1999)

Washington	3	2.0 (3,5)	0.90	0.82	Vander Hagen & Walker (1999)
average	9.5	2.7 (4.5)	1.02	0.73	
aeneus					
Texas	6	6.3 (2,2)	0.39	0.56	Carter (1986)
In sympatry					
ater					
Texas	10	2.5 (5,6)	0.33	0.21	This study
Arizona	4	1.4 (2,4)	0.64	0.93	Chace (2001)
average	7	2.0 (3.5)	0.49	0.57	
aeneus					
Texas	11	3.5 (5,6)	0.70	0.43	This study
Arizona	5	3.0 (4,4)	1.20	0.86	Chace (2001)
average	8	3.3 (4.5)	0.85	0.65	

[a] Species and size category data from each site listed in Appendix 7. [b] Number of mass-based categories. [c-d] Shannon-Weaver Index, [b] $H = \sum -p_i \ln (p_i)$, where p_i = percent of cowbird eggs in nests of each species' size category, c and [c] Evenness, $E = H/\ln(c)$.

DISCUSSION

Several types of data suggest that cowbirds compete intraspecifically for host nests. First, parasitism levels and female cowbird densities are positively correlated with total host densities (Gates and Gysel 1978, Verner and Ritter 1983, Rothstein et al. 1984, Airola 1986, Robinson et al. 2000, Thompson and Dijak 2000). Second, regional cowbird abundance and parasitism levels for some hosts were positively correlated (Fig. 4.2a) and host nest density was inversely related to the intensity of cowbird parasitism (Zimmerman 1983, Carello and Snyder 2000). Likewise, use of McGeen's (1972) cowbird pressure statistic to approximate cowbird densities demonstrated a similar density-dependent relationship (Fig. 4.2b). Finally, cowbird removal studies have demonstrated cowbird numbers were directly correlated with parasitism near the removal sites (De Groot and Smith 2001, Fig. 4.5). While most trends were not significant, they were all in the same direction, suggesting that cowbird reproductive success generally follows the relationship with host nest availability predicted by the competition hypothesis (Figs. 4.2-4.5), i.e. cowbird success decreases above threshold levels of parasitism.

In sympatry, *ater* and *aeneus* used different suites of hosts comprised of species equally available. The non-overlapping use was associated with host mass (Figs. 2.2, 4.9), which is linked to host quality (Weathers 1992). The restricted use of hosts by cowbirds in sympatry contrasted with a broader diversity of hosts used in allopatry across geographically diverse habitats and host communities (Tables 4.4-4.6). Therefore, when in sympatry, cowbirds appeared to partition hosts in a manner analogous to the host partitioning described for sympatric cuckoos (Friedmann 1928, Higuchi 1998).

These findings were quite robust for *ater* as the diversity of studies encompassed a variety of habitat types and host communities. Generally, where allopatric, each cowbird used a greater diversity of hosts than where sympatric. This trend was upheld when host diversity was analyzed using taxonomic or mass categories (Tables 4.6 and 4.7). Only in areas with low potential host diversity did host use by allopatric cowbirds approach that measured in sympatry. Indeed, the intensive nest searching effort in my study likely yielded higher levels of host diversity than measured for other sites which were restricted to certain strata, species, or habitat types. Chace's (2001) data support this interpretation as he recorded low host diversity and uneven host use based on samples within nesting communities. In both studies, *ater* did not use hosts often parasitized in allopatry (Friedmann 1963, Hill 1976a, Friedmann et al. 1977), namely, Western Tanagers in Arizona and Northern Cardinals, Orchard Orioles and Hooded Orioles in Texas (Chace 2001, this study). By contrast, my comparison of host use by *aeneus* was hampered by a lack of sites for *aeneus* in allopatry.

Carter's (1986) study provided the only site with community-based data for comparison. Differences in the diversity of host sizes were not in the direction predicted. However, the White-eyed Vireo (11 g) and Olive Sparrow (24 g) were the only small (< 25 g) potential hosts that occurred at Carter's (1986) site and he did not report finding any vireo nests despite their abundance, fourth most common among hosts, 1.1 pairs/ ha (Carter 1984, 1986). Therefore, the sole site for *aeneus* in allopatry consisted of a size-skewed sample of a host community with little potential for a greater diversity of host sizes to be used. This skew is more evident when average host size at Carter's (1986) site was compared to lists for species parasitized by *aeneus* (Table 4.6). For these

reasons, I considered the host community at Carter's (1986) site a poor one for measuring the diversity of hosts used. Indeed, the host use I observed matched that recorded elsewhere in a more general survey of the Rio Grande ecosystem, where sympatric *ater* and *aeneus* (see Warren 2002, Kostecke et al. 2004) parasitized mainly Bell's Vireo and Hooded Oriole nests, respectively (see also Wauer 1977). Likewise, data from general surveys of breeding birds in Oaxaca, Mexico, include use of only smaller hosts (mean = 13.3 g , Boucard's Wren, Blue-gray Gnatcatcher, and White-lored Gnatcatcher) for *ater* and larger hosts (mean = 38.2 g, 10 spp., range: 11-70 g) for *aeneus* (Rowley 1984, Forcey 2002).

Nonetheless, the magnitude of interspecific competition for hosts is not clear. I did not measure effects of nestling competition; however, energetic estimates and observational data for nestling growth suggest that *aeneus* would outcompete *ater* when reared by larger hosts (Eckerele and Breitwisch 1997). Being larger, *aeneus* nestlings grow relatively more slowly and require more food per feeding than *ater* (Carter 1986, Lowther 1993, 1995). This is supported by the studies that have shown *ater* does not compete well with larger hosts such as Northern Cardinals and Red-winged Blackbirds, which are 3-9 g larger than *ater*, depending on the subspecies of *ater* (Weatherhead 1989, Dunning 1993, Scott and Lemon 1996, Eckerele and Breitwisch 1997). Similarly, Peer and Sealy (2004a) found only *aeneus* fledged when nestlings of each species, *ater* and *aeneus*, were introduced into Great-tailed Grackle nests. Therefore, I suggest that interspecific competition is asymmetrical such that *ater* is more sensitive to the presence of *aeneus*, than *aeneus* is to that of *ater*.

Logically, this leads to hypotheses for why *aeneus* has not expanded its range further into areas occupied solely by *ater*. Indeed several large hosts, including those favored by *aeneus*, are available to the North. I attribute this mostly to the turnover in host communities, particularly with respect to the favored hosts of *aeneus*, the *Icterus* orioles (Friedmann 1929, Lowther 1995, Sealy and Underwood 2004, this study), which diminish in their abundance with increasing latitude. Likewise, frequently used hosts such as the Long-billed Thrasher and Olive Sparrow (Carter 1986) are not available and the Northern Mockingbird often ejects cowbird eggs, especially *aeneus* eggs (Peer et al. 2002). Alternatively, expansion by *aeneus* may be hindered by other factors such as interspecific competition for food as populations of other icterid species have increased in association with agriculture (see Whetje 2003). Nonetheless, *aeneus* continues to expand northward (Kostecke et al. 2004), albeit slowly compared to recent range expansions by *ater* and *bonariensis* (Rothstein 1994, Post et al. 1993, Sykes and Post 2001).

ALTERNATIVE HYPOTHESES

Few alternatives have been advanced to explain non-overlapping groups of hosts among sympatric brood parasites. Species often reduce competition through differential use of habitats and/or prey types (Gause 1934, Grant 1999). Through radio-tracking and censuses, Chace (2004) suggested sympatric *ater* and *aeneus* in southeastern Arizona did not avoid each other through strict habitat partitioning. Instead, cowbirds selected breeding sites primarily based on passerine richness and vegetation type, whereas distance from feeding areas did not figure as prominently in site selection. Thus, partitioning of habitat does not appear likely.

Likewise, cowbirds may avoid hosts more capable of defending their nests from parasitism. However, such a pattern was not observed (Table 4.2). Although *ater* was attacked during a parasitism attempt by a host typical of *aeneus* (Orchard Oriole), the encounter appeared similar to those recorded with typical hosts of *ater* (Table 4.2). Moreover, being larger, *aeneus* would be expected to access nests of smaller hosts but rarely did so (Table 2.2). Therefore, host use by each cowbird did not appear to be affected by host defensive behavior.

To explain similar, apparent partitioning of hosts by cuckoos (*Chrsococcyx* spp.), Brooker and Brooker (1990) suggested that such patterns resulted from direct removal of eggs by other cuckoos. They pointed out that in poorly illuminated domed nests, a dark, cryptically colored parasitic egg may have a selective advantage of not being removed during a subsequent cuckoo visit (Brooker and Brooker 1990). Their hypothesis was supported because hosts did not discriminate against non-mimetic eggs and cuckoos laid extraordinarily small dark eggs that match the size of host eggs (Brooker and Brooker 1990). Moreover, they cited several instances in which second Common Cuckoos appeared to have removed previously laid eggs (at 58% of 24 nests, Wyllie 1981, Davies and Brooke 1989). However, it is unclear just how strong such selective pressures would be, particularly when cuckoos appear relatively uncommon and parasitism frequencies around 5% were recorded across most of their range (see Brooker and Brooker 1990).

Provided cuckoos lay few eggs the selection pressure from differential egg losses would be great, yet cuckoos may lay 15-20 eggs per year (Chance 1940, Wyllie 1981, Nakamura and Miyazawa 1997). Moreover, pressures of nest predation and nestling competition would swamp most effects of such behavior. Likewise, Davies (2000)

explained the case for Dunnocks (cited as support by Brooker and Brooker 1990) as a case of evolutionary lag through which Dunnocks do not discriminate against cuckoo eggs. Still, the evidence provided by the Brookers (1990) - that cuckoos lay cryptic eggs despite no current host discrimination against less cryptic eggs - cannot be refuted.

By contrast, I never recorded direct agonistic behavior between *ater* and *aeneus* during 2,252 h of behavioral observation or differential responses toward cowbird eggs during laying visits or among monitored parasitized clutches, with either real or model cowbird eggs. Indeed, cowbirds continued to lay in active nests that contained a majority of, or only cowbird eggs, as in Carter's (1986) study. Thus, cowbirds appeared to be incapable of recognizing the eggs of either cowbird species, as multiple parasitism, particularly beyond three cowbird eggs is costly (Chapter 3).

Using video cameras, cuckoos could be similarly observed to measure their responses to different egg types placed in nests (Honza et al. 2002). Alternatively, I suggest that historic events other than egg morphology-oriented "competition past" likely directed cuckoo egg appearance. For instance, differential success with hosts of differing sizes appears to be a stronger form of selection among the cowbirds studied here. Similarly, brood parasites may be constrained with respect to other elements of nestling success, such as begging frequency or rate (Butchart et al. 2003, Glassey and Forbes 2003). Also, cuckoos might have experienced greater selection pressures on egg appearance from historic hosts now extinct or no longer geographically associated with the species of cuckoo. Molothrine cowbirds have experienced varied range expansions and likely contractions that would have brought them in contact with a wide array of

species. Historic hosts may have retained recognition abilities formed in response to parasites now in allopatry or extinct.

Indeed, attention must also be drawn to the fact that geographic variation in host responses to cowbird eggs vary. For example, the Northern Mockingbird, a common host for *aeneus* in Carter's (1984, 1986) study, rejected foreign eggs at other sites in Texas (Peer et al. 2002). Similarly, Bullock's Orioles accepted and cared for *aeneus* eggs and young at my site (Tables 3.6 and 3.7), but rarely accept eggs of *ater* elsewhere (Rohwer et al. 1989, Røskaft et al. 1993). Also noteworthy, in contrast to their use as hosts by *ater* elsewhere (Friedmann and Kiff 1985, Scott and Lemon 1996), and despite their abundance, Lark Sparrows and Chipping Sparrows were rarely parasitized. Thus, these species may not be favored by *ater* as hosts because they were relatively poor hosts.

In Colorado, *ater* parasitized Chipping Sparrow nests less often than other hosts (Ortega and Ortega 2001). The Ortegas suggested *ater* faired poorly with Chipping Sparrows because hosts fledged earlier than cowbirds. Similarly, Lark Sparrows, which can fledge at age seven to nine days (Baepler 1968), may be sub-optimal hosts. Also, Lark Sparrows may eject foreign eggs, as Peer et al. (2000) found Lark Sparrows ejected non-mimetic eggs that were smaller than cowbird eggs. Another study at my site has suggested Lark Sparrows may discriminate against dissimilar young when distributing food (H. McGaha, unpubl. data). However, cowbirds fledged normally from parasitized nests elsewhere (Newman 1970, Hill 1976a).

MECHANISMS FOR DENSITY-DEPENDENCE

Among birds, territories incorporating food and nest sites mediate levels of spatially

structured, density-dependent resource use (Rodenhouse et al. 2003). However, as brood

parasites, cowbirds are less spatially constrained as eggs can be laid at great and variable

distances from feeding areas (Curson and Matthews 2003). I do not suggest that cowbird

populations are limited only by the number of available host nests, because winter

competition for food clearly affects cowbird population sizes (Good 1979, Brittingham

and Temple 1983, Johnson et al. 1980). However, by what means do cowbirds exhibit a

functional response to host availability? Territorial behavior by females may provide the

mechanism for density-dependent host use and indeed *ater* appears to exhibit

semi-exclusive egg-laying ranges in at least some populations (Darley 1982, Hahn et al.

1999, Raim 2000, Shonk 2001). Territorial behavior may explain the pattern of habitat

use found among *ater* in New Mexico where larger, more fecund cowbirds commuted

shorter distances to laying areas than did smaller, less fecund cowbirds (Curson and

Matthews 2003). Likewise, within seasons, I frequently observed 1-2 *ater* females per

year that used localized areas within the site. I also recorded frequent chatter calls (n =

48) and a few instances of female-female head-up postures (n = 2), both of which

function when establishing territories or status (Darley 1971, Yokel 1986, Burnell and

Rothstein 1994, Raim 2000).

However, female *aeneus* often foraged and traveled together (Carter 1986, this

study). I suggest that *aeneus* females may assort in loosely density-dependent clusters

based on the dispersion of territorial males. Among *aeneus*, males defend exclusive

display areas of five to six hectares (Carter 1986) that females visit, presumably to

selectively assess and mate with certain individuals. To produce fertile eggs, laying birds

need to replenish sperm stores. Combined with last-male sperm precedence (Birkhead

and Møller 1992, Briskie 1996), the need for a reliable source of sperm may restrict female movements, particularly relative to the timing of fertilization. For laying birds, sperm may move rapidly to the infundibulum during an "insemination window" between laying and the ovulation of the next ovum (Cheng et al. 1983). The insemination window allows sperm to bypass that stored within the female and thus the window operates in the short-term, such that a well-timed mating will result in fertilization of the egg formed that day, but not others (Birkhead et al. 1996).

For cowbirds, laying is not disrupted by incubation, thus males may compete intensely for more morning copulations than among related species with parental care. Indeed, if a male could provide enough sperm to offset the reduced uptake during the insemination window, copulation during the window would yield greater assurance of paternity (Birkhead et al. 1996). My data are consistent with those suggesting jungle fowl hens and some songbirds are particularly attractive to males during the first hour or so after laying and may seek copulations predominately at this time (Fig. 4.9, Møller 1987, Thornhill 1988, Schulze-Hagen et al. 1995). Therefore, despite lacking territoriality, female *aeneus* should be spatially concentrated near male display areas, particularly to be near a preferred mate during the period when both ovulation and most nest searching takes place.

Indeed, I found individual females used the same areas within and between seasons (Fig. 2.6). Likewise, Carter (1984) found radio-tracked female *aeneus* commonly restricted their breeding activities to smaller areas within daily (dawn to dusk) ranges of 37 to 155 ha. Clotfelter (1995) observed some courtship outside of breeding areas, however, he witnessed only one copulation. By contrast, I found copulations

restricted to the breeding areas rather than at evening pre-roosting areas (Fig. 4.9). Male

hover displays peaked in the morning and evening periods, yet seven of the eight

copulations observed were in the evening, between 1721-1954 h CST. This suggests

most breeding activities occur at these times and may not be concentrated during the

insemination window. However, because most breeding activities occurred near areas

where laying occurred, females may be spatially constrained within areas where males

display. Interestingly, unlike most icterids with parental care, males may lack

information on the mating status of females. Thus, for a male, a high display rate likely

is adaptive, leading to more copulations than observed among species that follow each

other, i.e. mate-guarding among *ater*.

Finally, female *aeneus* exhibited greater inter-annual site fidelity than among *ater*.

This contrasts with findings for *ater* elsewhere, as *ater* often exhibits high (35-50%)

interannual site fidelity (Dufty 1982, Hahn et al. 1999, Raim 2000, Woolfenden et al.

2001). I rarely detected female *ater* in more than one season, thus, perhaps my site

represents a sink habitat for *ater* from which most females disperse after one season.

While nearby habitats offered less competition from *aeneus*, these lacked irrigation and

were much drier. Therefore, *ater* must choose between habitats with more productivity

in the presence of *aeneus* or reduced productivity free from competition with *aeneus*.

SUMMARY

Sympatric *ater* and *aeneus* used hosts of different body sizes. Such use of hosts

conformed to predictions based on competitive exclusion. All alternative hypotheses

were not supported, thus competition remains the most likely explanation for the patterns

of host use observed. However, further manipulative tests (exclusion of one cowbird) and data from more locations are required to determine more accurately if the lack of overlap in host use can be attributed solely to competition.

By not sharing commonly used hosts when in sympatry, the two generalist cowbirds demonstrated that laying, with respect to host species, is non-random. Despite this level of host selection, cowbirds did exhibit some sub-optimal laying (Chapter 3). These host generalists appeared capable of using hosts nearer that expected of specialists, which suggests transitions between generalism and specialism may be more likely than expected previously. However, as discussed in Chapter 2, greater annual productivity using one or a few hosts would be required to initiate specialism. *Aeneus* appeared to use the hosts capable of providing the highest annual productivity, whereas, *ater* experienced poor success with its hosts. Cross-fostering experiments are required to determine whether fledging success would be diminished using potential hosts.

Non-overlap in host use by sympatric cowbirds is of particular interest as cowbird breeding ranges are dynamic (Cruz et al. 1998) and likely varied considerably during the evolution of *Molothrus* spp., which arose 1.8-2.4 mya. Provided that cowbirds partitioned hosts, as currently found, varying degrees of co-occurrence may have strongly influenced cowbird characters, i.e. modal host size and, hence, cowbird body size, and possibly contributed to speciation among cowbirds. Finally, my findings may be applied to predict which songbird species may be more prone to cowbird use as range expansions occur.

CHAPTER 5. DIFFERENTIAL HOST USE BY SYMPATRIC COWBIRDS. II. EFFECTS ON OFFSPRING SEX RATIOS

Avian sex ratios often depend upon parental effects such as differential investment among young (Trivers 1973, Kilner 1998, Oddie 2000, Young and Badyaev 2004). However, not all birds care for their young. Most of these species have precocial young and therefore sex ratios are maintained through processes outside the nest, such as differential maternal investment in eggs (Lipar and Ketterson 2000, Oddie 2000, Badyaev et al. 2001, Young and Badyaev 2004), differential size-based mortality (Clutton-Brock et al. 1985), and frequency-dependent selection (Fisher 1930, Frank 1990).

Brood-parasites represent a special case for studying sex ratio maintenance because they rely upon other species to rear their young. Therefore, brood parasites cannot alter secondary sex ratios of their offspring directly, as species practicing parental care can (reviewed by Oddie 1998, Badyaev et al. 2002). This is interesting because populations of adult cowbirds are invariably male-biased (up to 6:1 Males:Females, n = 12 studies reviewed in Ortega 1998). Thus, male-bias must arise among cowbirds through either a male skew in primary sex ratio (egg production), egg size/provisioning, or differential survival during the stages leading to, and possibly during, adulthood.

Studies of sex ratios among Brown-headed Cowbirds have lacked data on hatching-year birds because few involved banding of this age class and, of those that did, the rate of hatching-year returns was extremely low (e.g. Weatherhead and Bennett 1992). Analysis of the onset of Brown-headed Cowbird sex ratio bias is limited to four studies, each at a different demographic stage. Within male-biased populations (Woolfenden et al. 2001, 2002), balanced sex ratios have been reported at laying

(Kasumovic et al. 2002), 7 days post-hatch (Weatherhead 1989), independence (Hill 1976b), and the onset of the first breeding season (Darley 1971). Balanced sex ratios, coupled with seemingly high estimates of annual egg production (> 25 eggs/female/year) (Walkinshaw 1949, Payne 1965, 1973a), led Darley (1971) and Hill (1976b) to attribute male-bias to differential female mortality associated with costs of reproduction. However, genetic-based estimates of annual egg production for Brown-headed Cowbirds are low (approx. mean: 4.4 (range: 1-17) eggs/female/year) (Hahn et al. 1999, Shonk 2001, Strausberger and Ashley 2003, Woolfenden et al. 2003) and adult mortality does not exceed that for species with parental care (Searcy and Yasukawa 1981, Woolfenden et al. 2001). Therefore, explanations for the timing of male-biased sex ratios among cowbirds remain unclear.

Because molothrine cowbirds are sexually dimorphic in size (Friedmann 1929, Ortega 1998) and common hosts range between 5-45 g (Friedmann 1929, Johnsgard 1997), chick sex may affect survival probability relative to host size (Scott and Lemon 1996, Lichtenstein 2001b). On this basis, Weatherhead (1989) hypothesized that cowbirds lay eggs so that the larger, more costly males were placed either in nests of larger or smaller hosts. Large hosts would be favored to minimize loss of female offspring from competition with larger host nestmates; alternatively, males in smaller hosts' nests might yield fitness gains associated with greater survival via higher feeding rate and/or monopolization of care. I tested Weatherhead's (1989) hypotheses in sympatric populations of Brown-headed Cowbirds and Bronzed Cowbirds in southern Texas because sympatric brood parasites often exhibit directional shifts in the sizes of hosts relative to those used in allopatry (Friedmann 1928, 1967; Nicolai 1964, Payne and

Payne 1967, Brooker and Brooker 1990, Higuchi 1998, Chace 2001, Chapter 4). As

body size relative to nestmates affects survival (see Badyaev et al. 2001, Dearborn and

Lichtenstein 2002) and sympatric cowbirds use hosts that differ in size (Chapter 4), I

tested (1) whether sympatric Brown-headed and Bronzed cowbirds differentially laid

eggs of either sex in nests of relatively small or large hosts and (2) whether cowbird

secondary sex ratios were affected by the use of certain-sized hosts. I also assessed

whether male skew occurs due to differential male recruitment or adult female mortality,

as the timing of sex-based selection is crucial to understanding cowbird life histories.

METHODS:

QUANTIFICATION OF SEX RATIOS AND DIMORPHISM

Offspring sex was determined for embryos and young through PCR amplification of

chromo-helicase-DNA binding (CHD1) genes from avian W and Z sex chromosomes as

described in more detail in Chapter 3 (see also, Griffiths et al. 1998). Eggs were

collected within the core egg-collection plot and data on young were collected from

surrounding areas as described in Chapters 2 and 3. I considered sex ratios among eggs

and young (10 - 40 d) as reflecting primary and secondary sex ratios, respectively. I

further refined my analysis by considering sex ratios at the age categories of 10-12 d and

>20 d as these criteria reflect survival to biologically meaningful stages of fledging and

independence. Although young may remain in nests as late as 10-12 d, growth is

asymptotic at this point and fledging is the norm (Carter 1986, Lowther 1993, Kilpatrick

2002). Ages for young not detected prior to hatching were estimated on the basis of

appearance and body measurements compared with young of known ages (see also Scott 1979, Carter 1984, Lowther 1993, Goguen 1999).

Sex ratio was also measured among independent young collected via a long-term trapping program at Ft. Hood, Killeen, Texas, previously described by Hayden et al. (2000). Independent young were also shot by Nature Conservancy staff for collection at this site. Most of these specimens (95%) were placed in the bird collection of the Field Museum of Natural History in Chicago, Illinois.

Host use with regard to cowbird sex was analyzed by categorizing hosts into relative units of 10% cowbird mass using data from Dunning (1993). This facilitated direct comparison of the sizes of hosts used by each cowbird species. Sexual dimorphism was tested for among eggs and young at 10-12 d and >20 d. Maximum length and width of each egg was recorded and used in the equation for egg volume: Volume = $0.498 \times$ Length $\times$ (Width)^2 (Spaw and Rohwer 1987). Cowbird eggs and young were weighed to the nearest 0.05 g using an electronic balance. I estimated energy requirements for each class of nestling, species and sex, using fledging mass and age data as described in Chapter 3 (Table 3.5).

POTENTIAL SOURCES OF SEX BIAS

Particularly in arid climates, arthropod availability and weather often interact to determine breeding season duration (Grant and Grant 1985, Rotenberry and Wiens 1991, Grant 1999, Morrison and Bolger 2002). Likewise, food availability may influence secondary sex ratio among species with sexually size dimorphic young (Teather and Weatherhead 1989, Oddie 2000). Therefore, I analyzed the duration of nesting attempts

relative to annual rainfall and temperature data (U. S. National Climatic Data Center, Asheville, North Carolina) to identify any variation that could have reduced food availability and, hence, nestling survival. Weather data were collected daily at Laughlin Air Force Base 33 km west of the study area. I considered days with temperatures exceeding 38 °C as extreme events that likely reduced arthropod activity and emergence, which in turn, reduced avian foraging success and productivity. To analyze temperature data, I tested for a relationship between days > 38 °C and number of host nests available.

To test whether interannual survival contributed to the male-biased adult populations, I banded and resighted young and adult cowbirds at my site. Young were banded at nests as well as caught in seed-baited walk-in tunnel traps. Adults were also caught in baited walk-in traps and lured into mist-nets using playback recordings.

RESULTS:

QUANTIFICATION OF SEX RATIOS AND DIMORPHISM

I recorded only 10 instances (involving six species) of overlap in host use for 557 cowbird eggs distributed among the 1,442 nests suitable for cowbird laying (Chapter 4). Individual cowbirds used up to five host species (Fig. 2.6). Host use was weakly associated with host abundance (Chapter 2, Table 2.2) and strongly associated with host body-size (Chapters 3 and 4).

Overall, 63% of the 287 eggs collected developed and yielded sex ratio data. Across hosts, primary sex ratios were equivalent (Table 5.1). Considering hosts of each species separately, primary sex ratio was not biased and host use for each sex was similar (Table 5.1, Fig. 5.1). In 2001, the drier year, secondary sex ratios were predominately

Table 5.1. Sex ratios among cowbird eggs.

	M : F (n eggs)	G (P-value)	% developed (n)
ater			
By year			
2000	0.95 (39)	0.03 (0.92)	67.2 (58)
2001	1.75 (22)	1.66 (0.23)	55.0 (40)
Total	1.18 (61)	0.41 (0.40)	62.2 (98)
aeneus			
By year			
2000	1.26 (52)	0.69 (0.41)	70.3 (74)
2001	1.30 (69)	1.18 (0.26)	60.0 (115)
Total	1.28 (121)	1.86 (0.13)	64.0 (189)
By host [a]			
20 g	1.21 (42)	0.91 (0.30)	74.4 (82)
23 g	1.61 (47)	5.53 (0.03)	71.3 (87)

[a] Orchard Orioles (20 g) and Hooded (23 g) Orioles, such analysis not attempted for *ater* as 93% (57) eggs sexed were from Bell's Vireo nests.
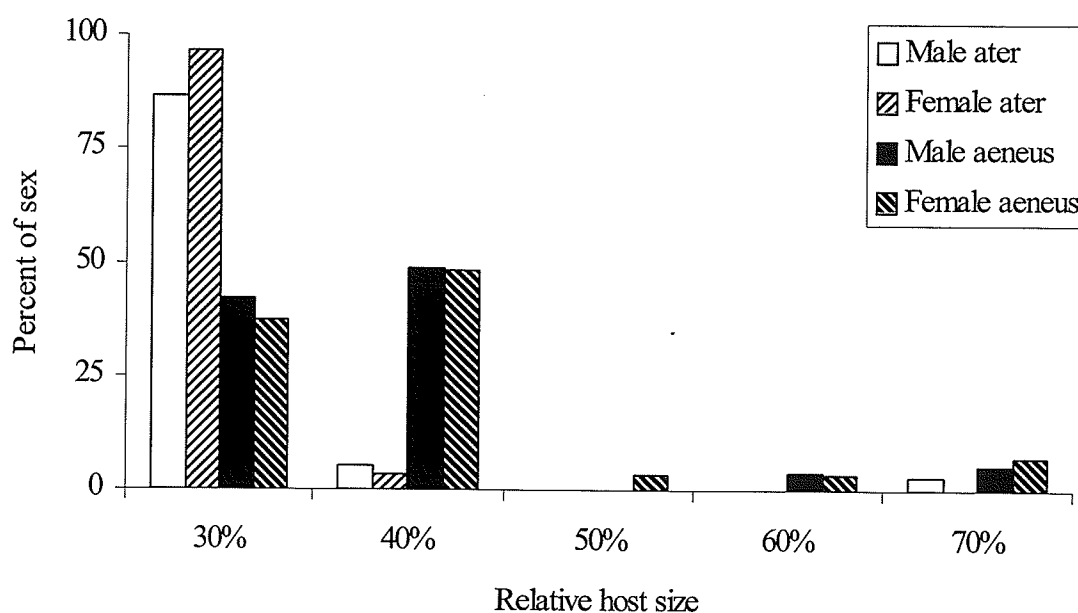
Figure 5.1. Use of hosts of different sizes by cowbirds with respect to eggs *and* young of either sex. Host sizes were relative to cowbird size (% of respective parasite as each cowbird used different sets of host species, see Table 2.2). Host use did not differ by sex among eggs laid by *aeneus*. Female-destined *ater* eggs were found in nests of smaller hosts more often than male eggs.

male-biased (Table 5.2). The secondary sex ratio for *ater* was significantly biased and that for *aeneus* tended strongly toward a male-bias (Table 5.2). Among young sampled within 2 d of fledging, 50% (n=12, two-tailed binomial test P_Z=1.00) of *ater* and 62% (n=29, P_Z=0.27) of *aeneus* were male, whereas, among independent juveniles 64% (n=66, P_Z=0.04) of *ater* and 47% (n=15, P_Z=1.00) of *aeneus* were male. Likewise, most independent juvenile *ater* at Ft. Hood (2003) were male (64%, n=108, P_Z=0.01).

Egg volume differed between sexes, however, annual variation strongly suggests that *ater* eggs are not sexually dimorphic (Fig. 5.2a). For *aeneus*, male eggs were consistently larger than female eggs, although this difference was significant only in 2002 (Fig. 5.2b). Young differed significantly in size at 2-3 d and 1-2 d post-hatch, for *ater* and *aeneus*, respectively (Fig. 5.3). At fledging, male cowbirds were significantly larger than females (*ater*: x = 5.5 g, P <0.001, df = 63; *aeneus*: x=10.1g, P < 0.001, df = 23). Size-based energetic estimates and measurements for each cowbird show that rearing males is more costly (Table 5.3). The size differences increased through independence (Fig. 5.4).

POTENTIAL SOURCES OF SEX BIAS

Host breeding season length varied significantly among years (Table 4.1), although cowbird laying dates were relatively invariable (Table 4.1). However, laying by *ater* peaked significantly later in 2000 than in 2001 and 2002 (Wilcoxon Z: -3.41, P < 0.001). Variation in breeding dates was correlated with annual differences in rainfall and temperature (Figs. 5.5 and 5.6). In 2001, the hottest and driest year, host and cowbird breeding seasons were shortest (mean among hosts: 18-22 d shorter, *ater*: 6-14 d shorter,

Table 5.2. Sex ratios among cowbird young >10 d.

	M : F (n young)	G (P -value)
ater		
2001	2.44 (31)	5.62 (0.02)
2002	1.04 (47)	0.02 (0.92)
Total	1.44 (78)	2.53 (0.12)
aeneus		
2001	2.00 (30)	3.40 (0.07)
2002	0.82 (20)	0.20 (0.86)
Total	1.38 (50)	1.29 (0.25)

ater
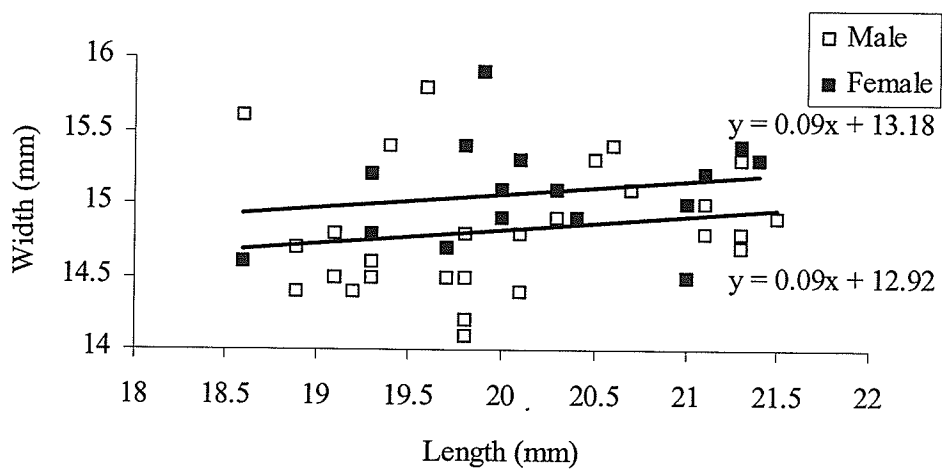
aeneus
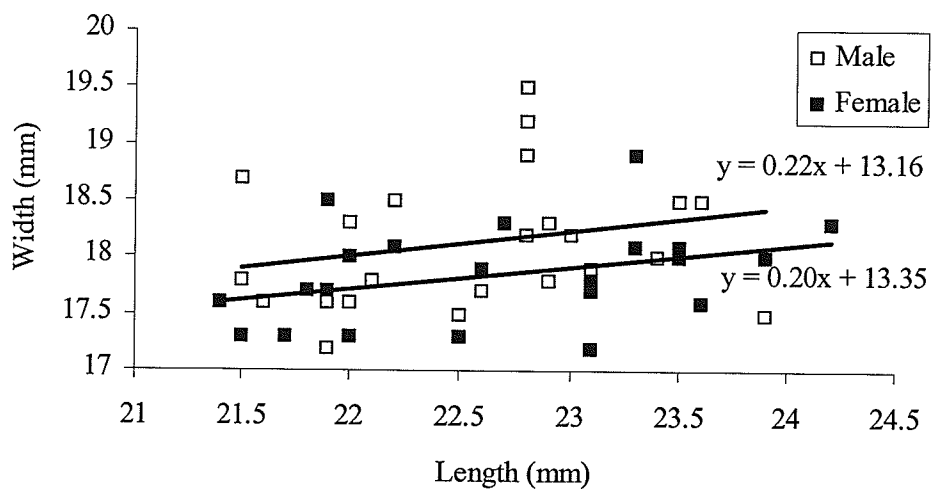
Figure 5.2. Overlap in dimensions of male and female eggs of *ater* and *aeneus*.
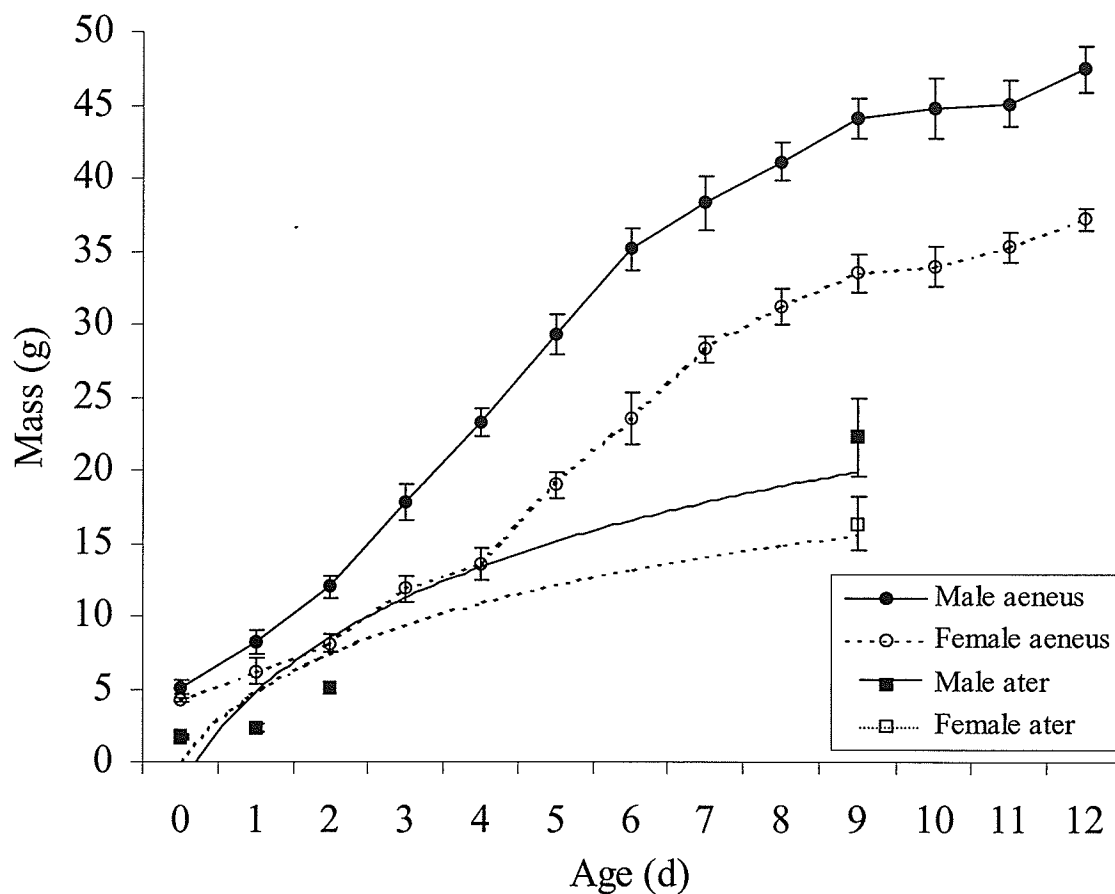
Figure 5.3. Nestling growth (mean ± SE) of male and female Bronzed and Brown-headed

cowbirds. Few data for *ater* available, therefore, growth curves were estimated using

logistic regression (males: y = 9.80 ln (x) −1.93, r = 0.93, P = 0.07; females: 7.07 ln (x) −

0.02, r = 0.96, P = 0.18). For both species, males were significantly larger than females.

Table 5.3. Differences in male and female nestling energetic requirements.

	Mass (g)	Days to fledge [a]	TME (kJ)[b]	PDME (kJ/d)[c]
Ater				
Male (21) [d]	31.1	9.5	591.8	103.5
Female (9)	26.1	9.5	509.7	88.3
Difference	5.0	0	82.1	15.2
Aeneus				
Male (14)	43.0	12-13	1102	130
Female (11)	32.9	11-12	911.4	106.1
Difference	10.1	1-2	190.6	23.9

[a]Time to fledging (Lowther 1993, 1995).

[b]Total metabolic energy provided across nestling stage.

[c]Peak daily metabolic energy.

[d]Number of young
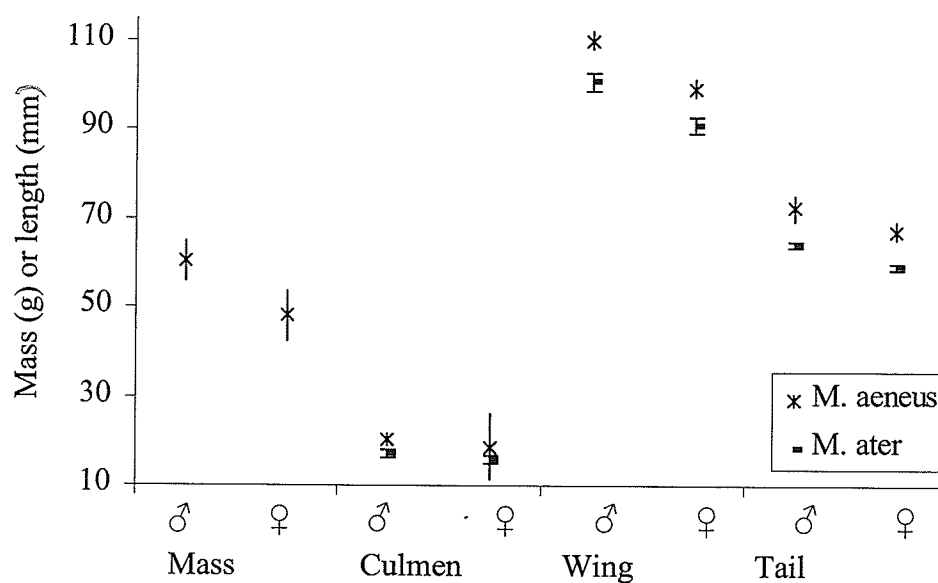
Figure 5.4. Among independent cowbirds (> 36 d), sex differences in size (mean ± SD depicted) were significant (P < 0.001) for all measures except culmen length among *aeneus* ($t_{142} = 1.57$, P = 0.07). Data from Carter (1984) (54 male and 93 female *aeneus*) and Ft. Hood, Texas (63 male and 34 female *ater*).
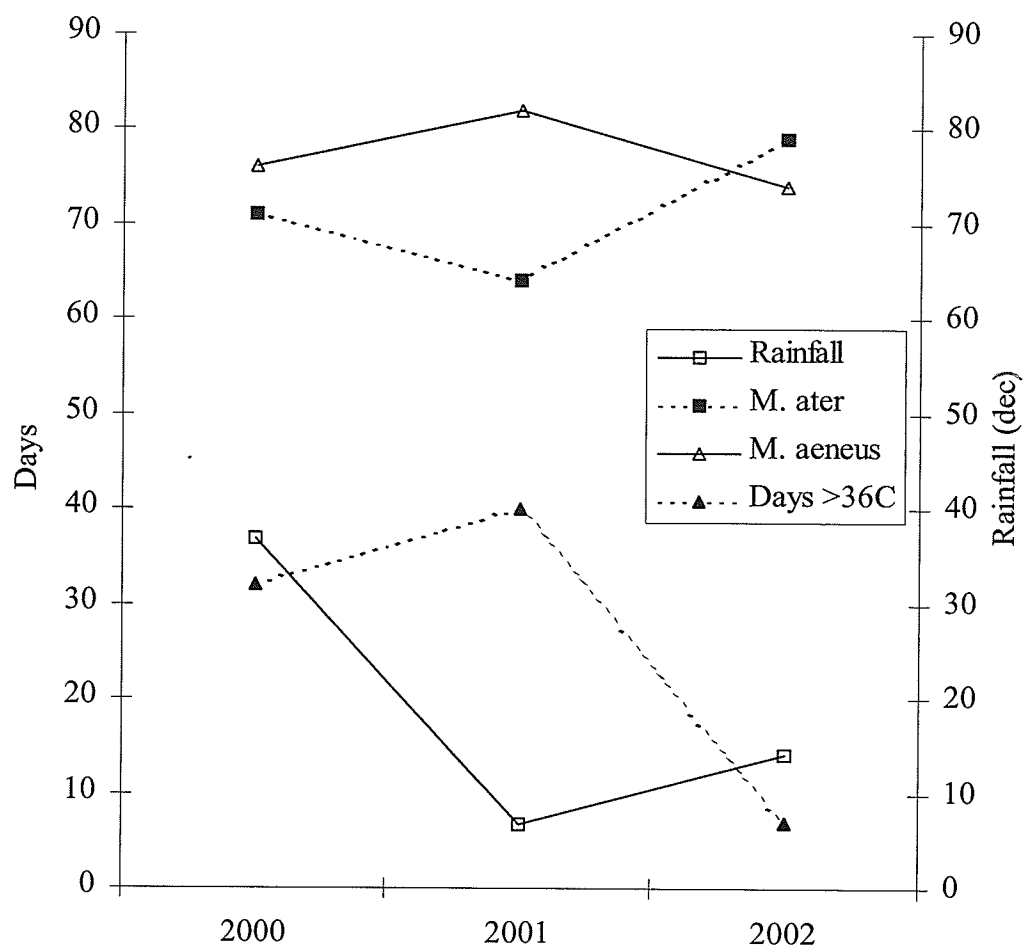
Figure 5.5. Overall trends in cowbird season duration (days laying) compared to rainfall and temperature (days > 38°C).

A

B
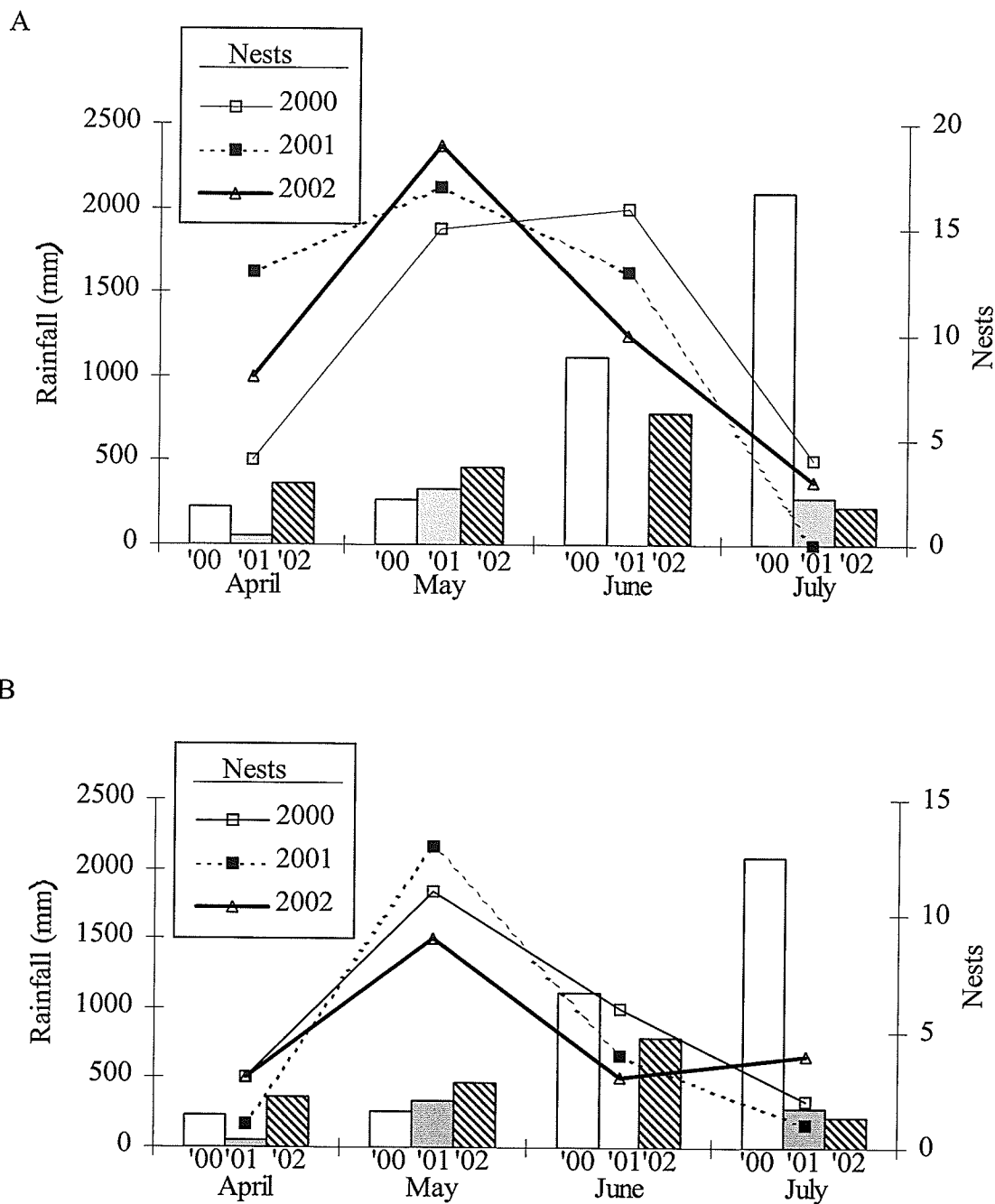
Figure 5.6. Seasonal nest availability (lines) of major cowbird hosts relative to rainfall (bars). Nests of Bell's Vireo A) and Orchard and Hooded orioles B) received 76% and 80% of *ater* and *aeneus* eggs, respectively. Nesting for hosts of each cowbird peaked in May and ended in July.

aeneus: 1-14 d shorter). For both cowbirds, secondary sex ratios were male-biased only in 2001 (Table 5.2). During the three seasons, laying by *ater* was moderately correlated with rainfall ($\rho = 0.5$, $P = 0.67$, Fig. 5.5), whereas that by *aeneus* was strongly correlated with temperature ($\rho = 1$, $P = 0.0$).

Between years, *aeneus* was resighted far more often than *ater* (Table 5.4). This was due largely to the more sedentary and conspicuous behaviors of *aeneus*, particularly feeding/courtship displaying in open, short-grass habitats. Few (3%, n = 68) of the cowbirds banded as young were re-detected.

DISCUSSION

QUANTIFICATION OF SEX RATIOS AND DIMORPHISM

As described in Chapter 4, *ater* used a reduced diversity of hosts and exhibited a directional shift to smaller hosts relative to those used in allopatry. *Ater* used primarily species ≤ 13 g, whereas *aeneus* parasitized hosts ≥ 18 g (Chapter 4). The shift in modal host size found in sympatry was not associated with assortative host use on basis of offspring sex. Yet, sex appeared to affect survivorship at an early age and to contribute to the male-bias associated with adult populations. However, I first address differences found in the magnitude of dimorphism among cowbird young.

Weatherhead (1989) found no significant dimorphism among 7 d old *ater* nestlings at Delta Marsh, Manitoba (males vs. females: 26.14 ± 3.76 g vs. 26.56 ± 4.94 g; n = 18). Lacking sexual size dimorphism, cowbirds would not be expected to use hosts in a sex-based manner and did not do so among nests of two hosts (Weatherhead 1989). By contrast, male nestlings of the other subspecies were significantly larger than females:

Table 5.4. Number of birds resighted per season [a]. For *ater*, resighting in 2000 was not possible as birds were not banded in 1999.

	ater		*aeneus*	
	Female	Male	Female	Male
2000	-	-	4	0
2001	9	3	11	12
2002	22	8	16	15
Total	28 (22.2%)	11 (4.7%)	24 (68.6%)	19 (47.5%)

[a] Birds resighted in both years were not double-counted when calculating overall resight totals.

M. a .ater at 8-9 d (t = 4.26, df = 12, P<0.005) (Scott and Lemon 1996), *M. a. obscurus*

(Fig. 5.3). Other than potential differences in dimorphism between subspecies, two

factors may have affected Weatherhead's (1989) result. First, *ater* typically fledge at

9-11 d (Lowther 1995) and data were available only to 7 d. The difference is not trivial

as cowbirds typically gain 6-9 g between 7 and 10 days (Scott 1979, Lowther 1995).

Secondly, the longer days (high-latitude) and superabundant food at Weatherhead's

(1989) wetland site may have diffused dimorphism among young (Teather and

Weatherhead 1989, Kilpatrick 2002). Indeed, nestling Red-winged Blackbirds at

Weatherhead's site were not dimorphic, in contrast to the significant differences between

sexes measured as early as 2 d elsewhere (Fiala 1981) and nearby (Glassey and Forbes

2003). This explanation was supported as *ater* young 7 d post-hatch were 3-6 g heavier

in Manitoba (Weatherhead 1989) compared with young from Kansas and Ohio (Scott

1979, Lowther 1995). The dimorphism among *aeneus* young is more pronounced,

evident 1-2 d post-hatch and manifested in a 10 g difference at fledging (Fig. 5.2).

Therefore, sex-based use of hosts offers potential gains to cowbirds.

Despite the differences among nestlings, I found no dimorphism among eggs.

However, I was unable to determine the number of eggs of each sex laid by individuals

and, therefore, could not detect trends, particularly among developing oocytes (Young

and Badyaev 2004), annual clutches, or order effects (Badyaev et al. 2002, Blanco et al.

2003). Nonetheless, cowbirds appear unlike other birds with dimorphic young (Oddie

2000), as they contribute little to ameliorate or exploit dimorphism among their offspring,

and instead defer control of offspring sex ratios to hosts.

Estimated energetic costs of rearing each sex of each cowbird species suggest that success with some hosts can be affected by differences associated with body size. For instance, Blue-gray Gnatcatchers rearing only one *ater* nestling incur energetic costs near those of rearing an entire brood of their own young (Root 1969, Kilpatrick 2002). Thus, for gnatcatchers, the sex-based difference in cowbird rearing costs occurs near the limit of care a pair can provide. However, hosts appear quite flexible with the energy devoted to parental care as single birds can fledge young despite losing the care normally provided by a mate (Gowaty 1996, Bart and Tornes 1989) or when experimentally handicapped (i.e. with tail-weights). Such flexibility includes rearing brood parasites, as Common Cuckoos and *ater* reared by differently sized hosts fledged at similar masses (Kilpatrick 2002, Butchart et al. 2003). Therefore, food provided by parents may not be limiting to young of either sex, despite the greater costs of rearing male cowbirds.

Despite the sex-based differences in rearing costs to hosts and differential use of hosts by body size, neither cowbird skewed its primary sex ratios among different hosts. This conforms to data from allopatric brood parasite populations: *ater* (Weatherhead 1989, Kasumovic et al. 2002) and Common Cuckoos (Kasumovic et al. 2002). Thus, to account for the male-biased adult sex ratios among cowbirds (Ortega 1998, Woolfenden et al. 2002), differential mortality of females must occur among either young or adults.

POTENTIAL SOURCES OF SEX BIAS

My results are contrary to those of Darley (1971), who found a 1:1 sex ratio among *ater* during their first breeding season. He attributed the male-bias within the adult population to differential mortality of adult females that occurred primarily after the onset of

breeding. However, others have found the ageing technique Darley (1971) used for yearling female *ater* to be problematic and only yearling males are reliably aged on basis of plumage characters (Ortega et al. 1996, Pyle 1997, Woolfenden 2001). If Darley (1971) had misclassified 19 (29%) adult females as yearlings, then the yearling cohort would have been significantly male-biased (G = 3.87, P < 0.05). Thus, Darley (1971) may have misclassified several birds, which would have resulted in the apparent balanced ratio. Future research should consider testing the differential female mortality hypothesis using female age-distribution data.

Hill (1976b) measured hatching-year sex ratios directly by trapping independent juvenile *ater* from July through October in Kansas. He found an overall sex ratio close to one; however, the ratio varied significantly over time and his samples included largely migrants. Hill (1976b) acknowledged that his sampling may have included sex-biased trapping due to differential migratory-based needs such as stopover and refueling requirements (see Baker 1978, Ketterson and Nolan 1983).

In contrast to Hill (1976b), I found juvenile *ater* were male-biased at two sites in Texas. As well, nestling survival was generally male-biased for *aeneus* and my limited data suggest this bias was positively correlated with host size (Fig. 5.7). Extrapolation of the fledging frequency for each sex on the basis of host size accounts for the male-bias found among juveniles trapped independent of host care. Intraspecific competition may impact cowbird sex ratio as the cowbirds differed in degree of multiple parasitism; *ater* did so moderately often (30.7 %), whereas *aeneus* frequently parasitized nests multiply (56.2%, see Chapter 3). Therefore, any size-based differential survival among *ater* would have depended less on males outcompeting females and more on males faring better than
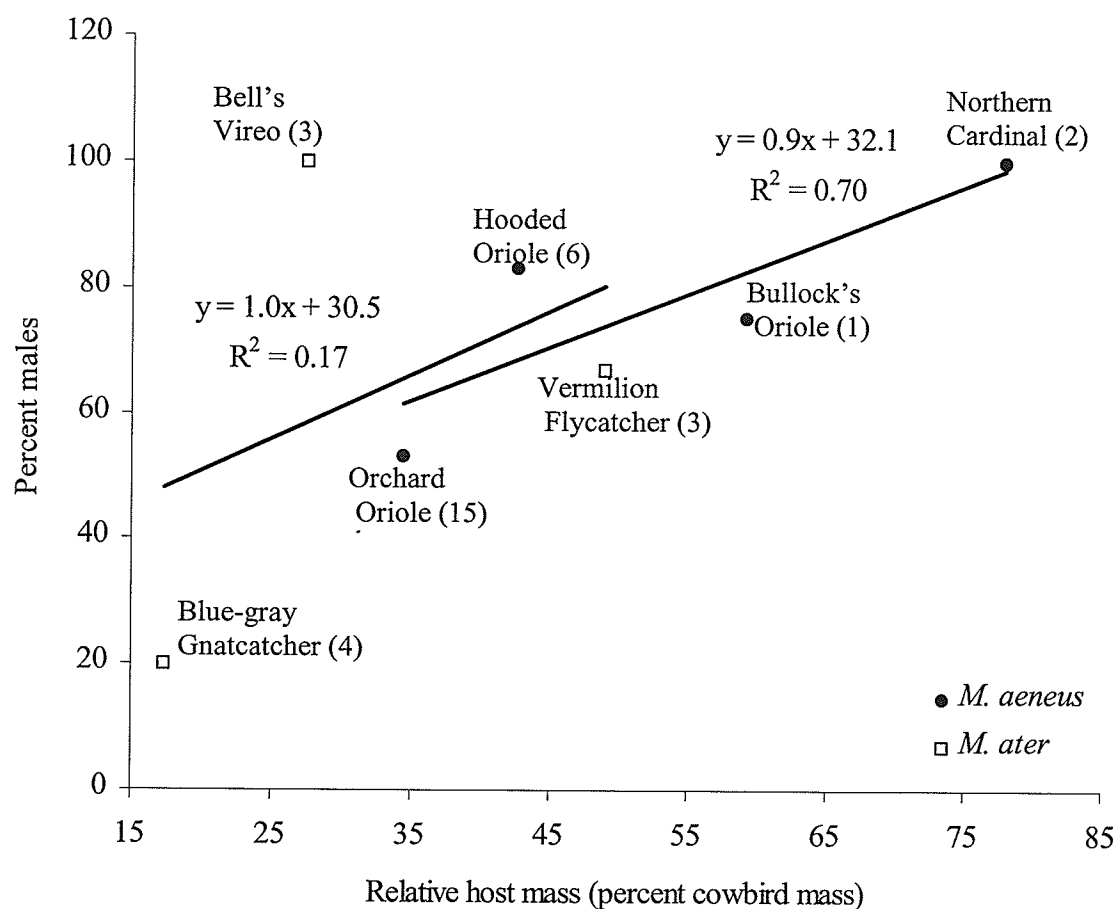
Figure 5.7. Sex-based fledging success of cowbirds relative to percent host size (based on cowbird species that parasitized each host and among young within two days of fledging). Proportionally, more males fledged from nests of smaller species, as measured among young ≤ 2 d prior to fledging.

females in host nests. By contrast, most *aeneus* nestlings competed with conspecifics in host nests.

For both species, the finding that larger nestlings within broods of several species are fed disproportionately (Price and Ydenberg 1995, Lichtenstein 2001b) suggests male cowbirds would be favored, whether competing against smaller females or hosts. As both cowbirds parasitized species up to seven times smaller than themselves (Table 2.2) and did not distribute eggs with regard to sex, I suggest that cohorts of cowbirds become male-biased prior to adulthood. More specifically, I suggest that the larger male young may be better equipped to monopolize host care and thus differentially survive to fledging and independence regardless of host size. Fledgling data for *aeneus* supported this hypothesis as 62% (n = 29) of fledglings were male. However, secondary sex ratios varied significantly between years (Table 5.2). This variation was associated with seasonal rainfall or high temperatures and, therefore, may reflect reduced food availability during periods of low rainfall (see Grant and Grant 1985, Brantley 1997).

Despite seasonal variability, male-bias among *ater* did not occur at the fledgling stage (50% male), but was delayed until independence (64-65% male, at both Texas sites). Thus, sex ratios became more male-biased during nestling development and fledging for *aeneus* and during independence for *ater*. Such a developmental pattern is common among emberizid finches, as despite relatively equal primary sex ratios, male-biased sex ratios occurred among juveniles of cardueline finch species (Shreeve 1980, Badyaev 2002), quelea (Ward 1965), and European Starlings (Fankhauser 1971). Shifts in sex ratio may not be due to body size alone as hormonal (Lipar et al. 1999) and/or immunity levels (Tschirren et al. 2003) can affect nestling behavior and survival.

Likewise, over-winter survival can override natal effects, further skewing sex ratios prior to first breeding through size-based dominance at feeding sites (Badyaev et al. 2002), thermal capacities (Weatherhead et al. 1984), or epizootic outbreaks (Faddoul et al. 1966, Johnson et al. 1980, Weatherhead and Bennett 1992). For instance, outbreaks of salmonellosis have killed hundreds to millions of blackbirds, including *ater* (Quist 2001, I. Tizard, pers. comm.). These factors may interact with physical condition and social dominance (Darley 1982) such that females experience differential mortality (see Baker 1978).

SOCIAL DOMINANCE

I suggest that social dominance, outside of and during migration, can further exacerbate the aforementioned factors to become widespread and consistent sources of mortality among cowbirds. Studies of captive cowbirds have clearly identified social structure in cowbird populations (Rothstein et al. 1986, Smith et al. 2002, West et al. 2002). Associations among captive cowbirds reflected those observed in nature (Payne 1973, Good 1979, Teather and Robertson 1985, Yokel 1989, Woolfenden et al. 2002). Captive cowbirds of all ages assorted positively by sex and age (King et al. 2002, Smith et al. 2002), and such behavior creates associations under which competition and social dominance would likely affect survival. Essentially, groups could exclude one another from resources such that the lowest ranking group (juvenile females) would suffer the greatest mortality.

For instance, Weatherhead and Bennet (1992) found differences in blood parasite levels among cowbirds of different ages and sexes; juveniles and females had the highest

levels of *Plasmodium* infection. By contrast, Johnson et al. (1980) found predominately

male *ater* died from intestinal coccidiosis in one of two years. They attributed this to

differential male exposure at residential feeders where color-marked males were sighted

more often than females. In this case, male dominance may have been associated with

novel risk of infection at feeders. Regardless, evidence is clear that cowbirds suffer

physiological stress and differential survival among sexes and cohorts outside the

breeding season. Good's (1979) study demonstrated this directly, as she measured

adrenal mass among male *ater* collected from winter roosts. Males in better condition

roosted in higher density roosts which appeared favored due to higher overnight

temperatures and reduced mortality (Good 1979). Thus, among male *ater* at winter

roosts, social dominance/size was associated with survival. Likewise, Dolbeer and Smith

(1985) found males ate significantly more corn than females, which consumed

significantly more grass seeds than males. Pathogenic infection likely interacts with

physical condition and feeding success bi-directionally, as poor condition and/or

infection can reduce ability to obtain food, or vice-versa (see Weatherhead et al. 1995).

For instance, Good (1979) found that cowbird condition and mortality were associated

with differences in adrenal mass, liver glycogen level and gizzard/crop contents. Males

found dead below roosts had significantly lower glycogen levels (evidence of poor recent

feeding) and fewer gizzard contents as well as greater infection levels, primarily coccidial

(*Eimeria* spp.) (Good 1979). Thus, Good (1979) suggested the greatest source of

cowbird mortality occurs during migration.

Indeed, House Finches (Badyaev et al. 2002) and *ater* often feed in identical

situations and form juvenile flocks that migrate later than adults (Friedmann 1929; Coon

1974; Hill 1974, 1976b). Further investigation is required to determine patterns of social dominance among juveniles in flocks and roosts in nature. As male-bias increases during the non-breeding season, it appears that cowbird adult sex ratio is not greatly influenced by adult female mortality directly associated with reproduction. This pattern is consistent with those found among several species with similar life histories (Ward 1965, Shreeve 1980, Badyaev et al. 2002).

SUMMARY

Young of both *ater* and *aeneus* were significantly sexually size dimorphic early in their development. The dimorphism was not due to differences in egg size. The primary sex ratio was not skewed, nor were eggs differentially placed among host nests on the basis of their sex. Data for secondary sex ratios suggests a male-bias associated with host use, however, they reflect environmental variability and therefore consistent trends in sex ratios may be obscured. Nonetheless, data collected on independent juveniles suggests that male-bias occurs earlier than can be attributed to differential female mortality associated with egg production.

These data demonstrate that cowbird-host relationships are complex and that host communities can affect cowbird demography. Cowbird management and insight into cowbird-host evolutionary interactions can be improved through more holistic study of the stage-based selective pressures faced by cowbirds. For instance, studies of cowbird recruitment, with an emphasis on condition at fledging, during fall migration and on their wintering grounds, may provide the greatest gains in our understanding of cowbird life histories and limits to population growth.

CHAPTER 6. CONCLUSIONS

FUTURE DIRECTIONS

I have raised several questions about the development of host use among cowbirds and other brood parasitic birds. Through my analyses, I have demonstrated that host specialism is not a terminal derived state. I have also presented field data that clearly show generalist cowbirds can differentially use hosts and, therefore, discriminate among host species. Specifically, cross-fostering experiments and/or biomarkers may be employed to determine whether host races occur among *rufoaxillaris* young (see Gibbs et al. 1997, 2000). Such information would allow an assessment as to whether natal imprinting influences host use by *rufoaxillaris*.

More host use data for sympatric and allopatric cowbirds from other locations should be collected for comparison, to provide insights on the development of apparent competitive exclusion among sympatric cowbirds. Such data are needed to test more thoroughly hypotheses explaining the evolution of host use among cowbirds. Ultimately, inferences may be drawn about the ancestral state of host use such that the coevolutionary or phylogenetic hypothesis may be excluded. For instance, the specialist cowbird, *rufoaxillaris*, may not exhibit mtDNA differentiation between populations that do not use the purported model for nestling mimesis, *Agelaioides badius*. In this case, the coevolutionary hypothesis would not be supported. This is a necessary step for appropriately viewing comparisons made among brood parasitic groups, i.e. cuckoos versus cowbirds.

At a finer-scale, questions concerning molothrine sexual selection may aid our understanding of the development of brood parasitism and sexual processes among

blackbirds. For instance, did diminishing paternal care or extreme size-dimorphism make brood parasitism a more profitable strategy than the dominant one of parental care? Specifically, cowbirds could attain greater dimorphism if their young were cared for assortatively by different sized groups of hosts. On the other hand, how do host communities affect sexual selection among cowbirds? Do communities influence sex ratio and size dimorphism among cowbirds? Such questions are appropriate as subspecific variation in presumably important sexual characters is great – some subspecies exhibit slightly reversed size dimorphism (*M. aeneus armenti*, Lowther 1995), while for most males are larger. Such differences, normally viewed as trivial among birds, are likely not so among obligate brood parasites. Because they depend on reproductive success via host care, obligate brood parasites may be greatly affected by small phenotypic differences. For example, selection for body size mediated by abiotic constraints may alter the biological availability of groups of hosts, i.e. small desert-dwelling cowbirds may have poor success with larger hosts. Likewise, genetically linked differences in the appearance of eggs or chicks could have great significance for effective host availability, i.e. flange color among *ater* (Rothstein 1978) or egg maculation among *bonariensis* (Fraga 1985).

Population growth is associated with the extensive range expansions by the three widespread generalists: *aeneus* expanded recently into the southern United States (Cruz et al. 1998, Kostecke et al. 2004); *ater* spread west of the Sierra mountains of California in the 1890's (Rothstein 1994); *bonariensis* moved across the Caribbean and north to the coastal eastern United States (Sykes and Post 2001). Thus, natural ecological

experiments are underway and cowbird host use in these areas should be closely

monitored (see Cruz et al. 1998).

PRACTICAL APPLICATIONS

Understanding cowbird host use may facilitate better management decisions for songbird

population sustainability and cowbird control. This is particularly so, because cowbird

populations are subsidized by human activities (primarily agriculture, silviculture, and

lawns) and their breeding ranges are dynamic. Cowbirds are abundant: estimates for *ater*

suggest 40 - 100 million birds (Smith and Rothstein 2000). Because populations are

large, cowbirds may have broad and acute impacts on host populations, particularly on

those already jeopardized via habitat loss, i.e. processes such as narrowing riparian

corridors, forest fragmentation, or fire suppression. However, the impact of cowbirds on

communities appears minimal relative to predation, at least in the midwestern United

States (De Groot and Smith 2001). Yet, cowbirds, particularly the more tropical species,

regularly act as nest predators as well and no studies similar to De Groot and Smith

(2001) have been attempted on those species.

Provided cowbirds partition hosts relatively rapidly, as in Texas, managers may

predict with relative accuracy which species may be more prone to cowbird use as range

extensions occur. One such site, Ft. Hood, Bell Co., Texas, where only *ater* occurred

until recently (see Kostecke et al. 2004) supports relatively large populations of two

endangered hosts, historically heavily used by *ater*, the Black-capped Vireo and Golden-

cheeked Warbler (*Dendroica chrysoparia*). Based on my data, use of these species by

ater will likely increase as competition for larger hosts increases as *aeneus* moved in.

However, a long-term cowbird removal program is in place and, thus, *aeneus* may face locally reduced competition for smaller hosts. Such a site may provide interesting comparisons with areas where cowbird trapping has not been heavily practiced.

LITERATURE CITED:

Abramsky, Z., M. L. Rosenzweig, and B. Pinshow. 1991. The shape of a gerbil isocline measured using principles of optimal habitat selection. Ecology 72:329-340.

Airola, D. A. 1986. Brown-headed Cowbird parasitism and habitat disturbance in the Sierra Nevada. Journal of Wildlife Management 50:571-575.

Alatalo, R. V., L. Gustafsson, M. Linden, and A. Lundberg. 1985. Interspecific competition and niche shifts in tits and the Goldcrest: an experiment. Journal of Animal Ecology 54:977-984.

Alderson, G. W., H. L. Gibbs, and S. G. Sealy. 1999a. Parentage and kinship analyses in an obligate brood parasitic bird, the Brown-headed Cowbird (*Molothrus ater*) using microsatellite DNA markers. Journal of Heredity 90:182-190.

Alderson, G. W., H. L. Gibbs, and S. G. Sealy. 1999b. Determining the reproductive behavior of individual Brown-headed Cowbirds using microsatellite DNA markers. Animal Behaviour 58:895-905.

Alvarez, F. 1999. Attractive non-mimetic stimuli in Cuckoo *Cuculus canorus* eggs. Ibis 141:140-150.

American Ornithologists' Union. 2000. Forty-second supplement to the American Ornithologists' Union Check-list of North American Birds. Auk 117:847-858.

Avise, J.C. and D. Walker. 1998. Pleistocene phylogeographic effects on avian populations and the speciation process. Proceedings of the Royal Society of London, B 265:457-463.

Badyaev, A. V., G. E. Hill, M. L. Beck, A. A. Dervan, R. A. Duckworth, K. J. McGraw, P. M. Nolan, L. A. Whittingham. 2002. Sex-biased hatching order and adaptive population divergence in a passerine bird. Science 295:316-318.

Badyaev, A. V., L. A. Whittingham, and G. E. Hill. 2001. The evolution of sexual size dimorphism in the House Finch. III. developmental basis. Evolution 55:176-189.

Baepler, D. H. 1968. Lark Sparrow. Pp. 886-902, in Life histories of North American Cardinals, Grosbeaks, Buntings, Towhees, Finches, Sparrows, and Allies. (O.L. Austin, ed.). U. S. National Museum Bulletin 237.

Baicich, P. J. and C. J. O. Harrison. 1997. A Guide to the Nests, Eggs, and Nestlings of North American Birds, second edition. Academic Press. San Diego, CA.

Baker, R. R. 1978. The Evolutionary Ecology of Animal Migration. Holmes and Meier. New York, NY.

Barber, D. R. and T. E. Martin. 1997. Influence of alternate host densities on Brown-headed Cowbird parasitism rates in Black-capped Vireos. Condor 99:595-604.

Bart, J. and A. Tornes. 1989. Importance of monogamous male birds in determining reproductive success: evidence for House Wrens and a review of male-removal experiments. Behavioral Ecology and Sociobiology 24:109-116.

Bedell, M. 1995. On a wing and a prayer. Kurtis Productions, Chicago, IL (film).

Birkhead, T. R. and A. P. Møller. 1992. Sperm Competition in Birds: Evolutionary Causes and Consequences. Academic Press, San Diego.

Birkhead, T. R., E. J. A. Cunningham, and K. M. Cheng. 1996. The insemination window provides a distorted view of sperm competition in birds. Proceedings of the Royal Society of London, B. 263:1187-1192.

Blanco, G., J. Martínez-Padilla, J. A. Dávila, D. Serrano, and J. Vinuela. 2003. First evidence of sex differences in the duration of avian embryonic period: consequences for sibling competition in sexually dimorphic birds. Behavioral Ecology 5:702-706

Blankespoor, G. W., J. Oolman, and C. Uthe. 1982. Eggshell strength and cowbird parasitism of Red-winged Blackbirds. Auk 99:363-365.

Bonsall, M. B. and M. P. Hassell. 1997. Apparent competition structures ecological assemblages. Nature 388:371-373.

Bonsall, M. B., M. P. Hassell, and G. Asefa. 2002. Ecological trade-offs, resource partitioning, and coexistence in a host-parasitoid assemblage. Ecology 83:925-934.

Bowers, M. A. and J. H. Brown. 1982. Body size and coexistence in desert rodents: chance or community structure? Ecology 63:391-400.

Brantley, S. L. 1997. Temporal patterns in surface-active arthropods at the Sevilleta LTER, New Mexico: associations with El Niño for three trophic groups. Supplement to the Bulletin of the Ecological Society of America 78:60.

Briskie, J. V. 1996. Spatiotemporal patterns of sperm storage and last male sperm precedence in birds. Functional Ecology 10:375-383.

Briskie, J. V. and S.G. Sealy. 1990. Evolution of short incubation periods in the parasitic cowbirds, *Molothrus* spp. Auk 107:789-794.

Briskie, J.V., S.G. Sealy, and K. A. Hobson. 1990. Differential parasitism of Least Flycatchers and Yellow Warblers by the Brown-headed Cowbird. Behavioral Ecology and Sociobiology 27:403-410.

Brittingham, M. C. and S. A. Temple. 1983. Have cowbirds caused forest songbirds to decline? BioScience 33:31-35.

Brooke, M. de L. and N. B. Davies. 1991. A failure to demonstrate host imprinting in the cuckoo (*Cuculs canorus*) and alternative hypotheses for the maintenance of egg mimicry. Ethology 89:154-166.

Brooker, L. C. and M. G. Brooker. 1990. Why are cuckoos host specific? Oikos 57:301-309.

Brooker, M. G. and L. C. Brooker. 1992. Evidence for individual female host specificity in two Australian Bronze Cuckoos (*Chrysococcyx* spp.). Australian Journal of Zoology 40:485-493.

Broom, M. and G. D. Ruxton. 2002. A game theoretical approach to conspecific brood parasitism. Behavioral Ecology 13:321-327.

Brown, B. T. 1993. Bell's Vireo, No. 35 in The birds of North America, (A. Poole and F. Gill, eds.) Acad. Nat. Sci., Philadelphia, PA, and Am. Ornithol. Union, Washington, D.C.

Brown, B. T. 1994. Rates of brood parasitism by Brown-headed Cowbirds on riparian passerines in Arizona. Journal of Field Ornithology 65:160-168.

Brown, J. S. 1989. Desert rodent community structure: a test of four mechanisms of coexistence. Ecological Monographs 59:1-20.

Brush, T. 2000. Bronzed Cowbirds (*Molothrus aeneus*) still parasitize Hooded Orioles (*Icterus cucullatus*) in the lower Rio Grande valley of Texas. Bulletin of the Texas Ornithological Society 33:9-10.

Bryant, D. M. and V. M. T. Bryant. 1988. Assimilation efficiency and growth of nestling insectivores. Ibis 130:268-274.

Budnik, J. M., D. E. Burhans, M. R. Ryan, and F. R. Thompson, III. 2001. Nest desertion and apparent nest protection behavior by Bell's Vireos in response to cowbird parasitism. Condor 103:639-643.

Burgham, M. C. and J. Picman. 1989. Effect of Brown-headed Cowbirds on the evolution of yellow warbler anti-parasite strategies. Animal Behaviour 38:298-308.

Burhans, D. E., F. R. Thompson, III, and J. Faaborg. 2000. Costs of parasitism incurred by two songbird species and their quality as cowbird hosts. Condor 102:364-373.

Burnell, K. and S. I. Rothstein. 1994. Variation in the structure of female Brown-headed Cowbird vocalizations and its relation to vocal function and development. Condor 96:703-715.

Butchart, S. H. M., R. M. Kilner, T. Fuisz, and N. B. Davies. 2003. Differences in the nestling begging calls of hosts and host-races of the Common Cuckoo, *Cuculus canorus*. Animal Behaviour 65:345-354

Carello, C. A. and G. K. Snyder. 2000. The effects of host numbers on cowbird parasitism of Red-winged Blackbirds. Pp. 110-114, in Ecology and Management of Cowbirds and Their Hosts, (J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, eds.). University of Texas Press, Austin, TX.

Carter, M. D. 1984. The Social Organization and Parasitic Behavior of the Bronzed Cowbird in South Texas. Ph.D. dissertation, University of Minnesota.

Carter, M. D. 1986. The parasitic behavior of the Bronzed Cowbird in South Texas. Condor 88:11-25.

Chace, J. F. 2001. Host and Habitat Partitioning by Sympatric Brood Parasites in Arizona. Ph.D. dissertation. University of Colorado, Boulder, CO.

Chace, J. F. 2004. Habitat selection by sympatric brood parasites in southeastern Arizona: the influence of landscape, vegetation, and species richness. Southwestern Naturalist 49:24-32.

Chance, E. 1940. The Truth About the Cuckoo. Country Life, London, UK.

Chakrabroty, R., T. R. Meagher, and P. E. Smouse. 1988. Parentage analysis with genetic markers in natural populations. I. The expected proportion of offspring with unambiguous paternity. Genetics 118:527-536.

Cheng, K. M., J. T. Burns, and F. McKinney. 1983. Forced copulation in captive mallards. III. sperm competition. Auk 100:302-310.

Clayton, N. S., J. C. Reboreda, and A. Kacelnik. 1997. Seasonal changes of hippocampus volume in parasitic cowbirds. Behavioural Processes 41:237-243.

Clements, J. F. 2003. Birds of the World. 5th edition. Ibis Publishing, Vista, CA.

Clotfelter, E. D. 1995. Courtship displaying and intrasexual competition in the Bronzed Cowbird. Condor 97:816-818.

Clutton-Brock, T. H., T. H. Albon, and F. E. Guinness. 1985. Parental investment and sex differences in juvenile birds and mammals. Nature 313:131-133.

Coe, S. J. and J. T. Rotenberry. 2003. Water availability affects clutch size in a desert sparrow. Ecology 84:3240-3249.

Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. American Naturalist 122:661-696.

Coon, D. W. 1974. Daily Movement of the Brown-headed Cowbird in south-central Texas During Winter. Ph.D. dissertation. Texas A&M University, College Station, TX.

Cruz, A., T. D. Manolis, and J. W. Wiley. 1985. The Shiny Cowbird: a brood parasite expanding its range in the Caribbean region. Ornithological Monographs 36:607 -619.

Cruz, A., W. Post, J. W. Wiley, C. P. Ortega, T. K. Nakamura, and J. W. Prather. 1998. Potential impacts of cowbird range expansion in Florida. Pp. 313-336, in Parasitic Birds and Their Hosts: Studies in Coevolution, (S. I. Rothstein and S. K. Robinson, eds.). Oxford University Press, Oxford, UK.

Cruz, A. and J. W. Wiley. 1989. The decline of an adaptation in the absence of a presumed selection pressure. Evolution 43:55-62.

Curson, D. R., C. B. Goguen, and N. E. Matthews. 2000. Long-distance commuting by Brown-headed Cowbirds in New Mexico. Auk 117:795-799.

Curson, D. R. and N. E. Matthews. 2003. Reproductive costs of commuting flights in Brown-headed Cowbirds. Journal of Wildlife Management 67:520-529.

Darley, J. A. 1971. Sex ratio and mortality in the Brown-headed Cowbird. Auk 88:560-566.

Darley, J. A. 1982. Territorial behavior of the female Brown-headed Cowbird (*Molothrus ater*). Canadian Journal of Zoology 61:65-69.

Davies, N.B. 2000. Cuckoos, Cowbirds, and Other Cheats. T. & A. D. Poyser, London, UK.

Davies, N. B., and M. de L.Brooke. 1989. An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts. I. Host egg discrimination. Journal of Animal Ecology 58:207-224.

Davis, S. K. 2003. Nesting ecology of mixed-grass prairie songbirds in southern Saskatchewan. Wilson Bulletin 115:119-130.

Davis, S. K. and S. G. Sealy. 2000. Cowbird parasitism and nest predation in fragmented grasslands of southwestern Manitoba. Pp. 220-228, in Ecology and Management of Cowbirds and Their Hosts, (J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, eds.). University of Texas Press, Austin, TX.

De Groot, K. L. and J. N. M. Smith. 2001. Community-wide impacts of a generalist brood parasite, the Brown-headed Cowbird (*Molothrus ater*). Ecology 82:868 -881.

Dearborn, D. C. 1998. Begging behavior and food acquisition by Brown-headed Cowbird nestlings. Behavioral Ecology and Sociobiology 43:259-270.

Dearborn, D. C., A. D. Anders, F. R. Thompson, III, and J. Faaborg. 1998. Effects of cowbird parasitism on parental provisioning and nestling food acquisition and growth. Condor 100:326-334.

Dearborn, D. C. and G. Lichtenstein. 2002. Begging behavior and host exploitation in parasitic cowbirds. Pp. 361-388, in The Evolution of Begging: Competition, Cooperation, and Communication, (J. Wright and M. L. Leonard, eds.). Kluwer Academic Publishing, Norwell, MA.

Dickman, C. R., K. Green, P. L. Carron, D. C. D. Happold, and W. S. Osborne. 1983. Coexistence, convergence and competition among *Antechinus* (Marsupialia) in the Australian high country. Proceedings of the Ecological Society of Australia 12:79-99.

Dolbeer, R. A. and C. R. Smith. 1985. Sex-specific feeding habits of Brown-headed Cowbirds in northern Ohio in January. Ohio Journal of Science 85:104-107.

Dufty, A. M., Jr. 1982. Responses of Brown-headed Cowbirds to simulated conspecific intruders. Animal Behaviour 30:1043-1052.

Dufty, A. M., Jr. 1983. Variation in the egg markings of the Brown-headed Cowbird. Condor 85:109-111.

Dunning, J. B. 1993. Handbook of Avian Body Masses. CRC Press, Boca Raton, FL.

Eadie, J., P. Sherman, and B. Semel. 1998. Conspecific brood parasitism, population dynamics, and the conservation of cavity-nesting birds. Pp. 306-340, in Behavioral Ecology and Conservation Biology, (T. Caro, ed.). Oxford University Press, Oxford, UK.

Eastzer, D., P. R. Chu, and A. P. King. 1980. The young cowbird: average or optimal nestling? Condor 82:417-425.

Eckerle, K. P. and R. Breitwisch. 1997. Reproductive success of the Northern Cardinal, a large host of Brown-headed Cowbirds. Condor 99:169-178.

Edvardsen, E., A. Moksnes, E. Røskaft, E. Øien, and M. Honza. 2001. Egg mimicry in cuckoos parasitizing four sympatric species of *Acrocephalus* warblers. Condor 103:829-837.

Ellison, W. G. 1992. Blue-gray Gnatcatcher, No. 23 in The birds of North America, (A. Poole and F. Gill, eds.) Acad. Nat. Sci., Philadelphia, PA, and Am. Ornithol. Union, Washington, D.C.

Evans, D. R. and J. E. Gates. 1997. Cowbird selection of breeding areas: the role of habitat and bird species abundance. Wilson Bulletin 109:470-480.

Faddoul, G. D., G. W. Fellows, and J. Baird. 1966. A survey of the incidence of salmonellae in wild birds. Avian Disease 10:89-94.

Fankhauser, D. P. 1971. Annual survival rates of blackbirds and starlings. Bird-Banding 42:36-42.

Fiala, K. L. 1981. Reproductive cost and the sex ratio in Red-winged Blackbirds. Pp. 198-214, in Natural Selection and Social Behavior, (R. D. Alexander and D. W. Tinkle, eds.). Chiron Press, NY.

Finch, D. M. 1983. Brood parasitism of the Abert's towhee: timing, frequency and effects. Condor 85:355-359.

Fisher, R. A. 1930. The Genetical Theory of Natural Selection. Clarendon Press, Oxford, UK.

Fleischer, R. C. 1985. A new technique to identify and assess dispersion of eggs of individual brood parasites. Behavioral Ecology and Sociobiology 17:91-99.

Fleischer, R. C. and S. I. Rothstein. 1988. Known secondary contact and rapid gene flow among subspecies and dialects in the Brown-headed Cowbird. Evolution 42:1146-1158.

Fleischer, R. C. and N. G. Smith. 1992. Giant Cowbird eggs in the nests of two icterid hosts: The use of morphology and electrophoretic variants to identify individuals and species. Condor 94:572-578.

Fleischer, R. C., A. P. Smyth, and S. I. Rothstein. 1987. Temporal and age-related variation in the laying rate of the Brown-headed Cowbird in the eastern Sierra Nevada, CA. Canadian Journal of Zoology 65:2724-2730.

Flood, N. J. 1990. Aspects of the breeding biology of Audubon's Oriole. Journal of Field Ornithology 61:290-302.

Forcey, J. M. 2002. Notes on the birds of central Oaxaca, Part III: Hirundinidae to Fringillidae. Huitzl 3:43-55.

Fraga, R. M. 1978. The Rufous-collared Sparrow as a host of the Shiny Cowbird. Wilson Bulletin 90:271-284.

Fraga, R. M. 1979. Differences between nestlings and fledglings of Screaming and Bay-winged Cowbirds. Wilson Bulletin 90:151-154.

Fraga, R. M. 1983. The eggs of the parasitic Screaming Cowbird (*Molothrus rufoaxillaris*) and its host the Bay-winged Cowbird (*M. badius*): is there evidence for egg mimicry? Journal of Ornithology 124:187-193.

Fraga, R. M. 1984. Bay-winged Cowbirds (*Molothrus badius*) remove ectoparasites from their brood parasites, the Screaming Cowbirds (*M. rufoaxillaris*). Biotropica 16:223-226.

Fraga, R. M. 1985. Host-parasite interactions between Chalk-browed Mockingbirds and

Shiny Cowbirds. Ornithological Monographs 36:829-844.

Fraga, R. M. 1996. Further evidence of parasitism on Chopi Blackbirds (*Gnorimopsar*

chopi) by the specialized Screaming Cowbird (*Molothrus rufoaxillaris*).

Condor 98:866-867.

Fraga, R. M. 1998. Interactions of the parasitic Screaming and Shiny cowbirds

(*Molothrus rufoaxillaris* and *M. bonariensis*) with a shared host, the Bay-winged

Cowbird (*M. badius*). Pp. 173-193 in, Parasitic Birds and Their Hosts: Studies

in Coevolution, (S. I. Rothstein and S. K. Robinson, eds.). Oxford University

Press, Oxford, UK.

Fraga, R. M. 2002. Notes on new or rarely reported Shiny Cowbird hosts from

Argentina. Journal of Field Ornithology 73:213-219.

Frank, S. A. 1990. Sex allocation theory for birds and mammals. Annual Review of

Ecology and Systematics 21:13-55.

Fretwell, S. D. 1977. Is the Dickcissel a threatened species. American Birds 31:923-932.

Friedmann, H. 1928. The origin of host specificity in the parasitic habit in the

Cuculidae. Auk 45:33-38.

Friedmann, H. 1929. The cowbirds: a study in the biology of social parasitism.

C. Thomas, Publ., Springfield, IL.

Friedmann, H. 1963. Host relations of the parasitic cowbirds. United States National

Museum Bulletin 233:1-276.

Friedmann, H. 1967. Alloxenia in three sympatric African species of *Cuculus*.

Proceedings of the U. S. National Museum 124:1-14.

Friedmann, H., L. F. Kiff, and S. I. Rothstein. 1977. A further contribution to knowledge of the host relations of the parasitic cowbirds. Smithsonian Contributions to Zoology No. 235.

Friedmann, H. and L. F. Kiff. 1985. The parasitic cowbirds and their hosts. Proceedings of the Western Foundation of Vertebrate Zoology 2:225-304.

Futuyma, D. J. 1998. Evolutionary Biology. Third edition. Sinauer Associates, Inc. Sunderland, MA.

Futuyma, D. J. and M. Slatkin. 1983. Coevolution. Sinauer Associates, Inc. Sunderland, MA.

Gärtner, K. 1982. Zur Ablehnung von Eirn und Jungen des Kuckucks (*Cuculus canorus*). Ornithologische Mitteilungen 33:115-131.

Gates, J. E. and L. W. Gysel. 1978. Avian nest dispersion and fledging success in field-forest ecotones. Ecology 59:871-883.

Gause, G. F. 1934. Struggle for Existence. Hafner, New York, NY.

Gibbs, H. L., P. Miller, G. Alderson, and S. G. Sealy. 1997. Genetic analysis of Brown-headed Cowbirds *Molothrus ater* raised by different hosts: data from mtDNA and microsatellite DNA markers. Molecular Ecology 6:189-193.

Gibbs, H.L., M. Sorenson, K. Marchetti, M. de L. Brooke, N. B. Davies, and H. Nakamura. 2000. Genetic evidence for female host-specific races of the Common Cuckoo. Nature 407:183-186.

Glassey, B. and S. Forbes. 2003. Why Brown-headed Cowbirds do not influence Red-winged Blackbird Parent behaviour. Animal Behaviour 65:1235-1246.

Godfray, H. C. J. 1994. Parasitoids: Behavioural and Evolutionary Ecology. Princeton University Press, Princeton, NJ.

Goertz, J. W. 1977. Additional records of Brown-headed Cowbird nest parasitism in Louisiana. Auk 94:386-389.

Goguen, C. B. 1999. Brown-headed Cowbird Movements, Habitat Use, and Impacts on Hosts in a Grazed and Ungrazed Landscape. Ph.D. dissertation, University of Wisconsin, Madison, WI.

Good, H. L. B. 1979. The Structure of an Urban Winter Blackbird Roost. Ph.D. dissertation. Rice University, Houston, TX.

Goodnight, K. F. and D. C. Queller. 1999. Computer software for performing likelihood tests of pedigree relationship using genetic markers. Molecular Ecology 8:1551 -1161.

Gowaty, P. A. 1996. Battles of the sexes and origins of monogamy. Pp. 21-52, in Partnerships in Birds: the Study of Monogamy, (J. M. Black, ed.). Oxford University Press, Oxford, UK.

Grant, N. D., and S. G. Sealy. 2002. Selection of Red-winged Blackbird (*Agelaius phoeniceus*) hosts by the Brown-headed Cowbird (*Molothrus ater*). Bird Behavior 15: 21–30.

Grant, P. R. 1999. Ecology and Evolution of Darwin's Finches. Second edition. Princeton University Press, Princeton, NJ.

Grant, P. R. and B. R. Grant. 1985. Responses of Darwin's finches to unusual rainfall. Pp. 417-447, in El Niño en las Islas Galápagos: El Evento de 1982-1983, (G. Robinson and E. M. del Pino, eds.). Fundación Charles Darwin para las Islas Galápagos, Quito, Ecuador.

Greene, E. 1999. Demographic consequences of Brown-headed Cowbird parasitization of Lazuli Buntings. Studies in Avian Biology 14:144-152.

Griffith, J. T. and J. C. Griffith. 2000. Cowbird control and the endangered Least Bell's Vireo: a management success story. Pp. 342-356, in Ecology and Management of Cowbirds and Their Hosts, (J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, eds.). University of Texas Press, Austin, TX.

Griffiths, R., M.C. Double, K. Orr, and R.J.G. Dawson. 1998. A DNA test to sex most birds. Molecular Ecology 7:1071-1075.

Grzybowski, J. A. and C. M. Pease. 2000. Comparing the relative effects of brood parasitism and nest predation on seasonal fecundity in passerine birds. Pp.145-155, in Ecology and Management of Cowbirds and Their Hosts. (J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, eds.). University of Texas Press, Austin, TX.

Haas, C.A. and K. H. Haas. 1998. Brood parasitism by Brown-headed Cowbirds on Brown Thrashers: frequency and rates of rejection. Condor 100:535-540.

Hahn, D. C. and J. S. Hatfield. 1995. Parasitism at the landscape scale: cowbirds prefer forests. Conservation Biology 6:1415-1424.

Hahn, D. C., J. A. Sedgwick, I. S. Painter, and N. J. Casna. 1999. A spatial and genetic analysis of cowbird host selection. Studies in Avian Biology 18:204-217.

Halterman, M. D., S. Allen, and S. A. Laymon. 1999. Assessing the impact of

Brown-headed Cowbird parasitism in eight National Parks. Studies in Avian

Biology 18:153-159.

Hamilton, W. J., III. and G. H. Orians. 1965. Evolution of brood parasitism in altricial

birds. Condor 67:361-382.

Hassell, M. P. and R. M. May. 1986. Generalist and specialist natural enemies in insect

predator-prey interactions. Journal of Animal Ecology 55:923-940.

Hathcock, C. R. 2001. Factors Affecting Reproductive Success in Hosts of the Bronzed

Cowbird (*Molothrus aeneus*) in the Lower Rio Grande Valley, Texas. M.Sc.

thesis, University of Texas-Pan American, Edinburg, TX.

Hathcock, C. R. and T. Brush. 2004. Breeding abundance and nest-site distribution of the

Altamira Oriole at Santa Ana National Wildlife Refuge, Texas.

Southwestern Naturalist 49:33-38.

Hauber, M. E. and D. C. Dearborn. 2003. Avian reproduction without parental care:

what to look for in genetic studies of obligate brood-parasitic mating systems.

Auk 120:1-13.

Hauber, M. E., P. W. Sherman, and D. Paprika. 2000. Self-referent phenotype matching

in a brood parasite: the armpit effect in Brown-headed Cowbirds (*Molothrus

ater*). Animal Cognition 3:113-117.

Haverschmidt, F. 1968. Birds of Surinam. Oliver and Boyd, Edinburgh, UK.

Hayden, T. J., D. J. Tazik, R. H. Melton, and J. D. Cornelius. 2000. Cowbird control
program at Fort Hood Texas: lessons for mitigation of cowbird parasitism on a
landscape scale. Pp. 357-370 in Ecology and Management of Cowbirds and Their
Hosts, (J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy,
eds.). University of Texas Press, Austin, TX.

Hearne, C. M., S. Gosh, and J. A. Todd. 1992. Microsatellites for linkage analysis of
genetic traits. Trends in Ecology and Evolution 8:288-294.

Higuchi, H. 1998. Host use and egg color of Japanese cuckoos. Pp. 80-93. In Parasitic
birds and their hosts. (S. I. Rothstein and S. K. Robinson, eds.). Oxford University
Press, Oxford, UK.

Higuchi, H. and S. Sato. 1984. An example of character release in host selection and egg
colour of Japanese cuckoos, *Cuculus* spp. in Japan. Ibis 126:398-404.

Hill, D. P. and S. G. Sealy. 1994. Desertion of nests parasitized by cowbirds: have Clay-
colored Sparrows evolved an anti-parasite defense? Animal Behaviour 48:1063
-1070.

Hill, R. A. 1974. Host-parasite Relationships, Summer Movements, and Population
Structure of the Brown-headed Cowbird in a Prairie Habitat of West-central
Kansas. M.Sc. thesis, Fort Hays Kansas State College, KS.

Hill, R. A. 1976a. Host-parasite relationships of the Brown-headed Cowbird in a prairie
habitat of west-central Kansas. Wilson Bulletin 88:555-565.

Hill, R. A. 1976b. Sex ratio determination of immature Brown-headed Cowbirds.
Bird-Banding 47:112-114.

Hofslund, P. B. 1957. Cowbird parasitism of the northern Yellow-Throat. Auk 74:42-48.

Holford, K. C. and D. D. Roby 1993. Factors limiting fecundity of captive Brown-headed Cowbirds. Condor 95:536-545.

Honza, M., B. Taborsky, M. Taborsky, Y. Teuschl, W. Vogl, A. Moksnes, and E. Røskaft. 2002. Behaviour of female Common Cuckoos, *Cuculus canorus*, in the vicinity of host nests before and during egg laying: a radiotelemetry study. Animal Behaviour 64:861-868.

Hoover, J. P. 2003. Multiple effects of brood parasitism reduce the reproductive success of Prothonotary Warblers. Animal Behaviour 65:923-934.

Hosoi, S. A. and S. I. Rothstein. 2000. Nest desertion and cowbird parasitism: evidence for evolved responses and evolutionary lag. Animal Behaviour 59:823-840.

Hoy, G. and J. Ottow. 1964. Biological and oological studies of the molothrine cowbirds (Icteridae) of Argentina. Auk 82:186-203.

Jackson, N. H. and D. D. Roby. 1992. Fecundity and egg-laying patterns of yearling brown-headed cowbirds. Condor 94:585-589.

Jaramillo, A. P. 1993. Parasite-host Coevolution in the Cowbirds *Molothrus rufoaxillaris* and *Molothrus badius*: Egg Mimcry in Shape and Size. M.Sc. thesis, University of Toronto, Toronto, ON.

Jaramillo, A. P. and P. Burke 1999. New World Blackbirds: the Icterids. Princeton University Press, Princeton, NJ.

Johnsgard, P. A. 1997. The Avian Brood Parasites. Oxford University Press, Oxford, UK.

Johnson, D. M., G. L. Stewart, M. Corley, R. Ghrist, J. Hagner, A. Keterrer, B. McDonnell, W. Newsom, E. Owen, and P. Samuels. 1980 . Brown-headed Cowbird (*Molothrus ater*) mortality at an urban winter roost. Auk 97:299-320.

Johnson, K. P. and S. M. Lanyon. 1999. Molecular systematics of the grackles and allies and the effects of additional sequence (cyt *b* and ND2). Auk 116:759-768.

Joseph, L., T. Wilke, and D. Alpers. 2002. Reconciling genetic expectations from host specificity with historical population dynamics in an avian brood parasite, Horsfield's Bronze-cuckoo *Chalcites basalis* of Australia. Molecular Ecology 11:829-837.

Kasumovic, M. M., H. L. Gibbs, B. E. Woolfenden, S. G. Sealy, and H. Nakamura. 2002. Primary sex-ratio variation in two brood-parasitic birds: Brown-headed Cowbird (*Molothrus ater*) and Common Cuckoo (*Cuculus canorus*). Auk 119:561-566.

Kattan, G. H. 1993. Reproductive Strategy of a Generalist Brood Parasite, the Shiny Cowbird, in the Cauca Valley, Colombia. Ph.D. dissertation, University of Florida, Gainesville, FL.

Kattan, G. H. 1995. Mechanisms of short incubation period in brood-parasitic cowbirds. Auk 112:335-342.

Kattan, G. H. 1997. Shiny cowbirds follow the "shotgun" strategy of brood parasitism. Animal Behaviour 53:647-654.

Ketterson, E. D. and V. Nolan, Jr. 1983. The evolution of differential bird migration. Current Ornithology 1:357-402.

Kilner, R. 1998. Primary and secondary sex ratio manipulation by Zebra Finches.

Animal Behaviour 56:155-164.

Kilner, R. M. 2003. How selfish is a cowbird nestling? Animal Behaviour 66:569-576.

Kilpatrick, A.M. 2002. Variation in growth of Brown-headed Cowbird (*Molothrus ater*)

nestlings and energetic impacts of their host parents. Canadian Journal of Zoology

80:145-153.

King, A. P., M. J. West, and D. J. White. 2002. The presumption of sociality: social

learning in diverse contexts in Brown-headed Cowbirds (*Molothrus ater*). Journal

of Comparative Psychology 116:173-181.

Koenig, W. D. 1982. Ecological and social factors affecting hatchability of eggs.

Auk 99:526-536.

Koskimies, P. and R. A. Vaisanen 1991. Mapping census of breeding land birds.

Pp. 63-74 in Monitoring bird populations. Finnish Museum of Natural History,

Helsinki.

Kostecke, R. M., K. Ellison, and S. G. Summers. Continued range expansion by

Bronzed Cowbirds in the southwestern United States. 2004. Southwestern

Naturalist 49:487-492.

Kotler, B. P. and J. S. Brown. 1999. Mechanisms of coexistence of optimal foragers as

determinants of the local abundance and distributions of desert granivores.

Journal of Mammalogy 80:361-374.

Kozlovic, D. R. 1998. Cowbird parasitism and productivity of House Finch hosts.

Canadian Journal of Zoology 76:1714-1721.

Krementz, D. G., J. D. Nichols, and J. E. Hines. 1989. Postfledging survival of European Starlings. Ecology 70:646-655.

Lack, D. 1968. Ecological adaptations for breeding in birds, Methuen, London.

Lanyon, S. M. 1992. Interspecific brood parasitism in blackbirds (Icterinae): a phylogenetic perspective. Science 225:77-9.

Lea, S. E. G. and G. H. Kattan. 1998. Reanalysis gives further support to the 'shotgun' model of Shiny Cowbird parasitism of house wren nests. Animal Behaviour 56:1571-1573.

Lichtenstein, G. 1998. Parasitism by Shiny Cowbirds of Rufous-bellied Thrushes. Condor 100:680-687.

Lichtenstein, G. 2001a. Selfish begging by Screaming Cowbirds, a mimetic brood parasite of the Bay-winged Cowbird. Animal Behaviour 61:1151-1158.

Lichtenstein, G. 2001b. Low success of Shiny Cowbird chicks parasitizing Rufous-bellied Thrushes: chick-chick competition or parental discrimination? Animal Behaviour 61:401-413.

Lichtenstein, G. and S. G. Sealy 1998. Nestling competition, rather than supernormal stimulus, explains the success of parasitic Brown-headed Cowbird chicks in Yellow Warbler nests. Proceedings of the Royal Society of London, B 265:249 -254.

Linden, M., L. Gustafsson, and T. Part. 1992. Selection on fledgling mass in the Collared Flycatcher and the Great Tit. Ecology 73:336-343.

Lipar, J. L. and E. D. Ketterson. 2000. Maternally derived yolk testosterone enhances the development of the hatching muscle in the Red-winged Blackbird *Agelaius phoeniceus*. Proceedings of the Royal Society of London, B 267:2005-2010.

Lipar, J. L., E. D. Ketterson, and V. Nolan. 1999. Intraclutch variation in testosterone content of Red-winged Blackbird eggs. Auk 116:231-235.

Longmire, J. L., J. L. Roach, M. Maltbie, P. S. White, O. L. Tatum, K. D. Makova, D. C. Hahn. 2001. Tetranucleotide microsatellite markers for the Brown-headed Cowbird *Molothrus ater*. Journal of Avian Biology 32:76-78.

Lowther, P. E. 1981. American Robin rears Brown-headed Cowbird. Journal of Field Ornithology 52:145-147.

Lowther, P. E. 1984. Cowbird nest selection. Wilson Bulletin 96:103-107.

Lowther, P. E. 1993. Brown-headed Cowbird (*Molothrus ater*). The birds of North America, no. 47 (A. Poole and F. Gill, eds.) Academy of Natural Sciences, Philadelphia, PA, and American Ornithologists' Union, Washington, D.C.

Lowther, P. E. 1995. Bronzed Cowbird (*Molothrus aeneus*). The birds of North America, no. 144 (A. Poole and F. Gill, eds.) Academy of Natural Sciences, Philadelphia, PA, and American Ornithologists' Union, Washington, D.C.

Lowther, P. E. 2001. New name for the Bolivian Blackbird. Bulletin of the British Ornithologists' Club 121:280.

Lowther, P. E. 2004. Molothrine cowbird host list. http://fm1.fielmuseum.org/aa/files/lowther/Cblist.pdf. Accessed 16 December.

Lowther, P. E. and W. Post. 1999. Shiny Cowbird (*Molothrus bonariensis*). The birds of

    North America, no. 399 (A. Poole and F. Gill, eds.) Academy of Natural Sciences,

    Philadelphia, PA, and American Ornithologists' Union, Washington, D.C.

Lyon, B. E. 1997. Spatial patterns of Shiny Cowbird brood parasitism on

    Chestnut-capped Blackbirds. Animal Behaviour 54:927-939.

Manolis, T. D. 1982. Host Relationships and Reproductive Strategies of the Shiny

    Cowbird in Trinidad and Tobago. Ph.D. dissertation, University of Colorado,

    Boulder, CO.

Marchant, S. 1960. The breeding of some S.W. Ecuadorian birds. Ibis 102:584-599.

Marshall, T. C., J. Slate, L. E. B. Kruuk, and J. M. Pemberton. 1998. Statistical

    confidence for likelihood-based paternity inference in natural populations.

    Molecular Ecology 7:639-655.

Martin, T. E. 1992. Breeding productivity considerations: what are the appropriate

    habitat features for management? Pp. 455-473, in Ecology and Conservation of

    Neotropical Migrant Landbirds, (J. M. Hagan, III, and D. W. Johnston, eds.).

    Smithsonian Institution Press, Washington, D.C.

Martinez J.G., Soler, J.J., Soler, M., and Burke, T. 1998. Spatial patterns of egg laying

    and multiple parasitism in a brood parasite: a non-territorial system in the Great

    Spotted Cuckoo (*Clamator glandarius*). Oecologia 117:286-294.

Mason, P. 1980. Ecological and Evolutionary Aspects of Host Selection in Cowbirds.

    Ph.D. dissertation, University of Texas, Austin, TX.

Mason, P. 1986a. Brood parasitism in a host generalist, the Shiny Cowbird: I. The quality

    of different species as hosts. Auk 103:52-60.

Mason, P. 1986b. Brood parasitism in a host generalist, the Shiny Cowbird: II. Host

  selection. Auk 103:61-69.

Mason, P. and S. I. Rothstein. 1986. Coevolution and avian brood parasitism: cowbird

  eggs show evolutionary response to host discrimination. Evolution 40:1207-1214.

Massoni, V. and J. C. Reboreda. 2002. A neglected cost of brood parasitism: egg

  punctures by Shiny Cowbirds during inspection of potential host nests.

  Condor 104:407-412.

Mattson, M. E. 1973. Host-parasite Relations of Canvasback and Redhead Ducklings.

  M.Sc. thesis. University of Manitoba.

May, R. M. and S. K. Robinson. 1985. Population dynamics of avian brood parasitism.

  American Naturalist 126:475-494

Mayfield, H. 1960. The Kirtland's Warbler. Cranbrook Institute of Science,

  Bloomfield Hills, MI.

Mayfield, H. F. 1965. Chance distribution of cowbird eggs. Condor 67:257-263.

McGaha, H. R. 2000. Effects of Dual Species Brood Parasitism on the Nesting Success

  of Northern Cardinals. M.Sc. thesis. Sam Houston State University, Huntsville,

  TX.

McGeen, D.S. 1972. Cowbird-host relationships. Auk 89:360-380.

McLaren, C. M., B. E. Woolfenden, H. L. Gibbs, and S. G. Sealy. 2003. Genetic and

  temporal patterns of multiple parasitism by Brown-headed Cowbirds (*Molothrus

  ater*) on Song Sparrows (*Melospiza melodia*). Canadian Journal of Zoology

  81:281-286.

McMaster, D.G., D. L. H. Neudorf, S. G. Sealy, and T. E. Pitcher. 2004. A comparative

analysis of laying times in passerine birds. Journal of Field Ornithology

75:113–122.

Mermoz, M. E. and G. J. Fernández. 2003. Breeding success of a specialist brood

parasite, the Screaming Cowbird, parasitizing an alternative host.

Condor 105:63-72.

Mermoz, M. E. and J. F. Ornelas. 2004. Phylogenetic analysis of life-history adaptations

in parasitic cowbirds. Behavioral Ecology 15:109-119.

Mermoz, M. E. and J. C. Reboreda. 1994. Brood parasitism of the Shiny Cowbird

Molothrus bonariensis, on the Brown-and-yellow Marshbird, *Pseudoleistes*

virescens. Condor 96:716-721.

Mermoz, M. E. and J. C. Reboreda. 1996. New effective host for the Screaming Cowbird.

Condor 98:630-632.

Mermoz, M. E. and J. C. Reboreda. 1999. Egg-laying behaviour by Shiny Cowbirds

parasitizing Brown-and-yellow Marshbirds. Animal Behaviour 58:873-882.

Mermoz, M. E. and J. C. Reboreda. 2003. Reproductive success of Shiny Cowbird

(*Molothrus bonariensis*) parasitizing the larger Brown-and-yellow Marshbird

(*Pseudoleistes virescens*) in Argentina. Auk 120:1128-1139.

Middleton, A. L. A. 1991. Failure of Brown-headed Cowbird parasitism in nests of the

American Goldfinch. Journal of Field Ornithology 62:200-203.

Mines, B. M. 1999. Hosts of the Pintailed Whydah (*Vidua macroura*) in southern

Africa. Bird Numbers 8:6.

Misenhelter, M. D. and J. T. Rotenberry. 2000. Choices and consequences of habitat occupancy and nest site selection in Sage Sparrows. Ecology 81:2892-2901.

Moksnes, A. and E. Røskaft 1995. Egg-morphs and host preference in the Common Cuckoo *Cuculus canorus*: an analysis of cuckoo and host eggs from European museum collections. Journal of Zoology 236:625-648.

Morel, M.-Y. 1973. Contribution à l'étude dynamique de la population de *Lagonosticta senegala* L. (estrildides) à Richard-Toll (Sénégal). Interrelations avec le parasite *Hypochera chalybeata* (Müller) (viduines). Mémoires du Muséum d'Histoire Naturelle Série A. 78:1-156.

Morrison, S. A. and D. T. Bolger. 2002. Variation in a sparrow's reproductive success with rainfall: food and predator-mediated processes. Oecologia 133:315-324.

Moynihan, M. 1968. Social mimicry: character convergence versus character displacement. Evolution 22:315-331.

Møller, A. P. 1987. Behavioural aspects of sperm competition in swallows *Hirundo rustica*. Behaviour 100:92-104.

Murray, B. G. 1969. A comparative study of the Le Conte's and Sharp-tailed sparrows. Auk 86:199-231.

Nakamura, H., S. Kubota, and R. Suzuki. 1998. Coevolution between the Common Cuckoo and its major hosts in Japan. Pp. 94-112, in Parasitic Birds and Their Hosts: Studies in Coevolution, (S. I. Rothstein and S. K. Robinson, eds.). Oxford University Press, Oxford, UK.

Nakamura, H. and Miyazawa, Y. 1997. Movements, space use and social organization
of radio-tracked Common Cuckoos during their breeding season in Japan.
Japanese Journal of Ornithology 46:23-53.

Nei, M. 1987. Molecular Evolutionary Genetics. Columbia University Press, New York,
NY.

Neudorf, D. L. and S. G. Sealy. 1994. Sunrise attentiveness in cowbird hosts.
Condor 96:162-169.

Newman, G. A. 1970. Cowbird parasitism and nesting success of Lark Sparrows in
southern Oklahoma. Wilson Bulletin 82:304-309.

Ney-Nifle, M., C. Bernstein, J. C. Reboreda, and A. Kacelnik. In press. Population
dynamics and avian brood parasitism: persistence and invasions in a three species
system. Journal of Animal Ecology.

Nicolai, J. 1964. Mimicry in parasitic birds. Scientific American 231:92-98.

Niles, D. M. 1970. A record of clutch size and breeding in New Mexico for the Bronzed
Cowbird. Condor 72:500-501.

Nilsson, P. A. and G. D. Ruxton. 2004. Temporally fluctuating prey and interfering
predators: a positive feedback. Animal Behaviour 68:159-165.

Nolan, V., Jr. 1978. The ecology and behavior of the Prairie Warbler *Dendroica
discolor*. Ornithological Monographs 26:1-595.

Oberholser, H.C. 1974. The bird life of Texas. University of Texas Press. Austin, TX.

Oddie, K. 1998. Sex discrimination before birth. Trends in Ecology and Evolution
13:130-131.

Oddie, K. 2000. Size matters: competition between male and female Great Tit offspring. Journal of Animal Ecology 69:903-912.

O'Loghlen, A. L. and S. I. Rothstein. 1995. Culturally correct song dialects are correlated with male age and female song preference in wild populations of Brown-headed Cowbirds. Behavioral Ecology and Sociobiology 36:251-259.

Omland, K. E. and S. M. Lanyon. 2000. Reconstructing plumage evolution in orioles (*Icterus*): repeated convergence and reversal in patterns. Evolution 54:2119-2133.

Orians, G. H., E. Røskaft, and L. D. Beletsky. 1989. Do Brown-headed Cowbirds lay their eggs at random in the nests of Red-winged Blackbirds? Wilson Bulletin 101:599-605.

Ortega, C. P. 1998. Cowbirds and other brood parasites. University of Arizona Press. Tucson, AZ.

Ortega, C. P., J. C. Ortega, S. A. Backensto, and C. A. Rapp. 1996. Improved methods for ageing second-year and after-second-year male Brown-headed Cowbirds. Journal of Field Ornithology 67:542-548.

Ortega, C. P. and J. C. Ortega. 2001. Effects of Brown-headed Cowbirds on the nesting success of Chipping Sparrows in southwest Colorado. Condor 103:127-133.

Ortega, C. P., J. C. Ortega, and A. Cruz. 1994. Use of artificial Brown-headed Cowbird eggs as a potential management tool in deterring parasitism, Journal of Wildlife Management 58:488-492.

Parker, T. H. 1999. Responses of Bell's Vireo to parasitism by the Brown-headed Cowbird in Kansas. Wilson Bulletin 111:499-504.

Payne, R. B. 1965. Clutch size and numbers of eggs laid by Brown-headed Cowbirds. Condor 67:44-60.

Payne, R. B. 1973. The breeding season of a parasitic bird, the Brown-headed Cowbird in central California. Condor 75:80-99.

Payne, R. B. 1976. The clutch size and numbers of eggs of Brown-headed Cowbirds: the effects of latitude and breeding season. Condor 78:337-342.

Payne, R. B. 1977a. Clutch size, egg size, and the consequences of single vs. multiple parasitism in parasitic finches. Ecology 58:500-513.

Payne, R. B. 1977b. The ecology of brood parasitism in birds. Annual Review of Ecology and Systematics 8:1-28.

Payne, R. B. and K. Payne. 1967. Cuckoo hosts in southern Africa. Ostrich 38:135-143.

Payne, R. B. and L. L. Payne. 1998a. Nestling eviction and vocal begging behaviors in the Australian glossy cuckoos *Chrysococcyx basalis* and *C. lucidus*. Pp. 152-172, in Parasitic Birds and Their Hosts: Studies in Coevolution, (S. I. Rothstein and S. K. Robinson, eds). Oxford University Press, Oxford, UK.

Payne, R. B. and L. L. Payne. 1998b. Brood parasitism by cowbirds: risks and effects on reproductive success in Indigo Buntings. Behavioral Ecology 9:64-73.

Payne, R. B., L. L. Payne, and J. L. Woods. 1998. Song learning in brood parasitic indigobirds *Vidua chalybeata*: song mimicry of the host species. Animal Behaviour 55:1537-1553.

Payne, R. B., L. L. Payne, J. L. Woods, and M. D. Sorenson. 2000. Imprinting and the origin of parasite-host species associations in brood-parasitic indigobirds, *Vidua chalybeata*. Animal Behaviour 59:69-81.

Payne, R. B. and M. D. Sorenson. 2004. Behavioral and genetic identification of a

hybrid *Vidua*: maternal origin and mate choice in a brood-parasitic finch.

Auk 121:156-161.

Payne, R. B., J. L. Woods, and L. L. Payne 2001. Parental care in estrildid finches:

experimental tests of a model of *Vidua* brood parasitism. Animal Behaviour

62:473-483.

Pearson, S. F. and S. Rohwer. 1998. Determining clutch size and laying dates using

ovarian follicles. Journal of Field Ornithology 69:587-594.

Pease, C. M. and J. A. Grzybowski. 1995. Assessing the consequences of brood

parasitism and nest predation on seasonal fecundity in passerine birds.

Auk 112:343-363.

Peer, B. D. and E. Bollinger. 1997. Explanations for the infrequent cowbird parasitism on

Common Grackles. Condor 99:151-161.

Peer, B. D., K. S. Ellison, and S. G. Sealy. 2002. Intermediate frequencies of egg

ejection by Northern Mockingbirds (*Mimus polyglottos*) sympatric with two

cowbird species. Auk 119:855-858.

Peer, B. D., S. K. Robinson, and J. R. Herkert. 2000. Egg rejection by cowbird hosts in

grasslands. Auk 117:892-901.

Peer, B. D. and S. G. Sealy 1999a. Laying time of the Bronzed Cowbird.

Wilson Bulletin 111:137-140.

Peer, B. D. and S. G. Sealy. 1999b. Parasitism and egg puncture behavior by

Brown-headed and Bronzed cowbirds in sympatry. Studies in Avian

Biology 18:235-240.

Peer, B. D. and S. G. Sealy. 2004a. The fate of grackle (*Quiscalus* spp.) defenses in the absence of brood parasitism: implications for long-term parasite-host coevolution. Auk 121:1172-1186.

Peer, B. D. and S. G. Sealy. 2004b. Correlates of egg rejection in hosts of the Brown-headed Cowbird. Condor 106:580-599.

Picman, J. 1989. Mechanisms of increased puncture resistance of eggs of Brown-headed Cowbirds. Auk 106:577-583.

Picman, J. 1997. Are cowbird eggs unusually strong from the inside? Auk 114:66-73.

Post, W. 1981. The prevalence of some ectoparasites, diseases, and abnormalities in the Yellow-shouldered Blackbird. Journal of Field Ornithology 52:16-22.

Post, W., A. Cruz, and D. B. McNair. 1993. The North American invasion pattern of the Shiny Cowbird. Journal of Field Ornithology 64:32-41.

Post, W. and J. W. Wiley. 1977. Reproductive interactions of the Shiny Cowbird and the Yellow-shouldered Blackbird. Condor 79:176-184.

Preston, F. W. 1948. The cowbird (*M. ater*) and the cuckoo (*C. canorus*). Ecology 29:115-116.

Pribil, S. and J. Picman. 1997. Parasitism of House Wrens by Brown-headed Cowbirds: why is it so rare? Canadian Journal of Zoology 75:302-307.

Price, M. V. 1986. Structure of desert rodent communities: a critical review of questions and approaches. American Zoologist 26:39-49.

Price, K. and R. Ydenberg. 1995. Begging and provisioning in broods of asynchronously-hatched Yellow-headed Blackbird nestlings. Behavioral Ecology and Sociobiology 37:201-208.

Purcell, K. L. and J. Verner. 1999. Abundance and rates of brood parasitism by Brown-headed Cowbirds over an elevational gradient in the southeastern Sierra Nevada. Studies in Avian Biology 18:97-103.

Pyle, P. 1997. Identification guide to North American birds, part 1. Slate Creek Press, Bolinas, CA.

Quist, C. F. 2001. Quarterly wildlife mortality report. Supplement to the Journal of Wildlife Diseases 37:1-10.

Rahn, H., L. Currant-Everett, and D. T. Booth. 1988. Eggshell differences between parasitic and nonparasitic Icteridae. Condor 90:962-964.

Raim, A. 2000. Spatial patterns of breeding female Brown-headed Cowbirds on an Illinois site. Pp. 87-99, in Ecology and Management of Cowbirds and Their Hosts, (J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, eds.). University of Texas Press, Austin, TX.

Reed, H. J. and N. H. Freeman. 1991. Does an absence of gape markings affect survival of leucistic young in the Zebra Finch? Bird Behaviour 9:58-63.

Robbins, M. B., and D. A. Easterla. 1981. Range expansion of the Bronzed Cowbird with the first Missouri record. Condor 83:270-272.

Robinson, S. K. 1988. Foraging ecology and host relationships of Giant Cowbirds in southeastern Peru. Wilson Bulletin 100:224-235.

Rodenhouse, N. L. and T. S. Sillett, P. J. Doran and R. T. Holmes. 2003. Multiple density-dependence mechanisms regulate a migratory bird population during the breeding season. Proceedings of the Royal Society of London, B 270:2105-2110.

Rohwer, S. and C. D. Spaw. 1988. Evolutionary lag versus bill-size constraints: a comparative study of the acceptance of cowbird eggs by old hosts. Evolutionary Ecology 2:27-36.

Rohwer, S., C. D. Spaw, and E. Røskaft. 1989. Costs to Northern Orioles of puncture-ejecting parasitic cowbird eggs from their nests. Auk 106:734-738.

Root, R. B. 1969. The behavior and reproductive success of the Blue-gray Gnatcatcher. Condor 71:16-31.

Røskaft, E., S. Rohwer, and C. D. Spaw. 1993. Costs of puncture ejection compared with costs of rearing cowbird chicks for Northern Orioles. Ornis Scandinavica 24:28-32.

Rotenberry, J. T. and J. A. Wiens. 1991. Weather and reproductive variation in shrubsteppe sparrows: a hierarchical analysis. Ecology 72:1325-1335.

Rothstein, S. I. 1975. An experimental and teleonomic investigation of avian brood parasitism. Condor 77:250-271.

Rothstein, S. I. 1977. Cowbird parasitism and egg recognition of the Northern Oriole. Wilson Bulletin 84:21-32.

Rothstein, S. I. 1978. Geographical variation in the nestling coloration of parasitic cowbirds. Auk 95:152-160.

Rothstein, S. I. 1990. A model system for coevolution: avian brood parasitism. Annual Review of Ecology and Systematics 21:481-508.

Rothstein, S. I. 1994. The cowbird's invasion of the Far West: history, causes and consequences experienced by host species. Studies in Avian Biology 15:301-315.

Rothstein, S. I. 2001. Relic behaviours, coevolution and the retention versus loss of host defences after episodes of avian brood parasitism. Animal Behaviour 61:95-107.

Rothstein, S. I., M. A. Patten, and R. C. Fleischer. 2002. Phylogeny, specialization, and brood parasite-host coevolution: some possible pitfalls of parsimony. Behavioral Ecology 13:1-10.

Rothstein, S. I. and S. K. Robinson. 1998. The evolution and ecology of avian brood parasitism, an overview. Pp. 3-56 in, Parasitic Birds and Their Hosts: Studies in Coevolution, (S. I. Rothstein and S. K. Robinson, eds.). Oxford University Press, Oxford, UK.

Rothstein, S. I., J. Verner, and E. Stevens. 1980. Range expansion and diurnal changes in dispersion of the brown-headed cowbird in the Sierra Nevada. Auk 97:253-267.

Rothstein, S. I., J. Verner, and E. Stevens. 1984. Radio-tracking confirms a unique diurnal pattern of spatial occurrence in the parasitic Brown-headed Cowbird. Ecology 65:77-88.

Rothstein, S. I., D. A. Yokel, and R. C. Fleischer. 1986. Social dominance, mating and spacing systems, female fecundity, and vocal dialects in captive and free-ranging Brown-headed Cowbirds. Current Ornithology 3:127-185.

Rowley, J. S. 1984. Breeding records of land birds in Oaxaca, Mexico. Proceedings of the Western Foundation of Vertebrate Zoology 2:74-224.

Sambrook, J., Fritsch, E. F., and Maniatis, T. 1989. Molecular cloning: a laboratory manual. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY.

Sauer, J. R., J. E. Hines, and J. Fallon. 2003. The North American Breeding Bird

    Survey, results and analysis 1966-2002. Version 2003.1, USGS Patuxent Wildlife

    Research Center, Laurel, MD.

Schoener, T. W. 1974. Resource partitioning in ecological communities.

    Science 185:27-39.

Schulze-Hagen, K., B. Leisler, T. R. Birkhead, and A. Dyrcz. 1995. Prolonged copulation,

    sperm reserves, and sperm competition in the aquatic warbler *Acrocephalus*

    paludicola. Ibis 137:85-91.

Scott, D. M. 1977. Cowbird parasitism on the Gray Catbird at London, Ontario. Auk 94:18

    -27.

Scott, D. M. 1978. Using sizes of unovulated follicles to estimate the laying rate of the

    Brown-headed Cowbird. Canadian Journal of Zoology 56:2230-2234.

Scott, D. M. 1991. The time of day of egg laying by the Brown-headed Cowbird and other

    icterines. Canadian Journal of Zoology 69:2093-2099.

Scott, D. M. and C. D. Ankney. 1980. Fecundity of the Brown-headed Cowbird in southern

    Ontario. Auk 97:677-683.

Scott, D. M. and C. D. Ankney. 1983. The laying cycle of Brown-headed Cowbirds:

    passerine chickens? Auk 100:583-592.

Scott, D. M. and R. E. Lemon. 1996. Differential reproductive success of Brown-headed

    Cowbirds with Northern Cardinals and three other hosts. Condor 98:259-271.

Scott, D. M., P. J. Weatherhead, C. D. Ankney. 1992. Egg-eating by female Brown-headed

    Cowbirds. Condor 94:579-584.

Scott, T. W. 1979. Growth and age determination of nestling Brown-headed Cowbirds. Wilson Bulletin 91:464-466.

Sealy, S. G. 1992. Removal of Yellow Warbler eggs in association with cowbird parasitism. Condor 94:40-54.

Sealy, S. G. 1999. Cowbird parasitism on Lark Buntings: Frequency, acceptance, and fledging. Journal of Field Ornithology 70:182-186.

Sealy, S. G. and R. C. Bazin. 1995. Low frequency of observed cowbird parasitism on Eastern Kingbirds: host rejection, effective nest defence, or parasite-avoidance? Behavioral Ecology 6:140-145.

Sealy, S. G. and J. Lorenzana 1997. Feeding of nestling and fledgling brood parasites by individuals other than the foster parents: a review. Canadian Journal of Zoology 75:1739-1752.

Sealy, S. G., D. L. Neudorf, and D. P. Hill. 1995. Rapid laying by Brown-headed Cowbirds *Molothrus ater* and other parasitic birds. Ibis 137:76-84.

Sealy, S. G., D. L. Neudorf, K. A. Hobson, and S. A. Gill. 1998. Nest defense by potential hosts of the Brown-headed Cowbird: methodological approaches, benefits of defense, and coevolution. Pp.194-210. In Parasitic Birds and Their Hosts: Studies in Coevolution, (S.I. Rothstein and S.K. Robinson, eds.). Oxford University Press, Oxford, UK.

Sealy, S.G., J. E. Sánchez, R. G. Campos R., and M. Marin. 1997. Bronzed Cowbird hosts: New records, trends in host use, and cost of parasitism. Ornitologia Neotropical 8:175-184.

Sealy, S. G. and T. J. Underwood. 2004. Accepters and rejecters of cowbird parasitism in the New World orioles (*Icterus* spp.). Ornitologia Neotropical 15:331-347.

Searcy, W. A. and K. Yasukawa. 1981. Sexual size dimorphism and survival of male and female blackbirds (Icteridae). Auk 98:457-465.

Sedgwick, J. A. and F. L. Knopf. 1988. A high incidence of Brown-headed Cowbird parasitism of Willow Flycatchers. Condor 90:253-256.

Sherry, D. F., M. R. L. Forbes, M. Khurgel, G. O. Ivy. 1993. Females have a larger hippocampus than males in the brood-parasitic Brown-headed Cowbird. Proceedings of the National Academy of Science (USA) 90:7839-7843.

Shreeve, D. F. 1980. Differential mortality in the sexes of the Aleutian Gray-crowned Rosy Finch. American Midland Naturalist 104:193-197.

Shonk, K. 2001. Movement Patterns, Behavior, and Genetic Measures of Space Use by Brown-headed Cowbirds. M.Sc. thesis. McMaster University, Hamilton, ON.

Shy, M. M. 1982. Interspecific feeding among birds: a review. Journal of Field Ornithology 53:370-393.

Sick, H. 1993. Birds in Brazil. Princeton University Press, Princeton, NJ.

Siegel, S. 1956. Nonparametric Statistics for the Behavioral Sciences. McGraw-Hill, New York, NY.

Sillett, T. S., R. T. Holmes, and T. W. Sherry. 2000. Impacts of a global climate cycle on population dynamics of a migratory songbird. Science 288:2040-2042.

Skjelseth, S., A. Moksnes, E. Røskaft, H. L. Gibbs, M. Taborsky, B. Taborsky, M. Honza, and O. Kleven. 2004. Parentage and host preference in the Common Cuckoo *Cuculus canorus*. Journal of Avian Biology 35:21-24.

Skutch, A. F. 1996. Orioles, Blackbirds, and Their Kin: a natural history. University of Arizona Press, Tucson, AZ.

Slagsvold, T. and B. Hansen. 2001. Sexual imprinting and the origin of obligate brood parasitism in birds. American Naturalist 158:354-367.

Smith, J. N. M. and P. Arcese. 1994. Brown-headed Cowbirds and an island population of Song Sparrows: A 16-year study. Condor 96:916-934.

Smith, J. N. M. and S. I. Rothstein. 2000. Brown-headed Cowbirds as a model system for studies of behavior, ecology, evolution, and conservation biology. Pp. 1- 9, in Ecology and Management of Cowbirds and Their Hosts, (J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, eds.). University of Texas Press, Austin, TX.

Smith, N. G. 1968. The advantage of being parasitized. Nature 219:690-694.

Smith, N. G. 1979. Alternate responses by hosts to parasites which may be helpful or harmful. Pp. 7-15, in Host-Parasite Interfaces. Academic Press, New York, NY.

Smith, V. A., A. P. King, and M. J. West. 2002. The context of learning: association patterns in a flock of Brown-headed Cowbirds. Animal Behaviour 63:23-35.

Soler, J. J., J. M. Aviles, M. Soler, and A. P. Møller. 2003. Evolution of host egg mimicry in a brood parasite, the Great-spotted Cuckoo. Biological Journal of the Linnean Society 79:551-563.

Sorenson, M. D. and R. B. Payne. 2002. Molecular genetic perspectives on avian brood parasitism. Integrative and Comparative Biology 42:388-400.

Sorenson, M. D., K. M. Sefc, and R. B. Payne. 2003. Speciation by host switch in brood parasitic indigobirds. Nature 424:928-931.

Southern, W. E. 1958. Nesting of the Red-eyed Vireo in the Douglas Lake Region, Michigan. Jack-Pine Warbler 36:105-130.

Spaw, C. D. and S. Rohwer. 1987. A comparative study of eggshell thickness in cowbirds and other passerines. Condor 89:307-318.

Starck, J. M. and R. E. Ricklefs 2000. Avian growth and development: evolution within the altricial-precocial spectrum. Edited by J. M. Starck and R. E. Ricklefs. Oxford University Press, Oxford, UK.

Stevens, E. E. 1982. Variation in the Oral Flange Color of Brown-headed Cowbird Nestlings: an Adaptation for Brood Parasitism? M.A. thesis, University of California, Santa Barbara, CA.

Stotz, D. F., J. W. Fitzpatrick, T. A. Parker III, and D. K. Moskovits, 1996. Neotropical Birds: Ecology and Conservation. Chicago: University of Chicago Press.

Strausberger, B.M. 1998. Temporal patterns of host availability, Brown-headed Cowbird brood parasitism, and parasite egg mass. Oecologia 116:267-274.

Strausberger, B.M. and M.V. Ashley. 1997. Community-wide patterns of parasitism of a host "generalist" brood-parasitic cowbird. Oecologia 112:254-262.

Strausberger, B.M. and M.V. Ashley. 2001. Eggs yield nuclear DNA from egg-laying female cowbirds, their embryos and offspring. Conservation Genetics 2:385-390.

Strausberger, B. M. and M. V. Ashley. 2003. Breeding biology of brood parasitic Brown-headed Cowbirds (*Molothrus ater*) characterized by parent-offspring and sibling-group reconstruction. Auk 120:433-445.

Sturkie, P. D. 1976. Avian physiology, third ed. Springer-Verlag, New York.

Stutchbury, B. 1997. Effects of female cowbird removal on reproductive success of Hooded Warblers. Wilson Bulletin 109:74-81.

Sykes, P. W., Jr., and W. Post. 2001. First specimen and evidence of breeding by the Shiny Cowbird in Georgia. Oriole 66:45-51.

Takasu, F. 1998. Modeling the arms race in avian brood parasitism. Evolutionary Ecology 12:969-987.

Teather, K. L. and R. J. Robertson. 1985. Female spacing patterns in Brown-headed Cowbirds. Canadian Journal of Zoology 63:218-222.

Teather, K. L. and P. J. Weatherhead. 1989. Sex-specific mortality in nestling Great-tailed Grackles. Ecology 70:1485-1493.

Teuschl, Y., B. Taborsky and M. Taborsky. 1994. Habitat imprinting and egg mimicry in European cuckoos. Journal für Ornithologie 135:137.

Teuschl, Y., B. Taborsky and M. Taborsky. 1998. How do cuckoos find their hosts? The role of habitat imprinting. Animal Behaviour 56:1425-1433.

Thompson, F. R., III. 1994. Temporal and spatial patterns of breeding in Brown-headed Cowbirds in the midwestern United States. Auk 111:979-990.

Thompson, F. R., III., and W. D. Dijak. 2000. Differences in movements, home range, and habitat preferences of female Brown-headed Cowbirds in three Midwestern landscapes. Pp. 100-109, in Ecology and Management of Cowbirds and Their Hosts, (J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, eds.). University of Texas Press, Austin, TX.

Thompson, J. N. 1994. The Coevolutionary Process. University of Chicago Press, IL.

Thornhill, R. 1988. The junglefowl hen's cackle incites male competition. Verhulst

    Deutsch Zoolo Ges 81:145-154.

Trine, C. L. 2000. Effects of multiple parasitism on cowbird and Wood Thrush nesting

    success. Pp. 135-144 in Ecology and Management of Cowbirds and Their Hosts, (J.

    N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, eds.).

    University of Texas Press, Austin, TX.

Trine, C. L., W. D. Robinson, and S. K. Robinson. 1998.Consequences of Brown-headed

    Cowbird brood parasitism for host population dynamics. Pp. 273-295, in Parasitic

    Birds and Their Hosts: Studies in Coevolution, (S.I. Rothstein and S.K. Robinson,

    eds.). Oxford University Press, Oxford, UK.

Trivers, R. L. 1973. Parent-offspring conflict. American Zoologist 14:249-264.

Tschirren, B., P. S. Fitze, and H. Richner. 2003. Proximate mechanisms of variation in the

    carotenoid-based plumage coloration of nestling Great Tits (*Parus major*). Journal

    of Evolutionary Biology 16:91-100.

Underwood, T. J. 2003. Proximate and Ultimate Influences on Egg Recognition and

    Rejection Behaviour in Response to Avian Brood Parasitism. Ph.D. dissertation,

    University of Manitoba.

Underwood, T. J., S. G. Sealy, and C. M. McLaren. 2004. Eastern Wood-Pewees as

    Brown-headed Cowbird hosts: accepters but infrequently parasitized. Journal of

    Field Ornithology. 75:165–171.

Vander Hagen, W. M. and B. Walker. 1999. Parasitism by Brown-headed Cowbirds in

    the shrubsteppe of eastern Washington. Studies in Avian Biology 18:34-41.

Verner, J. and L. V. Ritter. 1983. Current status of the Brown-headed Cowbird in the Sierra National Forest. Auk 100:355-368.

Vogl, W., M. Taborsky, B. Taborsky, Y. Teuschl, and M. Honza. 2002. Cuckoo females preferentially use specific habitats when searching for host nests. Animal Behaviour 64:843-850.

Walkinshaw, L. H. 1949. Twenty-five eggs apparently laid by a cowbird. Wilson Bulletin 48:94-101.

Ward, P. 1965. Feeding ecology of the Black-faced Dioch *Quealea quealea* in Nigeria. Ibis 107:173-213.

Warren, P. 2002. Geographic variation and dialects in songs of the Bronzed Cowbird. Auk 119:349-361.

Wauer, R. H. 1977. Significance of Rio Grande riparian systems upon the avifauna. Pp. 165-174, in Proceedings of the Symposium on Importance, Preservation and Management of Riparian Habitat, (R. R. Johnson and D. A. Jones, eds.).

Weatherhead P. J. 1989. Sex ratios, host specific reproductive success, and impact of Brown-headed Cowbirds. Auk 196:358-366.

Weatherhead P. J. and Bennett. 1992. Ecology of parasitism of Brown-headed Cowbirds by haematozoa. Canadian Journal of Zoology 70:1-7.

Weatherhead, P. J., H. Greenwood, and R. G. Clark. 1984. On the use of avian mortality patterns to test sexual selection theory. Auk 101:134-139.

Weatherhead P. J., K. J. Metz, D. Shutler, K. E. Muma, and G. F. Bennet. 1995. Blood parasites and dominance in captive blackbirds. Journal of Avian Biology 26:121 -123.

Weathers, W. W. 1992. Scaling nestling energy requirements. Ibis 134:142-153.

Weathers, W. W. 2001. Erratum. Ibis 143:708.

Webster, M. S. 1994. Interspecific brood parasitism of Montezuma Oropendolas by Giant

Cowbirds: parasitism or mutualism? Condor 96:794-798.

Weller, M. W. 1968. The breeding biology of the parasitic Black-headed Duck.

Living Bird 7:169-207.

West, M. J., D. J. White, and A. P. King. 2002. Female Brown-headed Cowbirds',

Molothrus ater, organization and behaviour reflects male social dynamics. Animal

Behaviour 64:377-385.

Wetmore, A., R. F. Pasquier, and S. L. Olson. 1984. The Birds of the Republic of Panamá.

Smithsonian Institution Press, Washington, D. C.

Whetje, W. 2003. The range expansion of the Great-tailed Grackle (*Quiscalis mexicanus*

Gmelin) in North America. Journal of Biogeography 30:1593-1607.

Whitfield, M. 2000. Results of a Brown-headed Cowbird control program for the

Southwestern Willow Flycatcher. Pp. 371-377, in Ecology and management of

cowbirds and their hosts, (J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K.

Robinson, and S. G. Sealy, eds.). University of Texas Press, Austin, TX.

Wiley, J. W. 1985. Shiny Cowbird parasitism in two avian communities in Puerto Rico.

Condor 87:165-176.

Wiley, J. W. 1988. Host selection by the Shiny Cowbird. Condor 90:289-303.

Williams, P. L. 1988. Spacing Behavior and Related Features of Social Organization in

Northern Orioles of Central Coastal California. Ph.D. dissertation, University of

California, Berkeley.

Woodward, P. W. 1983. Behavioral ecology of fledgling Brown-headed Cowbirds and
their hosts. Condor 85:151-163.

Woolfenden, B. H. 2000. Demography and Breeding Behaviour of Brown-headed
Cowbirds: an Examination of Host Use, Individual Mating Patterns and Reproductive
Success Using Microsatellite DNA Markers. Ph.D. dissertation, McMaster
University, Hamilton, ON.

Woolfenden, B. E., H. L. Gibbs and S. G. Sealy. 2001. Demography of Brown-headed
Cowbirds at Delta Marsh, Manitoba. Auk 118:156-166.

Woolfenden, B. E., H. L. Gibbs and S. G. Sealy. 2002. High opportunity for sexual
selection in both sexes of an obligate brood parasitic bird, the Brown-headed
Cowbird (*Molothrus ater*). Behavioral Ecology and Sociobiology 52:417-425.

Woolfenden, B. E., H. L. Gibbs, S. G. Sealy, and D. G. McMaster. 2003. Host use and
fecundity of individual female Brown-headed Cowbirds.
Animal Behaviour 66:95-106.

Woolfenden, B. E., H. L. Gibbs, C. M. McLaren, and S. G. Sealy. 2004. Community-
level patterns of parasitism: Use of three common hosts by a brood parasitic bird,
the Brown-headed Cowbird. Écoscience 11:238-248.

Wyllie, I. 1981. The cuckoo. Universe Books, N.Y.

Yokel, D. A. 1986. Monogamy and brood parasitism: an unlikely pair.
Animal Behaviour 34:1348-1358.

Yokel, D. A. 1989. Intrasexual aggression and the mating behavior of Brown-headed
Cowbirds: their relation to population densities and sex ratios. Condor 91:43-51.

Yokel, D. A. and S. I. Rothstein. 1991. The basis for female choice in avian brood

parasite. Behavioral Ecology and Sociobiology 29:39-45.

Young, H. 1963. Breeding success of the cowbird. Wilson Bulletin 75:115-122.

Young, R. L. and A. V. Badyaev. 2004. Evolution of sex-biased maternal effects in birds:

I. Sex-specific resource allocation among simultaneously growing oocytes.

Journal of Evolutionary Biology 17:1355-1366.

Zar, J. H. 1984. Biostatistical Analysis. Second edition. Prentice-Hall, Inc. Englewood

Cliffs, NJ.

Zimmerman, J. L. 1983. Cowbird parasitism of Dickcissels in different habitats and at

different densities. Wilson Bulletin 95:7-22.

APPENDICES

APPENDIX 1. FOLLICULAR PRODUCTION AMONG BRONZED COWBIRDS

To determine whether gross differences in potential fecundity occurred between *aeneus* and other molothrines, I compared egg production in ovaries of *aeneus* with the descriptions for *ater* and *bonariensis*: each lays eggs in sets, one egg per day, separated by one to several days between bouts (Payne 1976, Jackson and Roby 1992, Kattan 1993). Thus, the mean number of eggs per bout can be combined with breeding season duration to estimate annual potential fecundity (Payne 1976; Scott and Ankney 1983; Kattan 1993, 1997). Ovaries were obtained from *aeneus* between April and June 2002 at other Texas sites (see Kostecke et al. 2004). I followed criteria established by Payne (1976) and Kattan (1993) for counting macroscopic follicles destined to become eggs in *ater*, but scaled allometrically for the larger egg size of *aeneus*, i.e. vitellogenic follicles with diameter greater than 5.0 mm were likely to ovulate (molothrine mass-to-egg and ovum diameter regression statistics, respectively (n = 3 species): $\beta = 1.5$, $R^2 = 0.94$, P= 0.15 ; $\beta = 0.98$, $R^2 = 0.98$, P = 0.08).

Potential fecundity by *aeneus* did not differ markedly from that measured among *ater* (Payne 1976, Curson and Matthews 2003) or *bonariensis* (Kattan 1993). Overall, females produced follicles in clusters of two to 12, ranging between 0.2 - 13.0 mm in diameter (n = 46 ovaries). Five *aeneus* females contained follicles more than 6 mm in diameter, among these, follicular development corresponded to consecutive daily laying bouts of 2 - 4 eggs (Fig. 3.3). Therefore, egg production by *aeneus* did not differ from that described among *ater* and *bonariensis* (Payne 1976, Kattan 1993).

APPENDIX 2. CARE BY NEW WORLD SONGBIRDS APPEARS UNAFFECTED BY CHICK APPEARANCE

Two types of evidence support the hypothesis that most New World songbirds do not discriminate against the young of heterospecifics. First, songbirds care for the young of other species (Shy 1982). Such situations arise infrequently when two species attempt to use the same nest (Shy 1982). Secondly, no difference in fledgling success was found among cowbirds with yellow or white colored mouthparts reared by an array of hosts in Texas.

Heterospecific Care Via Nest-sharing or Usurpation

Shy (1982) reviewed cases of interspecific feeding of nestlings and found 32 that were attributable to mixed clutches. Of these records, six involved species known to rear cowbirds: Gray Catbird, American Robin, Song Sparrow, and Northern Cardinal. At my Texas site, I found seven cases where Lark Sparrows laid in or usurped nests with eggs of Northern Mockingbirds (5) and Painted Buntings (2). I also found House Finch eggs in one nest each of Northern Mockingbird, Orchard Oriole and Hooded Oriole. Four of these cases resulted in care allocated to heterospecific young, which differ from young of the fosterers in size and appearance (Baicich and Harrison 1997). Lark Sparrows fed young mockingbirds and buntings, while mockingbirds fed young House Finches. In two cases, Lark Sparrows fledged mockingbirds, whereas I could not determine the fate of the buntings fed by the sparrows. The House Finches fed by mockingbirds disappeared after 4d and the nest fledged at least one mockingbird.

Equivocal Cowbird Fledging Success Despite Variation in Appearance

Songbird young can be largely categorized as possessing exterior rictal flange mouthparts that appear either white or yellow (Rothstein 1978). Bronzed Cowbirds are white-flanged, whereas Brown-headed Cowbirds have either white or yellow rictal flanges (Rothstein 1978). I found a negative association between host and cowbird flange color at my Texas site; significantly more white-flanged young fledged (G=5.00, P=0.03, n=107) despite 13 of the 16 host species having yellow-flanged young. Moreover, there was no differential success for Brown-headed Cowbirds of either flange color; the ratios found among nestlings did not change among fledglings (G=1.72, P=0.20, n=164). I found little evidence for selection favoring either flange color. Indeed, flange color was associated with sex as males were disproportionately white flanged (72% versus the 54% white flanged females, n=57). Thus, I concluded flange color varies neutrally at my Texas site. However, further manipulative tests are required to test the hypothesis directly.

APPENDIX 3. COMMON AND SCIENTIFIC NAMES FOR AVIAN SPECIES

MENTIONED IN TEXT*

Common Cuckoo (*Cuculus canorus*)
Great-spotted Cuckoo (*Clamator glandarius*)
Mourning Dove (*Zenaida macroura*)
White-winged Dove (*Z. asiatica*)
Inca Dove (*Columbina inca*)
Common Ground Dove (*C. passerina*).
Short-tailed Field Tyrant (*Muscigralla brevicauda*)
Eastern Wood Peewee (*Contopus virens*)
Acadian Flycatcher (*Empidonax virescens*)
Willow Flycatcher (*E. trailii*)
Eastern Phoebe (*Sayornis phoebe*)
Vermilion Flycatcher (*Pyrocephalus rubinus*)
Ash-throated Flycatcher (*Myiarchus cinerascens*)
Eastern Kingbird (*Tyrannus tyrannus*)
Couch's Kingbird (*T. couchii*)
Western Kingbird (*T. verticalis*)
Scissor-tailed Flycatcher (*T. forficatus*)
Red-eyed Vireo (*Vireo olivaceus*)
Bell's Vireo (*V. bellii*)
Hutton's Vireo (*V. huttoni*)
Black-capped Vireo (*V. atricapillus*)
White-eyed Vireo (*V. griseus*)
Yellow-throated Vireo (*V. flavifrons*)
Plumbeous Vireo (*V. plumbeus*)
Rufous Hornero (*Furnarius rufus*)
Green Jay (*Cyanocorax yncas*)
Purple Martin (*Progne subis*)
Barn Swallow (*Hirundo rustica*)
Bewick's Wren (*Thryomanes bewickii*)
House Wren (*Troglodytes aedon*)
Cactus Wren (*Campylorhynchus brunneicapillus*)
Black-tailed Gnatcatcher (*Polioptila melanura*)
Blue-gray Gnatcatcher (*P. caerulea*)
Eastern Bluebird (*Sialia sialis*)
American Robin (*Turdus migratorius*)
Wood Thrush (*Hylocichla mustelina*)
Gray Catbird (*Dumetella carolinensis*)
Chalk-browed Mockingbird (*Mimus saturninus*)
Northern Mockingbird (*M. polyglottos*)
Brown Thrasher (*Toxostoma rufum*)
Long-billed Thrasher (*T. longirostre*)
*Dunnock (*Prunella modularis*)

European Starling (*Sturnus vulgaris*)
Yellow Warbler (*Dendroica petechia*)
Golden-cheeked Warbler (*Dendroica chrysoparia*)
Worm-eating Warbler (*Helmitheros vermivora*)
Prothonotary Warbler (*Protonotaria citrea*)
Ovenbird (*Seiurus aurocapillus*)
Louisiana Waterthrush (*Seiurus motacilla*)
Kentucky Warbler (*Oporornis formosus*)
Common Yellowthroat (*Geothlypis trichas*)
Yellow-breasted Chat (*Icteria virens*)
Summer Tanager (*Piranga rubra*)
Western Tanager (*Piranga ludoviciana*)
Pyrrhuloxia (*Cardinalis sinuatus*)
Northern Cardinal (*Cardinalis cardinalis*)
Blue Grosbeak (*Guiraca caerulea*)
Lazuli Bunting (*Passerina amoena*)
Indigo Bunting (*Passerina cyanea*)
Painted Bunting (*Passerina ciris*)
Eastern Towhee (*Pipilo erythrophthalmus*)
Olive Sparrow (*Arremonops rufivirgatus*)
Black-throated Sparrow (*Amphispiza bilineata*)
Chipping Sparrow (*Spizella passerina*)
Le Conte's Sparrow (*Ammodramus leconteii*)
Lark Bunting (*Calamospiza melanocorys*)
Lark Sparrow (*Chondestes grammacus*)
Rufous-collared Sparrow (*Zonotrichia capensis*)
Song Sparrow (*Melospiza melodia*)
*Red-billed Quelea (*Quelea quelea*)
Western Meadowlark (*Stunella neglecta*)
Yellow-shouldered Blackbird (*Agelaius xanthomus*)
Red-winged Blackbird (*Agealius phoeniceus*)
Great-tailed Grackle (*Quiscalus mexicanus*)
Brown-and-yellow Marshbird (*Pseudoleistes virescens*)
Chopi Blackbirds (*Gnorimopsar chopi*)
Bullock's Oriole (*Icterus bullockii*)
Hooded Oriole (*Icterus cucullatus*)
Orchard Oriole (*Icterus spurius*)
White-edged Oriole (*Icterus graceannae*)
Black-cowled Oriole (*Icterus prosthemelas*)
House Finch (*Carpodacus mexicana*)
Lesser Goldfinch (*Carduelis psaltria*)
American Goldfinch (*Carduelis tristis*)
Common Diuca Finch (*Diuca diuca*)

* Old World species placed within AOU taxonomy (2000 and supplements) based on Clements (2003).

APPENDIX 4. ELEVATED LAYING POSTURE OF BROWN-HEADED COWBIRDS

Mermoz and Ornelas (2004) found that the only trait which differed between cowbirds and non-parasitic icteridae was eggshell thickness. The more thickly shelled eggs of cowbirds have been attributed to coevolution in response to host egg-pecking and ejection attempts (see Rohwer and Spaw 1988, Mermoz and Ornelas 2004). However, because cowbirds lack a brood patch and visits to nests are short (5-50 s, Sealy et al. 1995), eggshell thickening may have originated to protect cowbird eggs during laying. Thus, eggshell thickness may not purely reflect coevolution.

During 1999-2002, my assistants and I observed 119 cowbird nest visits, during which 70 eggs were laid. Of these, six were video-taped clearly enough for a detailed analysis of laying. Cowbirds compressed their bodies by stretching forward, then spreading and pulling in their wings. This was followed by tipping the body forward while raising the tail until the cloaca was an average of 1.3 ± 0.3 cm (n = 6) above the nest rim.

Accounting for average internal depth of nests (4.6 and 4.1 cm for Bell's Vireos and Blue-gray Gnatcatchers, respectively) (Ellison 1992, Brown 1993), Brown-headed Cowbirds laid eggs from 5.6 ± 0.5 cm (n = 5) above nest contents. Bronzed Cowbirds may have laid from slightly elevated positions, however nests and their substrates obscured accurate measurement of this behavior. Combining my data with others', 11 of 14 instances involved elevated laying by Brown-headed Cowbirds (Bedell 1995, 1; J. J. Tewksbury, pers. comm., 4; B. Kus, pers. comm., 3). These data support the hypothesis that eggshells were strengthened primarily for protection during laying.

However, this interpretation does not inherently negate the secondary further thickening of eggshell via selection from hosts, i.e. coevolution. Manipulative tests, such as dropping eggs of different shell thickness onto host eggs, are needed to more fully evaluate these hypotheses.

APPENDIX 5. ANALYSIS OF EGG DISTRIBUTION WITH POISSON SERIES

The Poisson technique tests for an over/under abundance of multiply parasitized nests. However, in practice, comparisons most often reflect deviations from expected values for the unparasitized and singly parasitized categories. Thus, estimation of the portion of unparasitized nests located, but not used by cowbirds, has been attempted (Lowther 1984). When parasitism is > 50 %, such estimation is inappropriate (Lowther 1984). Lea and Kattan (1998) circumvented this problem by comparing only parasitized nests to a Poisson series, using an improved method to estimate the average number of eggs per nest. Poisson series are generated by

$$P(r) = m^r e^{-m}/r!, \qquad (1)$$

where the predicted probability, $P(r)$, of nests containing r eggs, is derived from m, the average number of eggs per parasitized nest. Lowther (1984) estimated m using the ratio between one- and two-egg nests. This procedure does not use all the data and therefore distorts $P(r)$. Lea and Kattan (1998) solved equation (1) for m as

$$m^* = m/(1 - e^{-m}). \qquad (2)$$

This technique more accurately estimates m (see Lea and Kattan 1998). Lea and Kattan (1998) then used the Kolmogorov-Smirnov one-sample test to compare cumulative observed and expected distributions (Siegel 1956). The test is more powerful than the chi-square test (see Lowther 1984, Orians et al. 1989). I applied the Kolmogorov-Smirnov one-sample test as outlined by Zar (1984) to facilitate more accurate calculation of P-values.
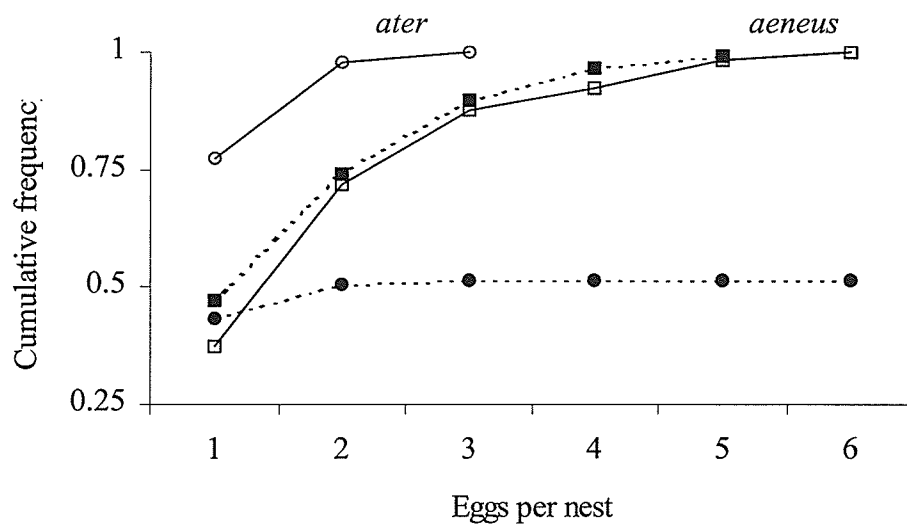
Figure A.1. Cumulative frequencies for observed (solid lines) and critical values (dashed lines) for comparison with Poisson series generated *sensu* Lea and Kattan (1998). Egg distribution by *ater* (circles) differed significantly from random ($D_{93} = 0.63$, $P < 0.001$), while that for *aeneus* did not ($D_{64} = 0.15$, $P = 0.11$).

APPENDIX 6. OBSERVATIONS OF SIMULTANEOUS NEST VISITS BY COWBIRDS

8 July 2000. At 0731, a female Bronzed Cowbird was followed by another female, they perched 5 m apart within 10 m of an empty Bullock's Oriole nest. At 0733, one female went to the nest and moved its head within. After 10 s, the cowbird left the nest at 0734 and the second cowbird flew to the nest and also moved its head within the nest. The nest remained inactive and no eggs were detected at this nest.

30 April 2001. Three Bronzed Cowbirds laid eggs in the same Orchard Oriole nest. The first cowbird arrived at 0647:19 and settled on the nest for 10 s. At 0648:52 two cowbirds arrived and left the nest after 3 s. The cowbirds made physical contact for 2 s, however, this interaction was not entirely visible. Three cowbird eggs were collected when the watch ended at 0655.

10 June 2002. On this morning, three Bronzed Cowbirds laid in a Hooded Oriole nest. The same or different cowbird(s) were repelled twice from the nest by a pair of Hooded Orioles. At 0637:26, a cowbird alit on the nest and forced her way onto the nest past the female oriole. While the female oriole hung from the nest, a second cowbird landed and hung from the nest. The second cowbird pecked the first near the tail. The first cowbird contracted her body in a series of motions associated with video taped egg laying postures by Brown-headed Cowbirds (Appendix 4). At 0637:34, the first cowbird left the nest emitting a 1.5 s chatter call. The second cowbird then entered the nest and contracted her body, presumably laying, 1-2 s prior to departing at 0637:38.

APPENDIX 7. SPECIES AND MASS DATA USED IN SHANNON-WEAVER

DIVERSITY INDEX CALCULATIONS

Potential Cowbird Hosts [a]	Mass (g) [b]
Eastern Wood Pewee (*Contopus virens*) [c]	14
Acadian Flycatcher (*Empidonax virescens*) [c]	13
Willow Flycatcher (*E. trailii*) [d]	14
Dusky Flycatcher (*E. oberholseri*) [e]	10
Black Phoebe (*Sayornis nigricans*) [f]	18
Eastern Phoebe (*S. phoebe*) [g]	20
Vermilion Flycatcher (*Pyrocephalus rubinus*) [f]	14
White-eyed Vireo (*Vireo griseus*) [c,h]	11
Bell's Vireo (*V. bellii*) [d,e,f]	9
Black-capped Vireo (*V. atricapillus*) [h]	9
Yellow-throated Vireo (*V. flavifrons*) [c]	18
Plumbeous Vireo (*V. plumbeus*) [i]	16
Cassin's Vireo (*V. cassinii*) [j]	15
Blue-headed Vireo (*V. solitarius*) [d]	15
Hutton's Vireo (*V. huttoni*) [i,j]	12
Warbling Vireo (*V. gilvus*) [d,i,k]	15
Red-eyed Vireo (*V. olivaceus*) [c,g,k,l]	18
Green Jay (*Cyanocorax yncas*) [m]	79
Bewick's Wren (*Thryomanes bewickii*) [f]	10
Blue-gray Gnatcatcher (*Polioptila caerulea*) [d,e,f]	6
Black-tailed Gnatcatcher (*P. melanura*) [e]	5
Eastern Bluebird (*Sialia sialis*) [l]	32
Veery (*Catharus ustulatus*) [g,k]	31
Hermit Thrush (*C. guttatus*) [g]	31
Wood Thrush (*Hylocichla mustelina*) [c,g,l]	47

Gray Catbird (*Dumetella carolinensis*) [k, l]	37
Northern Mockingbird (*Mimus polyglottos*) [m]	49
Brown Thrasher (*Toxostoma rufum*) [l]	69
Long-billed Thrasher (*T. longirostre*) [m]	70
Blue-winged Warbler (*Vermivora pinus*) [g]	10
Nashville Warbler (*V. ruficapilla*) [j]	9
Lucy's Warbler (*V. luciae*) [d, e]	7
Yellow Warbler (*Dendroica petechia*) [d, k, l]	9
Yellow-rumped Warbler (*D. coronata*) [e]	12
Black-throated Gray Warbler (*D. nigrescens*) [j]	8
American Redstart (*Setophaga ruticilla*) [g]	8
Worm-eating Warbler (*Helmitheros vermivorus*) [c]	13
Ovenbird (*Seiurus aurocapillus*) [c, g]	19
Louisiana Waterthrush (*S. motacilla*) [c, g]	21
Kentucky Warbler (*Oporornis formosus*) [c]	14
Common Yellowthroat (*Geothlypis trichas*) [d, e, l, k]	10
Hooded Warbler (*Wilsonia citrina*) [c]	10
Wilson's Warbler (*W. pusilla*) [e]	8
Painted Redstart (*Myioborus pictus*) [i]	8
Yellow-breasted Chat (*Icteria virens*) [c, d, e, f, h]	25
Hepatic Tanager (*Piranga flava*) [i]	38
Summer Tanager (*P. rubra*) [c, f]	28
Scarlet Tanager (*P. olivacea*) [c, g]	29
Western Tanager (*P. ludoviciana*) [i, j]	28
Olive Sparrow (*Arremonops rufivirgatus*) [m]	24
Eastern Towhee (*Pipilo erythrophthalmus*) [c, l, g]	39
Canyon Towhee (*P. fuscus*) [e]	44
Chipping Sparrow (*Spizella passerina*) [e, f, l]	12
Clay-colored Sparrow (*S. pallida*) [k]	12
Brewer's Sparrow (*S. breweri*) [n]	11
Field Sparrow (*S.pusilla*) [l]	13

Vesper Sparrow (*Poocetes gramineus*) [n]	25
Lark Sparrow (*Chondestes grammacus*) [f]	29
Sage Sparrow (*Amphispiza belli*) [n]	19
Song Sparrow (*Melospiza melodia*) [e, g, k, l]	21
Dark-eyed Junco (*Junco hyemalis*) [j]	19
Northern Cardinal (*Cardinalis cardinalis*) [c, e, f, h, l, o]	44
Rose-breasted Grosbeak (*Pheucticus ludovicianus*) [c, g, l]	46
Blue Grosbeak (*Passerina caerulea*) [d, e, f]	28
Indigo Bunting (*P. cyanea*) [c, f, l]	14
Painted Bunting (*P. ciris*) [f, h]	15
Dickcissel (*Spiza americana*) [o]	25
Red-winged Blackbird (*Agelaius phoeniceus*) [k, l, m, o]	42
Eastern Meadowlark (*Sturnella magna*) [o]	76
Brewer's Blackbird (*Euphagus cyanocephalus*) [e]	59
Common Grackle (*Quiscalus quiscula*) [o]	100
Orchard Oriole (*Icterus spurius*) [f, k, l]	20
Hooded Oriole (*I. cucullatus*) [f]	24
Bullock's Oriole (*I. bullockii*) [f]	34
Baltimore Oriole (*I. galbula*) [l]	33
House Finch (*Carpodacus mexicanus*) [l]	21
American Goldfinch (*Carduelis tristis*) [e]	13

[c] Trine et al. (1998), [d] Brown et al. (1994), [e] Halterman et al. 1999, [f] This study, [g] Hahn et al. 1999, [h] Barber and Martin 1997, [i] Chace (2001), [j] Purcell and Verner (1999), [k] Woolfenden (2001), Woolfenden et al. (2004), [l] Strausberger 1998, [m] Carter (1986), [n] Vander Hagen and Walker 1999, [o] Fleischer (1985).