Cowbird Removal as a Conservation Tool for Songbirds

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Abstract

The Brown-headed Cowbird (*Molothrus ater*) is an obligate brood parasite: it lays its eggs in other birds' nests, and the foster parents provide all subsequent parental care. Cowbird parasitism reduces host reproductive success (by removing host eggs, and by outcompeting host nestlings) and poses a conservation problem for some threatened or endangered songbirds. Red-winged Blackbird (*Agelaius phoeniceus*) populations were surveyed from 1993 to 2005 in wetlands near the periphery of the city of Winnipeg. Using a subset of this data, I examined the effect of cowbird egg removal in Red-winged Blackbirds, a frequent host. I examined whether cowbird removal: (1) improves the growth of host nestlings; and (2) enhances the survival of the host nestlings. Analysis revealed several main effects. Cowbirds that hatch early in relation to blackbirds depress host hatching success, yet do not compromise growth or survival of host nestlings to fledgling. Host egg removal by the female cowbird has lasting effects on the host brood proportions whereby the proportion of later-hatched host chicks increases. Cowbird parasitism may even skew surviving host sex ratios. These findings may aid the development of cowbird management programs, especially where hosts are threatened or endangered.

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Introduction

Concerns surrounding declining passerine bird species populations, many of which are Neotropical migrants, have prompted investigation into conservation and management techniques to re-establish population numbers and improve their habitats. Some passerine species, such as the Yellow Warbler (*Dendroica petechia*; Lichtenstein and Sealy 1998; Sealy 1992), Song Sparrow (*Melospiza melodia*; Smith *et al.* 2002; Arcese *et al.* 1996), Red-eyed Vireo (*Vireo olivaceus*; Graham 1988), Eastern Phoebe (*Sayornis phoebe*; Scott and Ankney 1980), Eastern Towhee (*Pipilo erythrophthalmus*; Burhans 2000), Chipping Sparrow (*Spizella passerina*; Graham 1988), and Ovenbirds (*Seiurus aurocapillus*; Hersek *et al*. 2002) are parasitized by Brown-headed Cowbirds (*Molothrus ater*), a common obligate brood parasite. Cowbirds can depress the growth and survival of host nestlings, hence, control of cowbird populations, particularly females (Smith *et al.* 2002), is one management option to impede the decline of songbird populations. Management strategies range from direct control of cowbird numbers via shooting, trapping, fertility control, egg / nestling removal, and egg addling, to indirect measures such as improving host population numbers via habitat improvement and reducing human influences (Goguen and Mathews 1999; Robinson 1999; Robinson *et al*. 1993; Smith 1999).

Here, I examined the efficacy of cowbird removal in a common host species, the Red-winged Blackbird (*Agelaius phoeniceus*). I tested two related hypotheses: (1) that the removal of cowbird eggs or nestlings from host nests improves the growth of host nestlings; and (2), that the removal of cowbird eggs

or nestlings enhances the overall survival of the host nestlings. I considered the potential benefits of cowbird egg and nestling removal from larger host species' nests, comparable in size to that of Red-winged Blackbirds. Hence, recommended conservation strategies and cowbird management techniques focused on larger host species.

Methods

The natural history of Brown-headed Cowbirds

Cowbirds are members of the New World Blackbirds (Family Icteridae) and include six species (Ortega 1998). The Brown-headed Cowbird (hereafter "cowbird") is the only brood parasite that is widespread in North America (Davies 2000). Historically, prior to European settlement, Brown-headed Cowbirds were closely associated with bison in the grassy plains of the mid-continent and would forage on insects and seeds unearthed by the ungulates (Davies 2000; Goguen and Mathews 1999). Though they are more common in their historic range, from south-central Canada and North Dakota to Oklahoma (Thompson *et al*. 2000) and west of the Mississippi River (Davies 2000) to the Sierra Nevada (Rothstein *et al*. 1980) over the past ~200 years, cowbirds have spread across nearly the entire North American continent south of the tree line (Davies 2000; Ortega 1998).

Cowbirds naturally inhabit a short grass and forest-edge habitat which offers both feeding grounds and perches from which cowbirds survey for host nests (Bull and Ferrand 1977; Jaramillo and Burke 1999). Settlers transformed the landscape through deforestation, irrigation, and the introduction of domesticated livestock and agriculture, thus creating open habitats where cowbirds thrived (Koford *et al*. 2000). Today, cowbirds are associated with anthropogenic landscapes and domesticated livestock since these mammals are associated with cowbird foods, in particular arthropods and grain (Davies 2000; Goguen and Mathews 1999). As the cowbirds' range expanded under these

favorable conditions, so did their host repertoire (Davies 2000). Many new host species were already affected by anthropogenic habitat loss or degradation, making them of special concern to conservation biologists.

Brown-headed Cowbirds are obligate brood parasites (Ortega 1998), and forego all parental responsibilities including nest building. They lay their eggs in the nests of other birds and dupe this 'host' into parenting the parasite offspring in addition to, or instead of, its own brood. Cowbirds breed in the spring and early summer coincident with their potential hosts (Jaramillo and Burke 1999; Johnsgard 1997; Ortega 1998). The timing of egg-laying is crucial, as they need to synchronize incubation and hatching with that of their hosts. Such synchrony is achieved by monitoring hosts nesting activity. Cowbirds deposit their eggs in host nests approximately 10 to 25 minutes before sunrise (Neudorf and Sealy 1994; Ortega 1998), and can do so in only 20 to 40 seconds (Johnsgard 1997).

Cowbirds are host generalists and interspecific brood parasites – that is the hosts are other bird species. While this strategy increases the annual fecundity of the brood parasite, the reproductive success of the host species can be jeopardized (Lorenzana and Sealy 1999). In contrast, intraspecific brood parasites lay their eggs in the nests of individuals that belong to the same species (Davies 2000), such as the European Starling (*Sturnus vulgaris*), Cliff Swallow (*Hirundo pyrrhonota*), and Wood Duck (*Aix sponsa*). Brown-headed Cowbirds are known to parasitize at least 220 avian species (Johnsgard 1997; Ortega 1998; Halterman *et al.* 1999) and have been raised successfully by approximately 144 of these species (Davies 2000). Most, but not all, of these

hosts are smaller than cowbirds. Although individual cowbirds are capable of laying up to 40 eggs during a breeding season (Ortega 1998; Scott and Ankney 1980), the effective annual fecundity is approximately two to eight surviving nestlings per female cowbird (Hahn *et al*. 1999; Johnsgard 1997).

Cowbird adaptations often lower their host's reproductive success. For example, female cowbirds often eject or ingest one or more host eggs at laying (Scott 1992; Wood and Bollinger 1997). Why they do so is unclear and several hypotheses have been advanced to explain the value of ingesting or removing host eggs from the nest. The "host deception model", for example, posits that reducing the number of eggs in a nest may prevent nest desertion should the host keep track of the number of eggs in her clutch (Sealy 1992; Wood and Bollinger 1997). Egg removal may also increase the effective incubation of the cowbird egg, which may, in turn, increase the likelihood of the cowbird nestling hatching (McMaster and Sealy 1997; Peer and Bollinger 2000). Furthermore, survival of the cowbird nestling may increase with fewer competitors in the nest. Alternatively egg ingestion may just be simple, opportunistic predation (Wood and Bollinger 1997).

Cowbirds lay unusually thick-shelled eggs. As such they are heavy and strong and may break host eggs, or make them impossible for the host to puncture or remove from the nest (Blankespoor *et al*. 1982; Mermoz and Ornelas 2004; Weatherhead 1991). Cowbird chicks that hatch prior to or concurrent with the host nestlings result in increased host hatching failure (Hauber 2003) since

the time spent incubating the clutch decreases as the female host must vacate the nest in search of food for the cowbird nestling.

Cowbirds have extremely short incubation periods (10-11 d; Briskie and Sealy 1987), which helps ensure that they hatch early relative to host nestlings. Once hatched, they grow rapidly and beg with high intensity (Dearborn and Lichtenstein 2002; Hauber 2003; Lichtenstein and Sealy 1998; Lichtenstein and Dearborn 2004). Especially in the nests of smaller host species, cowbird nestlings often outcompete the host nestlings by being first in line to receive nourishment (Dearborn 1998; Lichtenstein and Sealy 1998; Lorenzana and Sealy 1999). Host nestlings often die of starvation or are trampled by the cowbird (Hauber 2003). Host parents often work at supranormal levels to raise parasitized broods due to the heavy food demands of the cowbird nestling. This effort may prevent the host from renesting in species that breed more than once in a season. These, along with the reduced survival of host nestlings, represent negative effects on host reproductive success (Dearborn *et al*. 1998; Hauber and Montenegro 2002; Kilpatrick 2002).

The extra stress inflicted by cowbirds when combined with habitat loss, fragmentation, and predation can pose serious threats to the survival of already threatened avian species. This compound effect is at least partly responsible for the threatened status of several host species. Many of these species are small Neotropical migrants that are physically unable to defend a nest from an intruding female cowbird or remove cowbird eggs once parasitism has occurred. Several of the approximate 144 cowbird accepters are threatened or endangered due to

habitat loss, such as the Kirtland Warbler (*Dendroica kirtlandii*; Decapita 2000), Least Bell's Vireo (*Vireo bellii pusillus*; Griffith and Griffith 2000), the Black-capped Vireo (*Vireo atricapillus*; Hayden *et* al. 2000) and the Southwestern Willow Flycatcher (*Empidonax traillii extimus*; Briskie and Sealy 1987; Whitfield and Sogge 1999). Furthermore, these birds may fail to raise any of their own offspring if a cowbird egg hatches owing to their small size (Davies 2000; Robinson *et al*. 1993).

Brood parasitism is particularly detrimental to rare host species because the cowbird, a generalist, does not depend on any one species to ensure its reproductive success. Therefore, high local rates of parasitism can be maintained despite certain declining host populations when the area is shared with other abundant host species that act to ensure the cowbirds' reproductive success (Weatherhead 1989). Ultimately, the size of the host contributes to determining the resilience of the host species to parasitism (Kilpatrick 2002; Lorenzana and Sealy 1999).

The natural history of Red-winged Blackbirds

Red-winged Blackbirds (hereafter "blackbird") are a model candidate species in which to investigate the effects of cowbird brood parasitism. These blackbirds cope well with manipulation and are among, if not *the* most, abundant wild bird in North America (Jaramillo and Burke 1999) ranging from southeastern Alaska across sub arctic Canada and extending as far south as the Yucatan peninsula (Beletsky 1996; Bull and Ferrand 1977; Jaramillo and Burke 1999). Typical habitats of the Red-winged Blackbirds parallel those of cowbirds, such as

marshes and upland habitats (Bull and Ferrand 1977; Jaramillo and Burke 1999). Red-winged Blackbirds are cowbird egg 'accepters' and hence do not abandon a parasitized nest, but incubate and raise the cowbird chick (Carello and Snyder 2000; Kilner 2003). Furthermore, Red-winged Blackbirds are capable of simultaneously raising both their own young as well as young cowbirds due to their relatively large size (Clotfelter and Yasukawa 1999), whereas smaller host species are usually not capable of this *(*Kilner 2003; Lorenzana and Sealy 1999).

Blackbirds are a polygynous, colonial species. In southern Manitoba the males arrive on breeding grounds in April, and establish breeding territories by early to mid-May (S. Forbes, pers. comm.). Successful males establish and defend a territory of several thousand square meters, containing harems generally of six or less females, but occasionally as many as 15. Females arrive on breeding grounds in late April or early May in southern Manitoba and select mates and nesting sites based on the quality of the male's territory (Beletsky and Orians 1996).

In southern Manitoba, Red-winged Blackbird nesting occurs between the end of May and August, with a peak in mid-June. Females in southern Manitoba lay clutches of two to six eggs with a mode of four (S. Forbes unpublished data). Eggs are laid daily and incubation generally commences before the clutch is complete, resulting in hatching asynchrony. This results in an age-structured brood and a brood hierarchy. Providing that the female cowbird gauges egg deposition correctly, cowbird eggs should hatch with or sooner than blackbird

eggs which require incubation for 11 to 14 days (Beletsky and Orians 1996; Beletsky 1996).

There are several explanations as to why Red-winged Blackbirds accept cowbird eggs even though they are physically able to reject them (Clotfelter and Yasukawa 1999). The “evolutionary lag hypothesis” (Rothstein 1982; Davies 2000) suggests that the relatively recent sympatry of the host and parasite over most of the range of Red-winged Blackbirds (approximately 200 years) has not allowed sufficient time for the blackbirds to evolve a defense mechanism. Alternatively, the “equilibrium hypothesis” (Rohwer and Spaw 1988; Davies 2000) proposes that the cost of ejection or mistakenly ejecting their own egg may be more costly than raising the cowbird.

Birds that routinely reject cowbird eggs apparently recognize the cowbird eggs likely from their distinctive color and size. Rejection mechanisms include ejection from the nest, either by physical pushing, or puncturing the egg with their beak and flinging it from the nest. Alternatively, some species completely abandon the parasitized nest and renest elsewhere. Desertion may prove costly due to the investment involved in building another nest, especially if the breeding season is a short or nearing its completion (Davies 2000). Yellow Warblers, however, use a different protective mechanism. Upon discovery of a cowbird egg, these birds build a new nest floor over the parasitic egg. Several layers may be present in a warbler nest, or the nest may be abandoned (Graham 1988; Weatherhead 1989).

Terminology

Following earlier work on this same system (Forbes *et al.* 1997, Forbes and Glassey 2000, Forbes *et al.* 2001), I shall refer to host and parasite nestlings that hatched on the first day of the nestling period as core nestlings. Host nestlings that hatched one or more days later than the core brood are referred to as marginal nestlings. Cowbird nestlings sometimes hatch one or more days before the host brood. I shall refer to these as supracore nestlings.

Field methods

Blackbird populations were surveyed from 1993 to 2005 in wetlands near the periphery of the city of Winnipeg at two main sites, Lagimodiere Blvd. and Highway 101 and Inkster Blvd. and Highway 101, and three other sites that were sampled from intermittently over the 13 years (Figure 1). Field crews, consisting of Dr. Scott Forbes and up to eight summer students, surveyed the sites daily from late May until early July. Nests searches were conducted and entire breeding populations in designated areas were enumerated. From 200 to 600 nests were surveyed in a given breeding season. Nests were typically found during the nest-building stage and followed until the nestlings approached the age at fledging (until the eldest nestlings reached 10-d of age). Nests were marked, their locations mapped, and they were visited daily to record nest contents (the number of eggs or nestlings, the individual identity of each egg or nestling). Each nestling was individually marked using non-toxic felt markers applied to down tracts and weighed each day using portable electronic scales. The presence of cowbird eggs and nestlings was recorded in the same manner

as host nestlings (i.e., eggs were numbered, nestlings were individually marked and weighed daily).

Here I focus on the subset of nests that were either parasitized by Brown-headed Cowbirds naturally, or where cowbird eggs or hatchlings were experimentally transferred to Red-winged Blackbird nests. These data were gathered from 1993 to 2001. I compared nests where cowbird nestlings hatched successfully to nests where cowbirds were absent to estimate the impact of cowbird nestlings on host nestlings. A total of 1011 redwing nestlings were studied in 306 nests. Of these, 733 nestlings were in 216 unsuccessfully parasitized nests (UPN). That is, nests in which cowbird eggs were laid but failed to hatch; cowbird eggs were laid but were experimentally removed; cowbird eggs were experimentally added to nests but failed to hatch; or cowbird eggs were not laid or experimentally added to these nests. There were 278 nestlings in 90 successfully parasitized nests (SPN) where cowbird eggs were laid or experimentally added, hatched, and survived to fledgling. A maximum of one cowbird nestling occurred per nest (when occasionally two or more cowbird eggs were laid in a single nest, the surplus cowbird eggs were transferred to other nests). Experimentally transferred eggs were moved to nests at the same stage of incubation as the donor nest.

Data compilation

Field data were transferred from field notebooks to Microsoft Excel spreadsheets for analysis. I compiled growth and demographic data for SPNs and UPNs. I fit logistic growth curves to age and growth data for individual nestlings

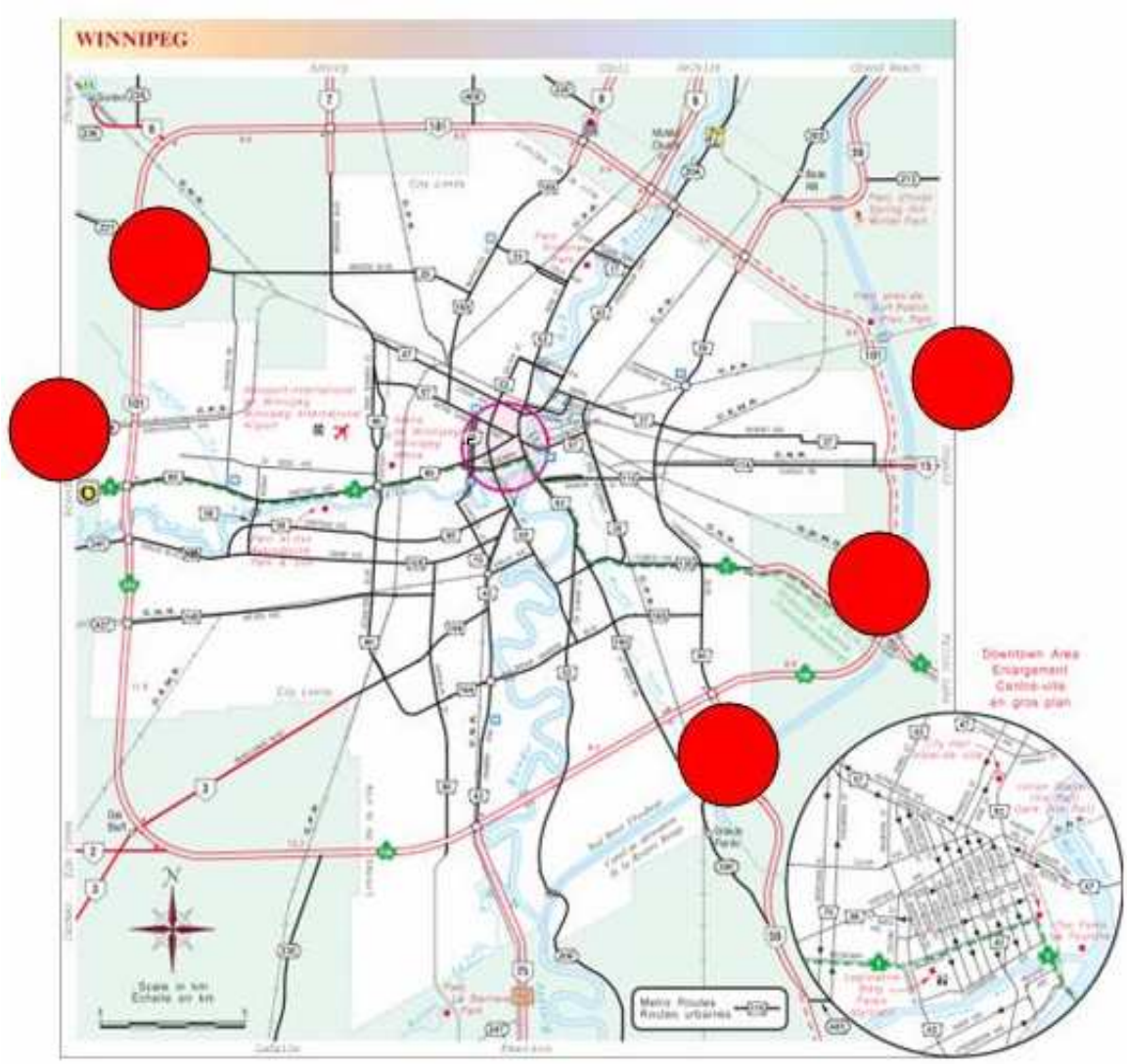

Figure 1: Map of Winnipeg, Manitoba and surrounding area. Dark circles indicate the five marsh sites where blackbird populations were surveyed from 1993 to 2005.

using a custom algorithm based on the least-squares method that derived the best-fit model using biologically plausible ranges of parameter values. The algorithm used a “brute force” approach (Haefner 1996) to search all parameter values for the instantaneous rate of growth, asymptotic mass, and inflection point to obtain the curve of best fit. This was defined as the model that minimized the squared deviations between observed data and the fitted model (least squares). All subsequent statistical analyses as described below were conducted in Microsoft Excel.

On the use of partial data sets to estimate growth parameters

A potential problem with logistic growth curves was the use of incomplete data sets. Nestlings follow a pattern of logistic growth with a discernible asymptote over their first eight to ten days in the nest. Individual nestlings, however, could often not be followed for this complete period – e.g., because the nestling was a victim of brood reduction, or taken by a predator, or lost in a flood. To determine if incomplete data sets generated unbiased estimates of the growth parameters, I randomly selected 50 core and 50 marginal host chicks surviving to nine days for analysis. These nestlings were randomly selected from the successfully and unsuccessfully parasitized groups using an Excel random number generator.

For each chick, logistic curves were fit successively from day two to the maximum observed age before fledging, yielding growth rate and asymptotic mass. I then compared the growth rates and asymptotic masses of the incomplete data sets to those of the complete data sets using simple linear

regression – e.g., by comparing day-eight parameters to day-nine parameters, day seven to day nine, day six to day nine, and so on, for each of the four groups (n = 25 UPN core, n = 25 UPN marginal, n = 25 SPN core, n = 25 SPN marginal). For each comparison, a corresponding scatter plot was created in Excel (see Results). These regressions allowed me to examine how closely the partial data set predicted the growth curves fit to the full data set, and whether these parameter estimates were biased – i.e., consistently under- or over-predicted growth rate or asymptotic mass.

Hatching failure

I examined the incidence of blackbird hatching failure in 48 SPNs (180 eggs) using a multiple regression analysis to determine whether the hatching asynchrony of the cowbird in conjunction with the initial clutch size affected the number of host hatchlings. I used the clutch size (and not individual eggs) as the unit of observation. A Student's t-test of the regression slope was used to assess the significance of the independent variates (host clutch size, cowbird hatching asynchrony). An analysis of variance was used to assess the significance of the overall regression.

Growth analysis

Following earlier procedures used on this same population (Forbes and Glassey 2000) chicks surviving to at least eight days (n=362) were sexed by plotting the mass frequency distribution of nestlings for the entire population in a given year. Red-winged Blackbirds are strongly sexually dimorphic (adult females average 30 to 35 g; adult males average 60 – 65 g) and by eight days post-hatch

show a strongly bimodal growth distribution. This method is reliable since, even in the presence of a cowbird, male Red-winged Blackbirds will not be as small as the female Red-winged Blackbirds.

Two multiple regression analyses were performed to examine the effects of cowbird presence, core brood size, marginal brood size, and nestling sex on the growth rate and asymptotic mass of host nestlings. Dummy variables were used for nestling sex and the presence or absence of a cowbird nestling. The significance of the independent variates was assessed with a Student's t-test of the regression slope. The significance of the overall regression was assessed by an analysis of variance.

Host demography

The effect of cowbird presence on host core and marginal brood size was examined in nests that contained nestlings surviving until at least eight days (UPN: n = 93; SPN: n = 48) which has been used in previous studies of this population as an index of fledging success (Forbes *et al*. 1997, Forbes *et al*. 2001). I compared the mean clutch size, brood size at hatching, and brood size at day eight of SPNs to those of UPNs using one tailed t-test analyses since it was expected *a priori* that the SPN clutch and brood sizes would be smaller due to the removal activities of the female cowbird. The Bonferroni multiple-comparison correction (α / n) was used on this family of tests to avoid inflating the Type I error rate.

Nestlings reaching eight days of age in the core (n = 121) and marginal (n = 98) broods were used as an index of fledging success. Multiple regression

models were built with day eight brood size as the dependent variate and the quality of year, size of core and marginal brood sizes at hatching, and the presence / absence of a cowbird as the independent variates. Year quality was a dichotomous variable (good or bad) based on whether fledging success was above or below the 13-year mean (2.70 fledglings / successful nest; 1993-2005) for this study population (S. Forbes unpubl. data). Dummy variables were used for year quality and the presence / absence of a cowbird. The significance of the independent variates was assessed with a Student's t-test of the regression slope, followed by assessing the overall regression significance with an analysis of variance.

The effect of cowbird presence on the sex ratio of host core and marginal broods was examined using only host nestlings that survived until at least eight days (brood n = 205). The proportion of males and females in the core and marginal brood was calculated for each nest. Student's t-tests were used to compare the sex ratios after the data had been arcsine-square root transformed.

Results

Using partial data sets to estimate growth parameters

Simple linear regression analysis of partial data sets revealed that using partial data sets to estimate nestling growth rate and asymptotic mass was of limited utility. The results of the regression analysis are summarized in Table 1, where day nine was used as the dependent variable to which day eight, day seven, day six…growth parameter estimates were sequentially compared. The reliability of using partial data sets was judged by statistical significance. Days yielding non-significant results were judged as poor estimates of growth rate or asymptotic mass. The regression slope, β, indicated whether parameter estimates were biased. A slope of 1.0 indicated an unbiased estimate. A slope less than 1.0 indicated that the partial dataset under-predicted the parameter estimate. A slope greater than 1.0 indicated that the partial dataset over-predicted the parameter estimates. This analysis examined how well a partial dataset would have predicted the parameter estimates generated from the complete dataset. It addressed the question of how much data is needed to get a reliable estimate of the logistic growth parameters.

As can be seen in Table 1, estimates of growth rate and asymptotic mass were found to only be reliable until day eight and day six respectively in core host broods without the presence of cowbirds. However, data sets of marginal host broods in unparasitized nests were statistically reliable until day seven for growth rate, and day eight for asymptotic mass. Similar results were found for growth rate and asymptotic mass estimates of core and marginal host broods

Table 1. Results of linear regression analysis on 100 randomly selected host nestlings (n = 25 UPN core, n = 25 UPN marginal, n = 25 SPN core, n = 25 SPN marginal). Each group was sequentially compared to itself at day nine to estimate the reliability of using partial datasets for estimating nestling growth rate and asymptotic mass. The regression coefficient (β) and the p-value (P) are shown for comparison of each day to day 9 for both the growth rate and asymptotic mass.

Unparasitized Group						Parasitized Group					
		Growth Rate		Asymptotic Mass				Growth Rate		Asymptotic Mass	
	Day 9 vs:	*β*	*P*	*β*	*P*		Day 9 vs:	*β*	*P*	*β*	*P*
Core chicks	Day 8	0.95	0.0002	1.025	0.003	**Core chicks**	Day 8	0.99	1.192E-06	0.97	7.9E-05
	Day 7	1.01	0.267	1.048	0.018		Day 7	0.96	3.915E-06	0.94	0.004
	Day 6	1.00	0.056	1.180	0.005		Day 6	1.00	0.316	0.90	0.477
	Day 5	1.00	0.594	1.238	0.418		Day 5	0.95	0.175	0.83	0.601
	Day 4	0.94	0.967	1.400	0.723		Day 4	0.95	0.215	0.89	0.183
	Day 3	0.99	0.981	1.201	0.912		Day 3	0.95	0.513	1.16	0.135
	Day 2	0.84	0.892	1.185	0.218		Day 2	0.93	0.434	0.86	0.607
Marginal chicks	Day 8	0.98	7.350E-07	1.001	4.54E-05	**Marginal chicks**	Day 8	0.89	0.026	0.95	2.47E-05
	Day 7	0.968	0.002	0.991	0.604		Day 7	0.89	0.109	0.91	0.001
	Day 6	0.94	0.370	1.064	0.250		Day 6	0.93	0.526	0.89	0.037
	Day 5	1.05	0.168	0.931	0.572		Day 5	1.01	0.686	0.83	0.038
	Day 4	1.05	0.293	0.946	0.851		Day 4	1.09	0.486	0.80	0.233
	Day 3	1.17	0.432	0.918	0.723		Day 3	1.14	0.594	0.85	0.003
	Day 2	0.97	0.604	1.040	0.936		Day 2	1.13	0.943	0.88	0.106

parasitized by cowbirds. Estimates of core chick growth rate and asymptotic mass were reliable at day seven. Marginal chicks in parasitized nests had only a narrow range whereby growth rate could be reliably estimated, starting on day eight. Parasitized marginal hosts' asymptotic mass was reliably estimated at day seven. Figures 2 and 3 display how the relationship between the complete and partial data sets decays with increasingly incomplete data sets.

Hatching failure in blackbird clutches

I expected clutch size to be a strong predictor of brood size at hatching, as is the case in unparasitized broods (S. Forbes, pers. comm.). However, clutch size did not significantly affect hatching brood size in SPNs contrary to expected results (Table 2: Multiple regression analysis; Student's $t = 1.328$; $df = 47$; $P = 0.191$). The hatching asynchrony of the cowbird was a nearly significant predictor of the hatching brood size of blackbirds (Student's $t = 1.929$; $df = 47$; $P = 0.060$): blackbird broods were smaller when cowbirds hatched before the first blackbirds (due to increased hatching failure of blackbird eggs) and larger when cowbirds hatched after the first blackbird nestlings.

Growth of host blackbird nestlings

I examined the growth of host nestlings that survived until at least eight days of age in relation to the presence of a cowbird, the size of the host core and marginal brood at hatching, and sex of the host nestling. The presence of a cowbird appeared to have little effect on either the growth rate of host nestlings ($R^2 = 0.013$; $t = 0.616$; $df = 361$; $P = 0.54$) or their asymptotic mass ($R^2 = 0.399$; $t = -0.189$; $df = 361$; $P = 0.85$). Similarly, the size of the marginal brood at hatching

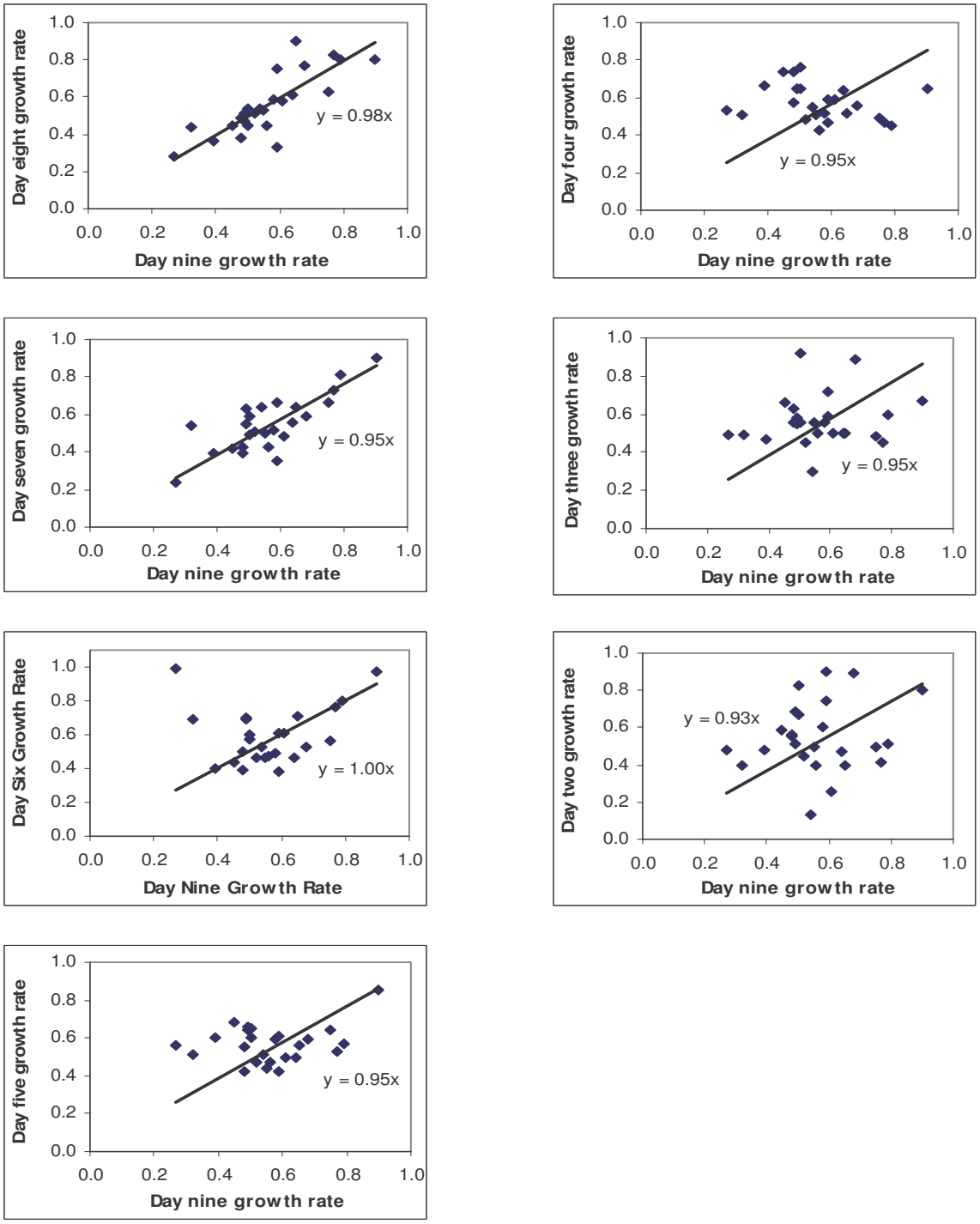

Figure 2. The relationship between the growth rates of core nestlings estimated from the first nine days of data and growth rates estimated from the first eight or fewer days of data. The purpose of this analysis was to determine if partial data sets provide reliable estimates of growth. Growth rates were obtained from fitted logistic growth curves.

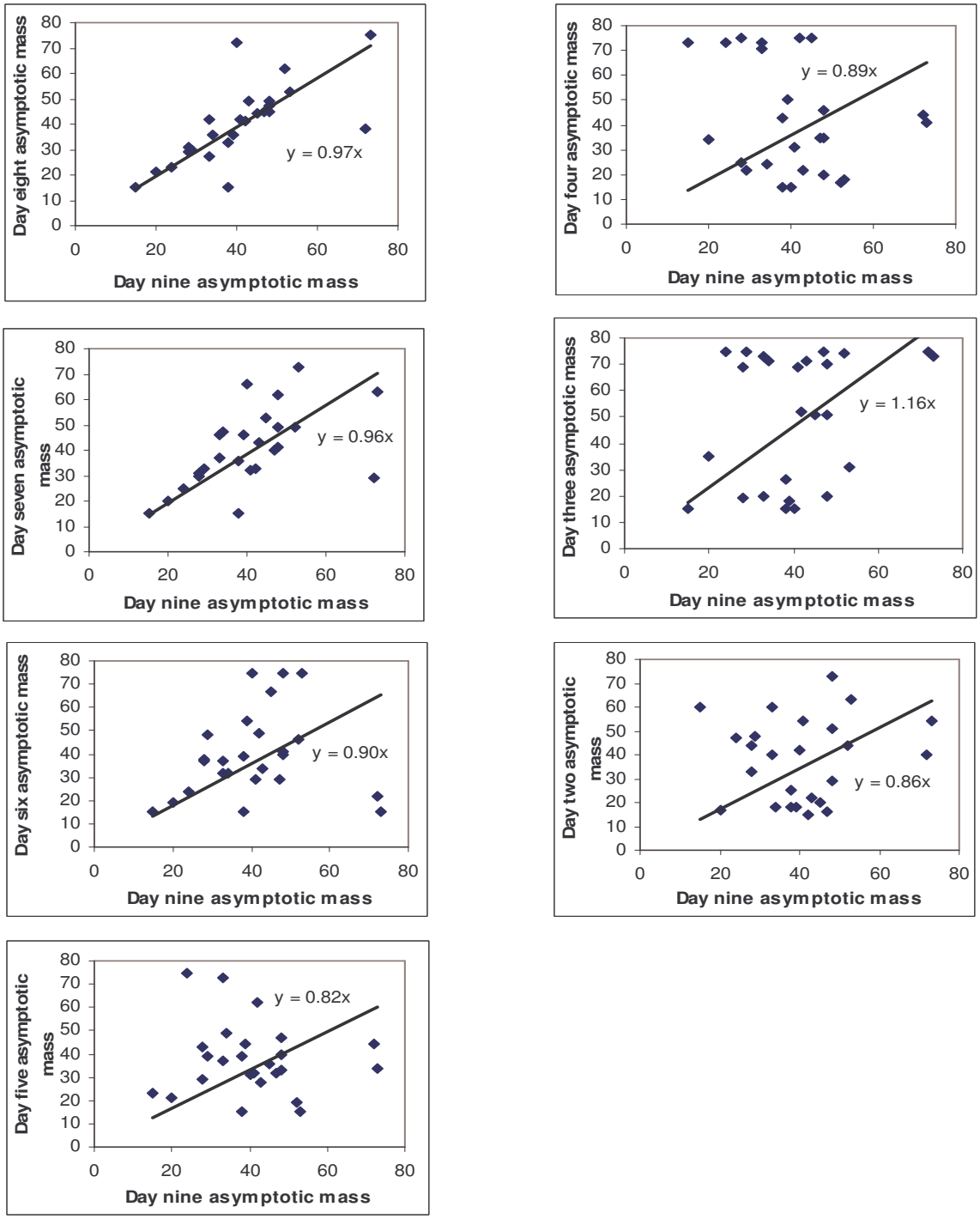

Figure 3. The relationship between the asymptotic masses of core nestlings estimated from the first nine days of data and the asymptotic masses estimated from the first eight or fewer days of data in successfully parasitized nests. The purpose of this analysis was to determine if partial data sets provide reliable estimates of growth. Asymptotic masses, measured in grams, were obtained from fitted logistic growth curves.

Table 2. The results of a multiple regression analysis examining the relationship between the size of the blackbird brood at hatching, cowbird hatching asynchrony, and the blackbird clutch size. The significance of the overall regression was assessed with an analysis of variance. The significance of the independent variates was assessed with a Student's t-test of the regression slope. The adjusted R^2 value F-statistic (F), degrees of freedom (df) and p-value (P) of the overall regression assessment are shown, as are the regression coefficients (β) and P values (P) for the independent variates in the multiple regression model.

ANOVA	***df***	***F***	***P***
Regression	2	3.830	0.029
Residual	45		
Total	47		
	β	***P***	
Cowbird HA*	0.311	0.060	
Clutch Size	0.267	0.191	
Adjusted R^2	0.107		

* HA denotes hatching asynchrony

had only very weak and non-significant effects on host nestling growth rate (R^2 = 0.013; t = 0.198; df = 361; P = 0.84) or asymptotic mass (R^2 = 0.399; t = -1.592; df = 361; P = 0.112). The size of the core brood at hatching had stronger but still non-significant effects on the growth and asymptotic mass of host nestlings (Table 3). As expected, nestling sex had a strong and significant effect on both growth rate and asymptotic mass. Results of the growth analysis are summarized in Table 3.

Host demography

Mean clutch size, day one brood size, and day eight brood size were all larger in the unsuccessfully parasitized group than in the successfully parasitized group (Table 4). Because I was making a family of comparisons on this data set, I used a Bonferonni correction to avoid inflating the Type I error rate which involved dividing alpha by the number of comparisons, which in this case was 0.0167 ($=\alpha / 3$). Day one core and marginal broods were also larger in the unparasitized group than those of the parasitized group, since these parameters are the constituents of the total brood size. By day eight, however, the proportions of core and marginal broods among the parasitized and parasitized groups deviated from the original trend such that the parasitized group displayed an increase in marginal brood size over that of the marginal brood size of the control group (Table 4). This analysis yielded only statistically significant results for the comparisons between total brood sizes at day five (P = 0.003), total brood sizes at day eight (P = 0.014), and core brood sizes at day eight ($P=2.9X10^{-5}$). However, several other groups of comparisons were approaching the significance

Table 3. Multiple regression analysis of the effect of core and marginal brood size at hatching, nestling sex, and the presence / absence of a cowbird on the growth rate and asymptotic mass of host nestlings surviving until at least eight days of age. The significance of the overall regression was assessed with an analysis of variance. The significance of the independent variates was assessed with a Student's t-test of the regression slope. The adjusted R^2 value, F-statistic (F), degrees of freedom (df) and p-value (P) of the overall regression are shown, as are the regression coefficients (β) and P values (P) for the independent variates in the multiple regression model.

	Growth Rate			**Asymptotic Mass**		
ANOVA	***df***	***F***	***P***	***df***	***F***	***P***
Regression	4	2.156	0.074	4	60.931	<<0.001
Residual	357			357		
Total	361			361		
	β		***P***	***β***		***P***
Size of core brood at hatching	0.015		0.135	-1.66		0.063
Size of marginal brood at hatching	0.002		0.843	-0.917		0.112
Sex of nestling (f = 1)	0.034		0.012	-13.213		<<0.001
Presence or absence of cowbird (CB=1)	0.009		0.538	-0.179		0.850
Adjusted R^2	0.013			0.399		

level and were suggestive of an actual significant difference between the means. These results may be attributed to low statistical power.

In both core and marginal broods, the presence of cowbirds and the size of the marginal brood did not significantly influence survivorship, however, year quality and the size of the core brood did. Year quality, which was measured by blackbird reproductive success that, in the past, has been linked to environmental conditions (Forbes *et al.* 2001), increased core host survival by a factor of 0.073 (P = 0.020), and marginal host survival by 0.235 (P = 0.004). The size of the core hatching brood had the opposite effect on core and marginal brood survival. Here, core and marginal host nestling survival declined by a factor of -0.076 (P = 0.001), and –0.252 (P = 0.0001) respectively (Table 5).

The presence of a cowbird nestling potentially had a complex effect on host nestling sex distribution among core and marginal broods. As illustrated in Table 6, the proportion of core males in SPNs was larger when in the presence of a cowbird than as was seen in UPNs. Conversely, the proportion of marginal males declined with parasitism. For female blackbird nestlings, the opposite trend held: the proportion of core females decreased, but the proportion of marginal females increased in response to cowbird presence. Upon statistical analysis, however, no significant relationship was established for any of the sex skewing observed as all p-values computed from Student's t-test analyses were not below 0.4. Again, the scope of this project was too small to detect such subtle effects as sex skewing, and lack of detectability may be explained by low statistical power.

Table 4. The effect of the presence of a cowbird on host core and marginal brood size among nests that contained nestlings surviving until at least eight days. A one tailed t-test analyses was used with α=0.0167 as per the Bonferroni multiple-comparison correction (α / n). Mean clutch and brood sizes, standard deviations (SD), clutch and brood sample size (n), and the p-values from the t-tests are reported.

	With cowbirds	SD	n	**Without cowbirds**	SD	n	***P***
Clutch	3.67	0.70	46	**3.91**	0.76	90	0.051
Total brood size at hatching	2.93	0.95	42	**3.31**	0.97	67	0.043
Core brood size at hatching	1.64	0.66	42	1.94	0.70	81	0.115
Marginal brood size at hatching	1.29	0.81	42	1.35	0.87	81	0.200
Total brood size at day five	2.56	0.923	41	2.98	1.066	49	0.003
Core brood size at day five	1.54	0.60	42	1.82	0.70	49	0.040
Marginal brood size at day five	1.02	0.82	41	1.16	0.83	49	0.131
Total brood size at day eight	2.34	1.04	41	2.62	1.05	68	0.014
Core brood size at day eight	1.54	0.60	41	1.73	0.75	82	2.93E-05
Marginal brood size at day eight	**0.90**	0.82	41	0.84	0.84	82	0.071

Table 5. The effect of year quality, size of core and marginal hatching brood size, and the presence / absence of a cowbird nestling on the survivorship of host nestlings reaching eight days of age following multiple regression analysis. The significance of the independent variates was assessed with a Student's t-test of the regression slope, followed by assessing the overall regression significance with an analysis of variance. The adjusted R^2 value F-statistic (F), degrees of freedom (df) and p-value (P) of the overall regression are shown, as are the regression coefficients (β) and p-values (P) for the independent variates in the multiple regression model.

	Core Host Brood			**Marginal Host Brood**		
ANOVA	***df***	***F***	***P***	***df***	***F***	***P***
Regression	4	4.23	0.003	4	6.31	0.0002
Residual	93			93		
Total	97			97		
	β		***P***	***β***		***P***
Year Quality (1 = good)	0.073		0.020	0.235		0.004
Size of core brood at hatching	-0.076		0.001	-0.252		0.0001
Size of marginal brood at hatching	-0.012		0.530	-0.015		0.814
Presence or absence of cowbird (CB=1)	0.007		0.839	-0.052		0.546
Adjusted R^2	0.097			0.180		

Table 6. Sex ratios of host core and marginal broods with members surviving to eight days in parasitized and non-parasitized nests. Sample sizes indicate the number of broods. None of the comparisons were significant (Student's t-test: $p > 0.4$)

	Core Brood		Marginal Brood	
	♂	♀	♂	♀
With Cowbirds	46%	54%	41%	59%
	(n=47)		(n=27)	
Without Cowbirds	41%	59%	47%	53%
	(n=87)		(n=44)	

Discussion

Bias analysis

Incomplete datasets prior to day seven or eight are unreliable estimators of growth rate and asymptotic mass (Table 1). This knowledge was fundamental to avoid reporting unrealistic cause and effect relationships within the nests. Both the statistical significance of the linear relationship and the slope of the line, β, were considered for delineating reliable data subsets where linear regressions yielding statistical significance and slopes greater than 0.9 were preferred. Accordingly, I only used nestlings surviving until at least eight days old in my analyses.

Effects of cowbirds on the hatching success of host clutches

Clutch size is usually a reliable predictor of the hatching brood size as the number of eggs determines the maximum number of nestlings. Indeed, in this population of blackbirds, the correlation between brood size at hatching and clutch size is usually above 90% (S. Forbes unpub. data). However, the presence of a cowbird disrupted this usual and predictable relationship. In fact, cowbird hatching asynchrony (whether they hatched before, at the same time or after the first host nestlings) was a better predictor of brood size at hatching than the original clutch size.

Others have noted that cowbirds increase the hatching failure rate of host eggs in phoebes (Hauber 2003), song sparrows (Arcese *et al.* 1996), vireos, flycatchers, and warblers (Wiley 1985). My findings are consistent with this earlier work. It appears that the post-hatching activities of the cowbird nestling

reduced host hatching success. Once a cowbird is hatched, its begging prompts the female host to leave the nest and gather food for the hatchling. In the meantime, the rest of the clutch cools down, thereby potentially reducing egg viability. This effect is especially important in nests in which the cowbird hatches before the host nestlings (supracore cowbirds) wherein the strongest effect was observed. Alternatively, these results may partially be explained by reduced effective incubation (McMaster and Sealy 1997). If, for instance, the addition of a cowbird egg into a nest where a host egg was not removed increased the clutch size beyond the capabilities of the incubating female, the eggs may not receive equal incubation or, collectively, may not reach optimal incubation temperature. The latter explanation, however, seems less likely due to the relative large size of Red-winged Blackbirds (Clotfelter and Yasukawa 1999), and their ability to incubate up to six eggs (Beletsky 1996).

Effects of cowbirds on the growth of host nestlings

The presence of a cowbird did not seem to affect the growth rate or the asymptotic mass of the surviving blackbird nestlings. These results were not surprising considering the larger size of blackbird nestlings relative to cowbird nestlings. As noted by Lorenzanna and Sealy (1999) larger host species are less vulnerable to some of the negative consequences associated with brood parasitism. Blackbird nestlings that survived until fledgling were effective competitors with the cowbirds. Although no relation was found between the core brood size and growth rate, and core brood size and asymptotic mass, this may be due to low statistical power in the present study.

I did not examine the parameters of the logistic growth curve for nestlings that did not survive at least eight days because my analysis of bias above indicated that these were unreliable indicators of growth performance. It is likely that nestlings that died due to brood reduction in cowbird SPNs grew more slowly than the survivors, but given that these data generated unreliable model results, I cannot address this question here.

While a significant effect of cowbirds on host chick growth was not detected in the present study, others have found such effects, particularly in smaller host species. For example, Dearborn *et al*. (1998) noted that parasitic cowbird nestlings caused a reduced host growth rate in Indigo Bunting (*Passerina cyanea*) chicks. This stems from two effects. First, host nestlings increase begging intensity in the presence of the cowbird (Glassey and Forbes 2003). The energy expended on begging may diminish the growth of host nestlings. But more importantly, cowbirds simply usurp food from host nestlings diminishing the growth of the latter (Dearborn *et al.* 1998, Lorenzana and Sealy 1999).

Marginal host chicks, due to their smaller size and inability to compete effectively, do not substantially lower the distribution of nest resources to siblings and, hence, did not influence the growth of host nestlings (Table 3). While a statistical effect was not observed between the core brood size and growth rate, slowed growth would be expected given the relative size and competitive competence typically demonstrated by core chicks, as shown earlier in this system (Forbes *et al.* 1997, Forbes and Glassey 2000). It is likely, however, that

low statistical power given the relatively small scope of this project made it impossible to detect such a trend. Furthermore, statistical analysis of the effects of core brood size on asymptotic mass were approaching statistical significance, highly suggesting that asymptotic mass would, in fact, decrease by 1.66 grams per additional core offspring. Studies by Bollinger (1994), Kalmbach and Becker (2005) and Magrath (1992) clearly demonstrate that hatching order can influence nestling growth rate, mass, and ultimately, survival.

As expected, nestling sex affected growth rate and asymptotic mass, since the early signs of sexual dimorphism can be seen in the nest as a divergence of nestling weight at approximately day five. Female blackbirds grew slightly faster than males, by about 0.03g per day, and they reach asymptotic mass sooner. Such a trend is typical of logistic growth curves. The asymptotic mass of surviving males was about 13g heavier than females.

Effects of cowbirds on host demography

The total size of host brood was smaller in SPNs (Table 4). Clutch size of the parasitized brood was reduced (by about 1/3 of an egg) presumably due to egg removal by laying female cowbirds. These findings are consistent with Lorenzana and Sealy (1999) who report that the majority of the cost of parasitism in host species weighing over 20g, Red-winged Blackbirds inclusive, is due to egg removal.

Blackbirds in this population typically lay one egg per day until the final clutch size is attained. Cowbirds monitor host nesting activity (Neudorf and Sealy 1994; Ortega 1998) and often lay their eggs among the core host eggs.

Not only does this assure that the cowbird nestlings will hatch sooner than host chicks (due to their short incubation time), but also that any of the host eggs removed by the female cowbird would have belonged to the core brood. As seen in Table 4, the reduced clutch size in SPNs translated into smaller brood size at hatching, and in particular, core brood size at hatching.

By midway to fledgling, the SPNs brood size was still significantly smaller than that in UPNs. However, by day eight the implications of cowbird host egg removal became apparent. Despite UPNs having a higher fledgling success rate, ultimately, the marginal chicks in SPNs survived better than those in UPNs. This phenomenon may be explained in terms of similar studies conducted by Forbes *et al*. (1997), and Forbes and Glassey (2000) in the same system. It is the size of the core brood that most strongly affects the survival of marginal nestlings (but not vice versa). Thus, the smaller SPN core brood size at hatching likely enhanced marginal chick survival in these nests. Forbes *et al*. (1997) found that when chicks were experimentally added to a nest, the brood enlargement positively correlated with marginal brood mortality. However, the same trend was not seen when manipulating the size of the marginal brood; the core brood fared equally as well regardless of marginal brood size. It was proposed that hatching asynchrony implements a brood hierarchy whereby marginal offspring are provisioned only after the needs of core chicks have been met. Thus, marginal chicks are expendable and parental concern lies mainly with the welfare of the core chicks (Forbes *et al*. 1997; Mock and Forbes 1995), which develop a competitive size advantage over the marginal chicks.

When the female cowbird removes host eggs from the nest, hence, she alleviated some of the stress imposed by core chicks, thus benefiting the smaller marginal chicks. Alternatively, increased marginal brood prevalence may be partly accounted for by an increased parental provisioning rate due to the increased begging that occurs in SPNs (Dearborn *et al*. 1998).

Effects of cowbirds on host nestling survival

Multiple regression analysis confirmed that cowbirds had no significant bearing on the survival of successful eight day old nestlings. The main detrimental effects cowbirds exert on surviving Red-winged Blackbirds occurred before hatching in the form of blackbird egg removal by cowbirds and decreased blackbird egg viability. Surviving marginal nestlings also did not affect core offspring survival since they only receive food once the core brood has been fed. Not surprisingly, the quality of the year and the size of the core brood at hatching significantly reduced core and marginal brood survival since both are implicated in food availability and distribution.

Effects of cowbirds on sex ratios of host nestlings

My results hint at sex-biased survival of nestling blackbirds subject to parasitism, but the sample size is relatively small, and none of these results approached statistical significance. Detecting modest differences in percent survival requires very large sample sizes, and low statistical power in my study may have obscured genuine results. Alternatively, there may have been no sex skewing at all in this population. Given that recent work has found that cowbirds skew the sex of nestling song sparrows (*Melospiza melodia*; Zanette *et al*. 2005),

I shall speculate on how cowbirds might skew sex ratios in blackbirds, while acknowledging that these results are not backed up by strong statistical support.

My results suggest that proportionately more core male, but fewer marginal male blackbirds survive in SPNs as compared to UPNs. When males hatch first in SPNs, their larger size works to their advantage and they are capable of competing for food and nest space. However, since marginal chicks are last to receive food provisions, male marginal chicks may be unable to sustain a larger body size.

The opposite effect may have occurred among the females in SPNs. Female marginal chicks fared better in SPNs than in UPNs since their smaller size allowed them to persist despite lower food rations. However, core female chicks in SPNs appeared to fare more poorly than core females in UPNs.

Implications for cowbird management

I studied a system where the parasite was smaller than the host species, and hence the results are likely to be most applicable for other large host species, less so for smaller hosts where the larger size of cowbird nestlings makes them effective competitors. Overall my results showed that the presence of a cowbird nestling had little effect on the post-hatching survival of Red-winged Blackbird nestlings. Rather, my results indicated that the most adverse effects of cowbirds on blackbirds occurred at or before hatching through reduced host clutch sizes (from egg removal by the female cowbird), and reduced host hatching success, particularly when the cowbird hatched before the host nestlings, presumably due to decreased effective incubation of host eggs.

Accordingly, optimal cowbird management for large host species should involve preventing cowbird eggs from being laid by culling adults while supplementing these efforts with cowbird egg / hatchling removal. Removal of older cowbird nestlings, however, is unlikely to have an effect on the growth and survival of large hosts. Similar sized host species that may benefit from these insights include the Wood Thrush (*Hylocichla mustelina*), whose population numbers have recently been declining (Trine 1998).

A consensus is emerging that cowbird management on a local scale is a feasible and realistic conservation tool for songbird with rapidly dwindling populations (Lopez-Ortiz *et al*. 2002; Smith *et al.* 2002; Wiedenfeld 2000). Cowbird management techniques that effectively lower local cowbird populations include shooting and trapping (Goguen and Mathews 1999; Robinson 1999; Robinson *et al*. 1993; Smith 1999). These are feasible solutions to prevent cowbird egg laying simply by significantly reducing the number of cowbirds in a location. Cowbird egg removal in conjunction with these efforts, or in lieu of these efforts, such as in remote areas where trapping often proves ineffective (Winter and McKelvey 1999), could reduce hatching failure and brood reduction. Long-term host population rehabilitation should focus on habitat restoration and removing human influences (Goguen and Mathews 1999; Robinson 1999; Robinson *et al*. 1993; Smith 1999), since habitat loss and degradation are the primary contributors to the endangered or threatened status of many cowbird hosts including Kirtland's Warbler, Golden-cheeked Warbler (*Dendrioca*

chysoparia), Southwestern Willow Flycatcher, California Gnatcatcher (*Polioptila californica*), Black-capped Vireo, and Least Bell's Vireo (Kus 2002).

As with any intervention program, forethought and caution must be exercised. One must consider that, though its range has drastically expanded, the cowbird is a native species to North America. An understanding of the location in question must be a prerequisite to any management strategy. Management efforts in wooded forest, for example, would be futile given that cowbirds do not densely inhabit such settings. The ecology of the declining host should be well investigated since declining host populations may not, in fact, be attributable to cowbird parasitism. As a general guideline, management implementation should not be considered when the frequency of parasitism does not exceed ~60% following monitoring of host populations for several years (Smith 1999). Furthermore, managers should be aware that cowbird control is a considerable undertaking as it needs to be ongoing at least until host populations have recovered substantially, since the removal of cowbirds from one year appears to have little effect on cowbird populations in subsequent years (Rothstein and Peer 2005).

Conclusions

1. The presence of a cowbird nestling decreased host hatching success, particularly when cowbirds hatched before host nestlings. Presumably, this was due to a decrease in the incubation time of the remaining, unhatched host nestlings.

2. Cowbird chicks had no effect on the growth of surviving host nestlings since those that survived were effective competitors with the cowbird nestlings.

3. Host core and marginal brood sizes were altered in the presence of a cowbird such that there was an increased survivorship in the marginal broods of SPNs as compared to UPNs despite lower fledgling success overall in the SPNs.

4. Survivorship of nestlings to fledgling age was not hindered by the presence of a cowbird chick.

5. The presence of a cowbird nestling may have had a complex effect on surviving host nestling sex ratio among core and marginal broods whereby there were more marginal females and more core males in parasitized broods. These results, however, were not statistically significant.

6. Recommended and effective cowbird management strategies for a large host include prevention of cowbirds from laying their eggs, and the prevention of cowbird eggs from hatching.

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