Hatching asynchrony, nestling competition, and the cost of interspecific brood parasitism

Mark E. Hauber

Department of Neurobiology and Behavior, Cornell University, Ithaca, NY 14853-2702, USA

All parental hosts of heterospecific brood parasites must pay the cost of rearing non-kin. Previous research on nest parasitism by brown-headed cowbirds (*Molothrus ater*) concluded that competitive superiority of the typically more intensively begging and larger cowbird chick leads to preferential feeding by foster parents and causes a reduction in the hosts' own brood. The larger size of cowbird nestlings can be the result of at least two causes: (1) cowbirds preferentially parasitize species with smaller nestlings and lower growth rates; and/or (2) cowbirds hatch earlier than hosts. I estimated the cost of cowbird parasitism for each of 29 species by calculating the difference between hosts' published brood sizes in nonparasitized and parasitized nests and using clutch size to standardize values. In this analysis, greater incubation length and lower adult mass, surrogate measures of the hatching asynchrony and size difference between parasite and hosts, were both related to greater costs of cowbird parasitism without bias owing to phylogeny. To establish causality, I manipulated clutch contents of eastern phoebes (*Sayornis phoebe*) and examined whether earlier hatching by a single cowbird or phoebe egg reduces the size of the rest of the original host brood. As predicted, greater hatching asynchrony increased the proportion of the original phoebe brood that was lost. This measure of the cost of parasitism was partially owing to increased hatching failure of the original eggs in asynchronous broods but was not at all related to the size differences of older and younger conspecific nestmates. However, proportional brood loss owing to an earlier hatching conspecific was consistently smaller than brood loss owing to asynchronous cowbirds in both naturally and experimentally parasitized phoebe nests. These results imply that although hatching asynchrony is an important cause of the reduction of host broods in parasitized clutches, competitive features of cowbird nestlings remain necessary to explain the full extent of hosts' reproductive costs caused by interspecific brood parasitism. *Key words:* asynchronous hatching, brood reduction, host-parasite interaction, parental care. *[Behav Ecol 14:227–235 (2003)]*

Hosts of heterospecific brood parasites that require parental care pay a cost for rearing non-kin (Payne, 1977; Rothstein 1990, Slagsvold 1998). For example, some parasitic young elicit more intensive parental assistance that lasts longer than that typically provided to conspecific young (Brooke and Davies, 1989; Dearborn et al., 1998). Many foster parents suffer immediate reproductive costs when their own offspring are displaced, pierced, or otherwise destroyed by parasitic young (Davies, 2000; Ortega, 1998; Rothstein and Robinson, 1998). Unlike certain avian brood parasites, such as *Cuculus* cuckoos and honeyguides, hatchling brown-headed cowbirds (*Molothrus ater*, hereafter cowbirds) rarely directly destroy or actively displace host eggs and nestlings (Dearborn, 1996). Yet, the presence of cowbird chicks is often accompanied by a reduction of the number of host chicks and fledglings (Kattan, 1996; Lorenzana and Sealy, 1999; Rothstein, 1975; Sedgewick and Iko, 1999). Despite the vast interest in brood parasitism in general (Davies, 2000), and cowbirds in particular (Morrison et al., 1999; Ortega, 1998; Smith et al., 2000), only recently have we begun to understand the mechanisms that cause these various costs of interspecific brood parasitism (Dearborn, 1998; Dearborn and Lichtenstein, 2002; Kilner et al., 1999; Lichtenstein and Sealy, 1998; McMaster and Sealy, 1999).

The difference between brood sizes of parasitized and nonparasitized nests may be caused by several mechanisms. For example, some female cowbirds preferentially select certain host types (e.g., according to host age, vocal behavior, location.; Hauber, 2000, 2001; Smith et al., 1984; Soler et al., 1995; Uyehara and Narins, 1995), thus biasing parasitized clutch sizes. Alternatively, female parasites themselves decrease the hosts' clutch sizes, as they often remove one or several host eggs before laying their own (Lowther, 1993; Scott et al., 1992; Sealy, 1994). Also, cowbird eggs have stronger, thicker shells and occasionally break the thinner, weaker-shelled host eggs (McMaster and Sealy, 1997; Weatherhead, 1991). The incubation efficiency of many original clutches is also decreased by the presence of larger or numerous cowbird eggs (Petit, 1991; Trine, 2000). Furthermore, when parasitism is followed by the hosts' attempts to remove cowbird eggs, these lead to accidental rejections of or damages to their own eggs at low but nonzero rates (Lorenzana and Sealy, 2001; Rohwer and Spaw, 1988, Røskraft et al., 1993; Sealy, 1996). Many of these mechanisms are also observed in other brood parasitic species (Davies, 2000).

In addition to these possibilities, cowbird and other parasitic nestlings themselves play a role in reducing host brood sizes (Dearborn and Lichtenstein, 2002; Lorenzana and Sealy, 1999). For example, earlier hatching by cowbirds disrupts the incubation pattern of hosts and could lead to hatching failure of host eggs with longer incubation periods (McMaster and Sealy, 1999; Walkinshaw, 1961). Previous studies also found that cowbird nestlings receive a disproportional amount of parental care, especially food delivered to the nest, compared with care given to their host nestlings (Dearborn, 1998; Lichtenstein and Sealy, 1998; Woodward, 1983). Mechanistically, superior competing abilities of cowbird nestlings over hosts for foster-parent care have been attributed to the parasites' louder and more intensive begging (Briskie et al., 1994; Broughton et al., 1987; Dearborn, 1998, 2000; Lichtenstein and Sealy, 1998; Woodward, 1983) and larger size (Hosoi and Rothstein, 2000; Lorenzana and Sealy,

1999). Larger size also causes additional reduction of host broods owing to trampling or displacement of nestmates (Dearborn, 1996; Hosoi and Rothstein, 2000; Lorenzana and Sealy, 1999). The size advantage of cowbird nestlings, in turn, may be owing to (1) female cowbirds' preferential parasitism of smaller and slower growing host species and/or (2) the earlier hatching of cowbirds compared to host eggs (i.e., hatching asynchrony). Again, many of these mechanisms are present in other brood parasitic species (Davies, 2000, Ortega 1998).

A previous meta-analysis showed that adult host mass (a surrogate measure of nestling size and growth rate, assuming that cowbird sizes and growth rates do not vary when raised by different host species) was negatively correlated with the extent of brood reduction in the presence of cowbird parasitism (Lorenzana and Sealy, 1999). This implied that, as already seen in experimental studies for a few taxa (Dearborn, 1998; Lichtenstein and Sealy, 1998), the relatively larger size of parasitic versus host nestlings was an important factor for the loss of host nestlings across several species (Lorenzana and Sealy, 1999). However, there has been no quantitative comparative examination of the hypothesis that the extent of hatching asynchrony between parasites and their hosts is positively related to the magnitude of the reduction of hosts' own broods when the hosts care for parasitic young (Hosoi and Rothstein, 2000; Ortega and Ortega, 2000). Also, to establish the causal relationship between hatching asynchrony and brood loss owing to parasitism requires experimental approaches.

The function of hatching asynchrony (HA) has been the subject of dynamic debates and intensive research effort (e.g., Clark and Wilson, 1981; Clotfelter and Yasukawa, 1999; Price and Ydenberg, 1995; Stoleson and Beissinger, 1995; Viñuela, 2000). It appears that within clutches, both naturally occurring HA and experimentally induced HA contribute to brood reduction, especially when resources provided by parents are limited or not easily divisible (Mock and Parker 1997). Most studies have concentrated on intraspecific HA, that is, HA that results from different hatching dates of eggs laid in the same clutch by the same female. Intraspecific HA is typically caused by the onset of incubation by laying females before completion of their clutches leading to the later hatching of last-laid eggs (Clotfelter and Yasukawa, 1999).

In contrast, interspecific HA is owing to the different developmental rates and, hence, hatching dates of eggs laid by different species in the same nest. Interspecific HA occurs in many nests parasitized by obligate brood parasites, in which the parasitic eggs typically hatch up to several days earlier than do the host eggs (Davies, 2000). The shorter incubation period of parasitic eggs relative to maternal body size is the result of natural selection for the faster development and earlier hatching of parasitic eggs compared with the rest of the host's clutch (Briskie and Sealy, 1990; Kattan, 1995; Krüger and Davies, 2002). Although the patterns of intra- and interspecific HA are different, they both may lead to brood reduction of the original clutch (Emlen, 1941; Mayfield, 1960; McMaster and Sealy, 1999).

In my research, I used comparative data from the published literature on brood sizes of several hosts of brown-headed cowbirds to examine whether the incubation period of the foster species (a surrogate measure of cowbird-host HA, assuming that cowbird incubation length does not vary when cared for by different host species) was a predictor of the reproductive costs (relative brood loss) associated with raising parasitic nestlings. In addition, I examined the costs of interspecific patterns of HA experimentally by simulating cowbird parasitism through the introduction of single, earlier-hatching parasitic or host eggs into nonparasitized clutches of

a common cowbird host, the eastern phoebe (*Sayornis phoebe*; Klaas, 1975; Rothstein, 1986), and by determining the extent of brood reduction after these manipulations.

MATERIALS AND METHODS

Comparative data set

Using data from this and published studies on the brood sizes of parasitized and nonparasitized host nests, I set out to examine the relationship between host incubation period and the cost of rearing cowbird young. In selecting these data, I relied heavily on the sample used by Lorenzana and Sealy (1999), but also expanded it with several recent studies. I used one data point for each host species by choosing a study that was based on the largest sample size and/or reported observations from parasitized nests that contained single cowbird nestlings only (Table 1). In this comparison, I only included information from clutches that were not lost in their entirety to predation (successful nests sensu Lorenzana and Sealy, 1999) and excluded unsuitable hosts of cowbirds, such as those feeding mostly a plant-based diet to their young (Kozlovic et al., 1996), because I was interested in the possible effects of the presence of cowbirds on host brood sizes owing to mechanisms internal to the nest (Dearborn, 2000). Although this restriction did not exclude all external causes of brood loss, such as partial clutch predation, it provided a data set that matched most closely the methodology followed in my experimental manipulation (see below). Life-history data for host species were obtained from Baicich and Harrison (1997), Hosoi and Rothstein (2000), and Lorenzana and Sealy (1999). Based on the results of Lorenzana and Sealy (1999), in my analyses I included host mass as an additional predictor of the cost of cowbird parasitism,

First, I examined whether the relationship between the dependent variable (the cost of interspecific brood parasitism) and the predictors (host incubation length and adult mass) could be confounded by events before the hatching of parasitic young (e.g., egg removal by female cowbirds, rejection errors of damaging/removing own eggs by the hosts). To this aim, I calculated the difference between the relative clutch sizes of parasitized and nonparasitized nests, using nonparasitized clutch size to standardize values as follows: (number of host eggs in parasitized nests − number of host eggs in nonparasitized nests)/typical clutch size of host species. I used a multiple linear regression with the [log $(X + 1)$]-transformed values of the relative clutch size against host incubation length and adult female mass. This preliminary analysis revealed no statistical relationship between the relative number of host eggs found in parasitized versus nonparasitized nests and either host incubation length ($p = .70$) or adult host mass ($p = .89$, $r^2 = .013$, $N = 15$ host species from Table 1 for which data were available from the literature).

Then, to examine the overall cost of parasitism (i.e., owing to factors during and subsequent to the hatching of parasitic chicks), I calculated a relative (standardized) cost value for each species by taking the difference between the reported mean brood sizes (number of host nestlings/nest at the age of the nestlings that was the last feasible point at which brood size could be measured without causing premature fledging) with and without cowbirds, and dividing it by the typical clutch size of that species. I again used a multiple linear regression with the log-transformed values of this cost of parasitism against host incubation length and adult female mass. Because the preliminary analysis of relative clutch sizes showed no relationship with either incubation length or host mass, a statistical effect between this second overall measure

Table 1.

Information on the brood sizes (i.e., number of host nestlings) of parasitized and nonparasitized nests of host species of brown-headed cowbirds from the published literature (see Methods)

English name	Group	Nest type	Adult mass (g)	Clutch size	Incubation (days)	Nonparasitized nestlings	Parasitized nestlings	Cost of parasitism
Willow flycatcher[a]	Others	Open cup	13.7	3.5	12.5	2.750	2.160	0.169
Eastern phoebe[b]	Others	Cliff open cup	19.8	5.0	15.0	4.620	0.667	0.791
Red-eyed vireo[c]	Others	Open cup	16.7	4.0	12.5	2.940	0.900	0.510
Solitary vireo[d]	Others	Open cup	16.6	4.0	15.0	2.140	0.520	0.405
Wood thrush[e]	Others	Open cup	47.4	3.5	13.0	2.940	2.070	0.249
California gnatcatcher[f]	Others	Open cup	6.0	4.0	14.0	2.900	0.000	0.725
Chestnut-collared longspur[g]	Finches	Open cup	18.9	4.0	12.0	3.610	3.500	0.028
Northern cardinal[h]	Finches	Open cup	37.6	3.5	12.0	2.000	1.920	0.023
Blue grosbeak[i]	Finches	Open cup	30.4	4.0	12.0	3.500	1.700	0.450
Indigo bunting[j]	Finches	Open cup	14.1	3.5	12.5	2.800	1.600	0.343
Painted bunting[k]	Finches	Open cup	13.0	3.5	11.5	2.400	1.500	0.257
Dickcissel[l]	Finches	Open cup	24.6	4.0	12.0	3.271	1.916	0.339
Yellow warbler[m]	Wood warblers	Open cup	9.2	4.5	11.0	3.230	2.500	0.162
Common yellowthroat[n]	Wood warblers	Open cup	9.9	4.0	12.0	3.321	1.854	0.367
Yellow-breasted chat[i]	Wood warblers	Open cup	23.3	4.0	11.5	2.900	2.300	0.150
Prothonotary warbler[o]	Wood warblers	Cavity	17.4	5.0	13.0	4.200	3.300	0.180
Ovenbird[e]	Wood warblers	Open cup	19.4	4.5	12.5	4.160	2.000	0.480
Louisiana waterthrush[p]	Wood warblers	Open cup	20.8	5.0	13.0	5.200	2.290	0.582
Grasshopper sparrow[g]	Sparrows	Open cup	17.0	4.5	11.5	3.720	2.400	0.293
Baird's sparrow[g]	Sparrows	Open cup	17.5	4.0	11.5	3.250	1.810	0.360
Lark sparrow[q]	Sparrows	Open cup	29.0	4.5	12.0	3.200	2.250	0.211
Dark-eyed junco[r]	Sparrows	Open cup	18.8	4.0	12.5	2.700	1.500	0.300
Song sparrow[s]	Sparrows	Open cup	20.5	4.0	13.0	3.874	2.667	0.302
Savannah sparrow[g]	Sparrows	Open cup	20.0	4.5	10.0	2.560	0.330	0.496
Field sparrow[t]	Sparrows	Open cup	12.5	4.0	10.5	3.400	2.500	0.225
Black-throated sparrow[u]	Sparrows	Open cup	14.0	3.5	12.0	1.600	0.20	0.114
Red-winged blackbird[v]	Blackbirds	Open cup	52.6	4.0	11.0	2.720	1.780	0.235
Bobolink[g]	Blackbirds	Open cup	42.0	5.5	12.0	4.000	4.000	0.000
Western meadowlark[g]	Blackbirds	Open cup	100.7	5.0	14.0	3.000	2.250	0.150
Brown-headed cowbird	Blackbirds		41.7		10–11			

Adult mass is given as adult female mass, when different from male mass.

[a] Whitfield in Lorenzana and Sealy, 1999.

[b] This study.

[c] Southern in Lorenzana and Sealy, 1999.

[d] Chace et al., 2000.

[e] Donovan et al. in Lorenzana and Sealy, 1999.

[f] Braden in Lorenzana and Sealy, 1999.

[g] Davis and Sealy, 2000.

[h] Eckerle and Breitwisch, 1997.

[i] Whitehead et al., 2000.

[j] Burhans et al., 2000.

[k] Whitehead et al., 2000.

[l] Zimmerman combined from Lorenzana and Sealy, 1999.

[m] Goossen and Sealy in Lorenzana and Sealy, 1999.

[n] Spautz, 1999.

[o] Petit, 1991.

[p] Eaton in Lorenzana and Sealy, 1999.

[q] Newman from Lorenzana and Sealy, 1999.

[r] Wolf, 1987.

[s] Cavalcanti combined from Lorenzana and Sealy, 1999.

[t] Burhans et al., 2000,

[u] Johnson M and van Riper C, personal communication.

[v] Røskraft et al., 1990.

of the cost of parasitism and the predictor variables would necessarily imply that there is a relationship between the cost of parasitism and the presence of a cowbird nestling per se owing to variation in either host incubation length and/or mass. Again, each species contributed a single data point to the analysis, and there was no relationship between the predictor variables themselves ($p = .42$, $r^2 = .02$, $N = 29$).

I used a post hoc test on the distribution of residual values from the multiple regression to examine potential phylogenetic confounds. I chose this methodology because the taxa in

the analysis were mostly drawn from among New World wood warblers and sparrows, and recent molecular studies showed that species-, genus-, and subfamily-level phylogenetic hypotheses for these two groups are only weakly supported (Klicka et al., 2000; Lovette and Bermingham, 1999). Nonetheless, I also calculated a set of independent contrast scores by using a specific phylogenetic hypothesis (data not shown). Even so, unstable phylogenetic trees weaken the conclusions drawn from comparative methods (e.g., using independent contrasts or pairwise comparisons; Hosoi and Rothstein, 2000), because these analytical tools are sensitive to changes in the classification of sister taxa.

Observations and experimental manipulations

Study species and site
Eastern phoebes (hereafter phoebes) are small insectivorous migrant birds in North America that often breed in close association with human settlements (Hauber, 2002; Weeks, 1978). Phoebe clutches have moderate levels of intraspecific hatching asynchrony, typically less than 1 day (Murphy, 1994). In contrast, parasitized phoebe clutches have substantial interspecific HA, as the incubation period of cowbirds is about 5 days shorter than that of phoebes (Hauber ME, personal observation; Lowther, 1993; Weeks, 1994).

In 2000 and 2001, I monitored nesting activities of phoebes in and around Ithaca, New York. Before the onset of breeding (typically late April or early May at this site) I checked for evidence of nest building and repair once a week (for details of the study site, public outreach efforts, and general methods, see Hauber, 2001). In short, during the egg-laying period, I monitored each nest at least once every 48 h. I noted the number of phoebe and cowbird eggs and nestlings at each visit. Nests lost because of predation or inclement weather were excluded from all analyses. Phoebes were not color-banded for individual identification, and data from each site and nesting attempt were considered single data points in the analyses, because I assigned experimental treatments haphazardly based solely on nests' availability. Therefore, I did not have a priori expectations of interaction-bias between the environmental or genetic differences and the manipulative treatments across phoebe nests. Also, all statistical tests were two-tailed.

Reproductive measures
Every first, and some second, breeding attempts of phoebes were left undisturbed in 2000 and used to obtain data on nonmanipulated brood sizes in parasitized and nonparasitized nests. Where and when logistically possible (Hauber, 2001), I examined the presence of unhatched phoebe eggs by counting the number of unhatched eggs at more than 2 days after the predicted hatching dates. For these nests I also calculated egg-to-nestling survival rates by dividing the number of 5-day-old phoebe nestlings with the number of phoebe eggs at clutch completion. I used clutch-size data from subsequent visits and assumed that a single egg is added each day (whether it be a phoebe or cowbird egg; Hauber ME, personal observation; Weeks 1994) to calculate clutch completion dates for each study nest. This was a valid assumption because the daily increase in total clutch size for those nests that were visited on two subsequent days during the laying cycle was close to 1.0 (mean change $\pm$ SE, 0.95 $\pm$ 0.067 eggs/day; one-sample t test, $p > .47$, $N = 15$ daily visits). In turn, I used these data to determine predicted hatching dates for each clutch as completion date + 15 days (Baicich and Harrison, 1997; Hauber ME, personal observation; Weeks, 1994).

Induction of HA
Some second nesting attempts in 2000 and first and second nesting attempts in 2001 were used for clutch manipulation experiments in which I removed either a single cowbird or phoebe egg from each manipulated nest and replaced it with a different phoebe or cowbird egg from another nest. Because several nests were lost owing to stormy weather and flooding streams, some clutches ($N = 5$) received a hatchling parasite or host chick (less than 1 day old) instead of an early hatching egg. In 2001, by using second nesting attempts only, I also examined the potential effect of experimentally introduced size difference among phoebe nestlings on brood reduction. In these manipulations, I introduced a single known-age phoebe nestling from a separate nest on the predicted day of hatching of the original brood and examined brood sizes 5 days later.

I transferred phoebe and cowbird eggs and chicks when they were available for manipulation within my study population to aim for experimental HA or age difference that varied between 0–6 days. These values are within the range of HA observed for nonparasitized (0–1 days) and parasitized phoebe nests (5–6 days, Hauber ME, personal observations). To ascertain that experimentally induced early hatching took place, I checked each manipulated nest within 48 h of the predicted hatching dates and determined actual HA. Because the actual variation of HA (-2–10 days) was greater than the natural range, I used regression analyses to examine the effects of experimentally induced HA and age difference on brood reduction. By using this method of analysis, nests with 0-day HA became experimental controls. Comparisons of the extents of brood reduction in naturally nonparasitized and experimental 0-day HA nests revealed no significant differences, indicating that the cross-fostering treatment alone did not have an effect (see Results).

In this second portion of the study, the cost of brood parasitism was quantified as follows: $\{1 - [\text{the number phoebe nestlings present on day 5 after predicted hatching date (day 0)/the number of intact phoebe eggs present at clutch completion}]\}$. Using this measure of phoebe clutch size in the calculations excludes the effect of female parasites' activities on clutch sizes (e.g., host selection, egg-pecking, and egg-removal). Also, I decided on using the number of 5-day-old host nestlings to estimate this proportional measure of brood reduction because, as before, I was interested in the possible effects of the presence of cowbirds on host brood sizes owing to mechanisms internal to the nest (Dearborn, 2000): as cowbirds both hatch and fledge at approximately 5 days earlier than do phoebes (Lowther, 1993; Weeks, 1994), surviving host nestlings would be about 5 days old when parasitic chicks leave the nest (Hauber ME, personal observation). After fledging by the parasite, other factors (e.g., survival of fledgling cowbirds, brood partitioning by host parents) may interact with, confound, or mask the potential effects of host-parasite HA. Nonetheless, in this study population, the number of 5-day-old phoebe nestlings closely matched the number of 10- and 15-day-old phoebe nestlings ($p < .0001$, $r_{Spearman} = .88$, $N_{10-5\ days} = 29$ breeding attempts; and $p = .023$, $r_{Spearman} = .72$, $N_{15-5\ days} = 11$ breeding attempts). I did not determine the extent of natural HA in nonmanipulated clutches or within the original clutches in manipulated nests, but I did examine hatching failure of phoebes' eggs as indicated above for nonmanipulated nests.

Ethical considerations
Observations and experimental manipulations at nests of eastern phoebes did not cause the abandonment of already established nests, probably because all the nests used in this

study were built near sites of frequent human activities. During transportation of eggs and nestlings, three phoebe and two cowbird eggs were destroyed accidentally, but all cross-fostered eggs and nestlings were accepted by the foster parents. Although this study undeniably introduced stress and mortality to some nonparasitized clutches, the sample sizes were kept small to minimize these effects. Also, other aspects of my research on phoebes and cowbirds alleviated the population-level detrimental impacts of these experiments, because in several separate studies, I removed early-hatching parasitic eggs and nestlings for hand-rearing in the laboratory (see Hauber et al., 2000, 2001).

RESULTS

Comparative data set

The analysis of relative brood sizes from parasitized and nonparasitized host nests, standardized by clutch size, showed that this overall measure of the cost of cowbird parasitism was positively associated with hosts' incubation period ($p = .0030$; Figure 1A) and negatively associated with adult mass ($p = .026$; Figure 1B): Log cost $= 0.60 - 0.070 \times$ incubation period $+ 0.003\times$ host mass (overall $p = .0034$, $r^2 = .31$, $N = 29$). The residual values of cost calculated from this regression analysis were randomly associated between species from the different taxonomic groups included in this analysis ($F = 0.31$, df $= 4,26$, $p = .87$, ANOVA). This suggests that no single group of closely related host taxa biased or contributed disproportionally to these conclusions. Accordingly, by using independent contrast scores (data not shown) in a multiple regression analysis I found that the relationships of the cost of parasitism with both incubation length ($p < .0001$) and host mass ($p = .0010$) remained consistent: log cost score $= 0.67 - 0.075 \times$ incubation period $+ 0.003 \times$ host mass (overall $p < .0001$, $r^2 = .57$, $N = 28$).

Overall, for the species included in these analyses, incubation lengths were longer and adult host masses were lower than those of the brown-headed cowbird (both $p < .0001$, one-sample Wilcoxon signed-rank tests; Table 1.).

Observations and experimental manipulations

For nonmanipulated broods during the first breeding attempts in 2000, the number of phoebe eggs that were found unhatched more than 2 days after their predicted hatching dates was greater in parasitized (0.60 ± 0.21, eggs $N = 15$) than in nonparasitized nests (0 ± 0, eggs $p < .001$, $N = 27$, Mann-Whitney test), but was not related to the number of cowbird eggs present at clutch completion in parasitized nests ($p > .83$, $r_{Spearman} = .22$, $N = 9, 3,$ and 3 parasitized nests with 1, 2, and 3 cowbird eggs/clutch, respectively).

There was no difference between phoebes' egg-to-chick survival rates for nonmanipulated first and second nesting attempts in either naturally parasitized or nonparasitized clutches in 2000 ($p = .88$ and $p = .46$, respectively, Mann-Whitney tests; for sample sizes, see Figure 3), therefore data from first and second clutches were pooled. Phoebe survival in naturally parasitized nests was negatively correlated with the number of cowbird nestlings reared in the nest ($p < .005$, $r_{Spearman} = -.78$, $N = 14$); specifically no phoebes survived in nests containing two or three cowbird nestlings ($N = 3$ and 2 parasitized nests, respectively).

By cross-fostering earlier hatching cowbird and phoebe eggs, I induced hatching asynchronies of -1 to 10 days with most introduced eggs hatching between 0 and 7 days earlier than the predicted hatching date of the original clutch (3.30 ± 0.54 days; Figure 2A,B). The proportion of unhatched

A

B
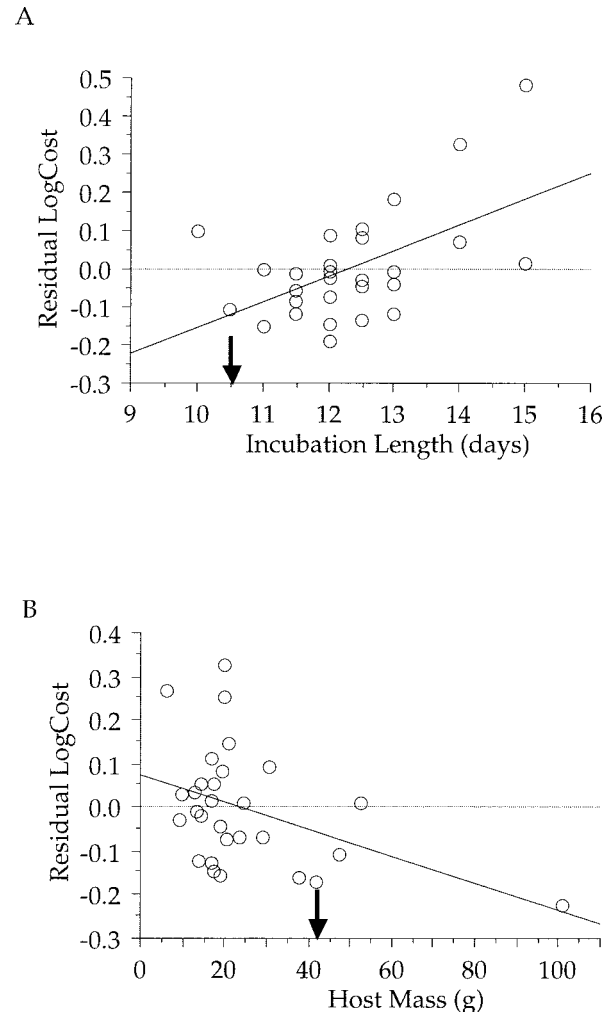
Figure 1
The relationships between the calculated costs of brood parasitism with cowbird hosts' incubation lengths (A) and adult host masses (B). Increasing y-axis values indicate increasing residual cost values that were taken from a simple regression analysis of log-transformed cost with host mass (A) and incubation length (B), respectively. Linear regression lines are indicated, and arrows point to the attributes of brown-headed cowbirds.

phoebe eggs (relative to the number of phoebe eggs at clutch completion) tended to be greater for clutches with increased HA with either earlier hatching cowbirds ($p = .051$, $r_{Spearman} = .80$, $N = 7$) or earlier hatching conspecifics ($p = .025$, $r_{Spearman} = .40$, $N = 31$). The extent of experimental HA was also related the cost of parasitism in manipulated nests: the introduction of earlier-hatching cowbirds or conspecific nestlings increased proportional brood loss of the original phoebe clutch (cowbirds: $p = .010$, $r_{Spearman} = .91$, $N = 7$; phoebes: $p < .0001$, $r_{Spearman} = .99$, $N = 32$; Figure 2A,B). To the contrary, introducing older conspecific nestlings into nonparasitized host broods on the day of hatching did not increase brood loss ($p > .66$, $r_{Spearman} = .12$, $N = 13$): only in one brood was there hatchling mortality after the introduction of a 6-day-old phoebe nestling (Figure 2C).

By using log-transformed values, I found that the species-identity of the cross-fostered earlier hatching eggs (i.e., cowbird versus phoebe) was a significant predictor of the cost of parasitism in host nests when the positive effect of

A

B

C
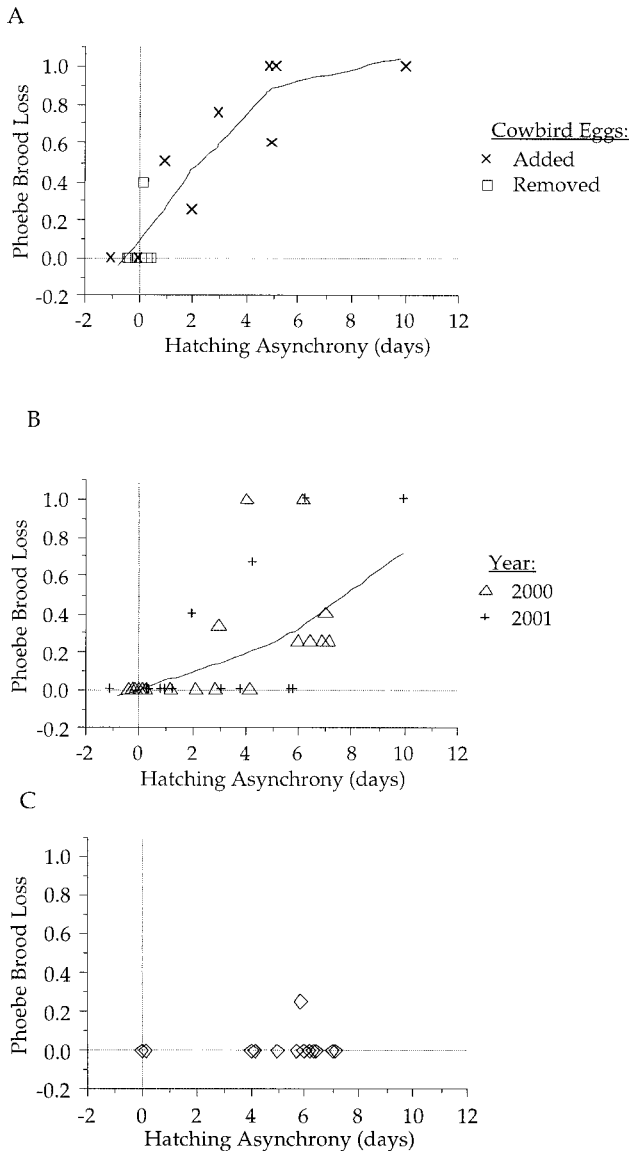
Figure 2
The relationship between eastern phoebes' brood losses (i.e., a cost of parasitism calculated as 1 − [egg-to-nestling survival rates of the original clutch to 5 days after hatching]) and the hatching asynchronies (in days) caused by experimentally replacing single brown-headed cowbird eggs (A) or single conspecific eggs (B) before hatching, and older conspecific nestlings (C) on the day of hatching. Brood losses in naturally parasitized phoebe nests from which cowbird eggs were removed for cross-fostering are also included in A. For illustrative purposes, data points with the same x-axis measures are scattered.

experimentally induced HA was taken into consideration ($F = 28$, df = 1,38, $p < .0001$): proportional brood loss was greater for cross-fostered cowbird eggs than for phoebe eggs ($F = 9.7$, df = 1,38, $p = .0036$). Also, proportional brood loss increased with greater experimental HA ($F = 16$, df = 1,42, $p = 0003$), and when earlier-hatching phoebe eggs versus older phoebe nestlings were introduced before versus on the day of hatching, respectively ($F = 11$, df = 1,42, $p = .0023$). I also calculated a linear regression equation for the earlier hatching conspecific egg-treatment: log nestling survival = 0.31 - 0.020 × hatching asynchrony (by phoebe nestling, in days; overall $p = .0005$, $r^2 = 0.32$, $N = 31$).

Phoebe survival rates in nonmanipulated nonparasitized nests in 2000 were similar to values predicted by this linear regression equation derived from the HA experiment in 2000 (using 0 days for HA, $p = .28$, $N = 31$; Figure 3), whereas phoebe survival in naturally parasitized nests was consistently lower than predicted by this model (using 5 days for HA, $p = .016$, $N = 11$, one-sample Wilcoxon signed-rank tests; Figure 3).

DISCUSSION

Comparative analyses of a sample of host species of brown-headed cowbirds showed that the extent of host-parasite hatching asynchrony was positively correlated with the cost of interspecific brood parasitism (measured as the relative extent of the hosts' brood losses between parasitized and non-parasitized clutches). This effect was statistically significant when the relatively larger size of cowbird nestlings compared with host nestmates was included as an independent predictor of the cost of parasitism, and phylogenetic relationships between the sampled taxa did not bias this conclusion. Experimental manipulation of hatching asynchrony in clutches of eastern phoebes also revealed that reproductive cost borne by foster parents for raising parasitic young (measured as the proportional loss of the original brood) was increased by greater HA. Brood loss was caused by the cross-fostering of either earlier-hatching cowbird or phoebe eggs, but not of older phoebe nestlings on the day of hatching, indicating that interspecific patterns of HA alone can be causal factors in lowering the reproductive output of parasitized broods. These data support the hypothesis that HA between parasitic and host young contributes to the reproductive costs caused by interspecific brood parasitism.

Despite the experimental evidence from manipulated phoebe nests, it is nonetheless possible that the apparent correlation between the cost of parasitism and host incubation length in the comparative data set was influenced by factors not included in the multivariate analysis. For example, Lichtenstein (2001) suggested that higher rates of host chick survival in nests of larger cowbird hosts were related not only to the better competitive abilities of host chicks versus parasites but also to the better abilities of foster parents in larger species to discriminate their own and the parasitic chicks. She based this prediction of better discrimination of chicks by hosts on her finding that, unlike smaller foster parents, larger hosts preferentially feed their own and not the parasitic young. Currently there are no published data to evaluate this "size-dependent discrimination" hypothesis in the hosts of brown-headed cowbirds.

Also, the cost of cowbird parasitism in this study was approximated by various measures of the extent of hosts' brood reduction in parasitized versus nonparasitized clutches. Brood reduction in nonparasitized clutches is typically attributed to sibling competition (including siblicide; Mock and Parker, 1997) and food limitation (Stoleson and Beissinger, 1995). If these factors should be related to, or interact with, incubation length and the probability of cowbird parasitism in host taxa, it is likely that this would lead to the finding of a statistical correlation between hatching asynchrony and cowbird parasitism. However, this possibility was reduced in the comparative analysis by using data on pairwise comparisons of parasitized versus nonparasitized brood sizes from sympatric populations of hosts.

Although interspecific patterns of HA decrease reproductive success in eastern phoebes, the exact mechanism by which earlier hatching influences the survival of later hatching nestmates remains unclear. Experimentally introduced earlier-hatching phoebe and cowbird eggs and nestlings in this
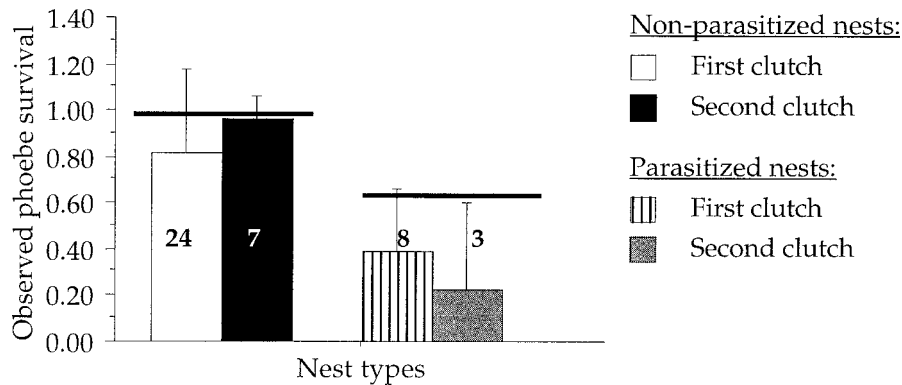
Figure 3
Observed egg-to-nestling survival rates (i.e., $1 -$ cost of parasitism from Figure 2) in nonmanipulated nests of eastern phoebes in 2000 (mean + SD). Horizontal lines indicate predicted values for nonparasitized and parasitized nests derived from a regression model based on transformed 2000 experimental values from Figure 2B. Sample sizes are indicated for each bar, and data for parasitized nests are taken only from clutches with single cowbirds.

study were all accepted, attended, and fed by foster parents. The acceptance of prematurely hatching conspecific and parasitic young by foster parents is not unique to phoebes (see Emlen, 1941; McMaster and Sealy, 1997), and may reduce the efficiency of incubation of the rest of the clutch by the brooding parent, leading to a decrease in the hatching success or hatchling condition of the original brood (McMaster and Sealy, 1999). In support of this possibility, I observed unhatched phoebe eggs only in naturally parasitized clutches and in those experimental clutches that had several days of HA.

However, small-to-moderate levels of experimentally induced HA (less than 7 days) alone did not prevent hatching failure of all of the original eggs. Nevertheless, those nestlings that managed to hatch were clearly smaller than the earlier hatched experimentally introduced nestmate. An older *and* larger nestling may be able to position itself within the nest and/or beg in a manner that results in competitive superiority for parental resources (e.g., preferential feeding by the parents; Dearborn, 1998; Lichtenstein and Sealy, 1998). This, in turn, may have caused the undernourishment and the eventual starvation of additional younger nestmates. Data from my experiments, however, do not support this possibility because the introduction of older and larger phoebe nestlings on the day of hatching of the original brood did not cause brood reduction even when the age difference reached 5–7 days (Figure 2C). To evaluate this "competitive asymmetry" hypothesis fully requires the monitoring of both pre- and posthatching development of the original brood, competitive interactions between nestmates, and parental feeding decisions (e.g., following the methodology of Dearborn, 1998; Lichtenstein and Sealy, 1998).

Whatever the exact mechanism, the extent of the cost of cowbird parasitism in manipulated and nonmanipulated phoebe nests was not explained solely by HA. Specifically, the cost of raising an earlier hatching conspecific consistently underestimated levels of brood reduction in both experimentally and naturally parasitized nests (Figures 2 and 3). This suggests that features of parasitic young other than earlier hatching also contribute to the reproductive costs of cowbird parasitism. For example, cowbird hatchlings are larger and grow more rapidly than do many hosts, such as phoebes (Lowther, 1993; Weeks, 1994). Accordingly, in addition to host incubation period, adult host mass was also an independent significant predictor of the cost of parasitism in the multiple regression analysis (Figure 1B). This result supports previous work that documented a negative relationship between adult host mass and the cost of parasitism but did not include incubation length as a co-variate in the analysis (Lorenzana and Sealy, 1999).

Yet other studies suggest that cowbird nestlings, like other

brood parasites that are reared with host nestmates (Soler et al., 1995), appear to be superior competitors for eliciting and receiving care from the foster parents than smaller host young (in eastern phoebes: Hauber, 2003; Woodward, 1983; in indigo buntings [*Passerina cyanea*]: Dearborn, 1998; and in yellow warblers [*Dendroica petechia*]: Lichtenstein and Sealy, 1998). These conclusions held true even when the effect of the difference between host and cowbird nestling mass and age were controlled for. Yet, cowbirds do not appear to be superior competitors for parental provisioning compared to host chicks when position relative to the feeding parent is also taken into consideration (Dearborn and Lichtenstein, 2002) or when competing with nestlings of larger hosts that also have shorter incubation lengths (Clotfelter and Yasukawa, 1999; Eastzer et al., 1980; Ortega and Cruz, 1991; Peer and Bollinger, 1997). Taken together, these observations suggest that, in addition to HA, the more intensive begging behavior of cowbirds also leads to preferential feeding by foster parents in nests of some host species (Hauber 2003) and, thus, contributes to the full extent of competitive failure and eventual demise of smaller and/or slower developing host nestlings.

Finally, on a few occasions, cowbird nestlings have been observed or assumed to have displaced foster siblings (Dearborn, 1996), even though this behavior is clearly not as frequent or predictable as the infamous behavioral adaptations typical of young *Cuculus* cuckoos that eject host nestmates and eggs (Davies, 2000). Nevertheless, the greater ease of displacement and/or competitive asymmetries between larger cowbird and smaller host chicks may be an important epiphenomenon of cowbirds' preferential parasitism of hosts that build open-cup nests rather than cavity nests (Burhans et al., 2000; Lowther, 1993; Ortega, 1998; Ortega and Ortega, 2000; Table 1.). For example, on the sudden departure of a brooding parent on two occasions during my nest visits, I saw small phoebe nestlings fall to the ground from a nest that appeared to be overcrowded by a large earlier-hatched experimental and two smaller naturally hatched nestmates.

Overall, the comparisons across host species and the reported experimental data indicate that hatching asynchrony between parasitic and host nestlings contributes to the costs paid by foster parents of brown-headed cowbirds. Specifically, more extensive HA increases brood loss of the original host clutch, in part because of greater hatching failure of host eggs in eastern phoebe nests. However, the full cost of cowbird parasitism cannot be explained by HA alone. Attributes of cowbird nestlings that have not been manipulated by these experiments (e.g., their larger size, greater growth rate, more intense begging responses versus host nestmates), and perhaps nest architecture that favors positional asymmetry,

may further contribute to the loss of reproductive output from parasitized broods of phoebes and probably of other smaller host species of nonevictor interspecific brood parasites.

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