What are the costs of raising a brood parasite? Comparing host parental care at parasitized and non-parasitized broods

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Abstract. Young obligate brood parasitic birds impose a cost on their hosts by exploiting care from unrelated foster parents. While raising parasitic young is detrimental to hosts' fitness because it reduces the clutch size and the fledging success of the original brood, the potential relationship between parental care provided for parasitized broods and foster parents' future reproductive output remains poorly understood. Using video-recordings of eastern phoebe (*Sayornis phoebe*) nests, a proportion of which were naturally parasitized by brown-headed cowbirds (*Molothrus ater*), we quantified and compared different aspects of parental behaviors of this common host species. We found that nest attendance rates, but not brooding, were positively related with the total number of nestlings (brood size) and the proportion of cowbirds reared in a brood (parasite load). However, phoebes' parental behaviors were not related to cowbird parasitism *per se* probably because parasitized broods overall contained fewer nestlings than did non-parasitized broods. Based on our correlational data we estimate that phoebe parents deliver 3.6 times greater parental effort to raise a parasitic cowbird chick than one of their own offspring. Differences in parental care provided for varying brood sizes and parasite loads may provide a mechanism to explain how raising brood parasitic young is related to reduced residual reproductive effort in Eastern phoebes and perhaps in other host species.
Key words: brood parasitism, coevolution, clutch size, laying date, manipulation, parental care.

Resumen. *¿Cuáles son los costes de criar un parásito de puesta? Comparación del coste del cuidado parental en nidadas parasitadas y no parasitadas.* Los pollos de las aves parásitas de cría obligadas imponen un coste sobre sus hospedadores explotando el cuidado de padres adoptivos no emparentados con ellas. Aunque la cría de pollos parásitos es negativa para la eficacia de los hospedadores, porque reduce el tamaño de puesta y el éxito de los volantones de la nidada original, las relaciones potenciales entre el cuidado parental proporcionado a las nidadas parasitadas y el éxito reproductor futuro de los padres adoptivos permanecen poco estudiadas. Mediante registros de vídeo de nidos de *Sayornis phoebe*, una parte de los cuales fueron parasitados de forma natural por *Molothrus ater*, hemos cuantificado y comparado diferentes aspectos del comportamiento parental de esta común especie hospedadora. Hemos hallado que las tasas de atención a los nidos, pero no la cría, se relacionan positivamente con el número total de polluelos (tamaño de puesta) y la proporción de parásitos criados en la nidada (carga parasitaria). Sin embargo, los cuidados parentales del hospedador no se relacionaron con el parasitismo *per se*, probablemente porque las nidadas parasitadas en conjunto tuvieron menos pollos que las no parasitadas. A partir de nuestros datos correlacionales estimamos que los padres hospedadores dedican 3.6 veces más cuidado parental a criar un pollo del parásito, que uno de su propia descendencia. Las diferencias en el cuidado parental proporcionado a puestas de diferentes tamaños y cargas parasitarias pueden proporcionar un mecanismo para explicar cómo la cría de pollos parásitos se relaciona con un éxito reproductor residual reducido en *Sayornis phoebe* y quizás en otras especies de hospedadores.

Introduction

Nestlings of interspecific brood parasites, by definition, exploit their hosts because parasitic young rely entirely on care provided by foster parents without increasing these hosts' inclusive fitness (Payne, 1977; Davies, 2000). Surprisingly, the mechanism of how costly parental care (Clutton-Brock, 1991) received by unrelated parasitic young is related to foster parents' residual reproductive efforts remain poorly understood. This is in spite of many detailed studies and reviews that examined the extent of the fitness loss that foster parents pay to raise broods parasitized by different obligately parasitic species (e.g., common cuckoos *Cuculus canorus*: Brooke & Davies, 1989, Oien et al., 1998; great spotted cuckoos *Clamator glandarius*: Soler et al., 1995; village indigobirds *Vidua chalybeata*: Payne et al., 2001; shiny cowbirds *Molothrus bonariensis*: Massoni & Reboreda, 1998, brown-headed cowbirds *M. ater*: Ortega, 1998, Lorenzana & Sealy, 1999, Hauber, in press). In particular, there has been much interest and considerable progress toward a better description and understanding of the mechanisms by which parasitic nestlings exploit host behaviors (Dearborn, 1998; Lichtenstein & Sealy, 1998; Kilner & Davies, 1999; Kilner et al., 1999; Lichtenstein, 2001; Dearborn & Lichtenstein, 2002; Hauber, 2003). Other aspects of brood parasitic adaptations (e.g., egg-pecking and host-egg removal by parasitic females, hatching asynchrony between parasites and hosts, competition or displacement of foster siblings by parasitic nestlings, etc., Ortega, 1998) are also described by many researchers with regards to contribution of these traits to decreases of the hosts' current (parasitized) reproductive success (Lorenzana & Sealy, 1999; Massoni & Reboreda, 2002; Hauber, in press).

It is less well understood for species in which parasites do not remove or eject all nestmates (e.g., *Clamator* cuckoos, *Vidua* finches, and *Molothrus* cowbirds: Arias de Reyna, 1998; Davies, 2000) whether brood parasitism also imposes costs (e.g. reductions in survival from fledging to independence, rates of overwinter return, and, ultimately, lifetime reproductive success) onto those of the hosts' own young that do survive to fledge despite the presence of a parasitic nestmate. To date a handful of studies have not detected such detrimental effects (Smith, 1981; Payne & Payne, 1998; Sedgewick & Iko 1999).

It also remains unclear whether parasitized adult hosts themselves pay a cost of raising parasitized broods with regards to their own residual reproductive value (e.g., reductions in seasonal survival, probability of laying a second clutch, overwinter return rate, and subsequent reproductive effort; Lorenzana & Sealy, 1999). For some hosts, such as those of the common cuckoo, it has been shown that rearing a parasitic chick reduces the probability of second clutching within the same breeding season (Brooke & Davies, 1989), while the few published studies on the residual fitness value of adults that had served as hosts for brown-headed cowbirds (*Molothrus ater*) have not detected any significant effect of parasitism in three North American host species (Smith, 1981; Payne & Payne, 1998;

Sedgewick & Iko, 1999; Hauber, 2001). Understanding the different mechanisms that contribute to the fitness reducing effects of brood parasitism across the many host species is essential to predict the overall impact of parasitism on the life-time reproductive success of parasitized *vs.* non-parasitized hosts (Lorenzana & Sealy, 1999). Measures of the different costs of parasitism are also important both to conservation biologists who are developing management strategies for endangered populations of frequently parasitized hosts (Morrison et al., 1999; Smith et al., 2000) and to evolutionary biologists who are examining the selective pressures that influence the rates of evolution (or non-evolution) of host-defenses against parasitism (Rothstein, 1986; Rothstein & Robinson, 1998).

On the one hand, it is theoretically likely for many host species that obligate brood parasitism has detrimental effects on foster parents' residual reproductive effort (Lorenzana & Sealy, 1999). Empirically, for example, hatchlings of common cuckoos displace host eggs and do not require more food than a typical host brood (Kilner et al., 1999). Still, fledgling cuckoos exploit the care of their foster parents for a longer period than typically required by host fledglings (Brooke & Davies, 1989). Hence, cuckoo parasitism decreases the probability of initiating successful second nesting attempts within the same breeding season (Davies, 2000). Hatchling *Molothrus* cowbirds and *Clamator* cuckoos do not typically displace their nestmates, but they exploit parental care of their hosts by begging more intensively (Broughton et al., 1987; Briskie et al., 1994) and receiving disproportionally more of the food delivered to the nest than typical for host nestmates (Dearborn, 1998; Lichtenstein & Sealy, 1998; Soler et al., 1999). Hence, foster parental care for broods with parasitic cowbirds may be more intense and costly than for non-parasitized broods, though so far there are few data to support this possibility (Hauber, 2002).

On the other hand, cowbird eggs typically hatch earlier, nestlings grow faster, and fledglings leave nests earlier than do most host siblings (Ortega, 1998; Hauber, in press). In addition, the superior competitive abilities of cowbirds for parental care (e.g., food delivery: Briskie et al., 1994; Dearborn et al., 1998; Hauber, 2003) frequently lead to reduced host brood sizes, thus fewer total number of nestlings are raised by parasitized than non-parasitized parents (Lorenzana & Sealy, 1999). Therefore, it is also theoretically possible that cowbird parasitism *per se* does not impose greater costs on foster parents than raising a full brood of their own offspring (Kattan, 1996; Clotfelter, 1997; Kilpatrick, 2002). Indeed, a handful of previous studies have not demonstrated a strong relationship between parasitism by brown-headed cowbirds and the survival and residual reproductive value of host parents (Payne & Payne, 1998; Sedgewick & Iko, 1999). This is quite surprising because in some host species significant differences were found in aspects of parental behaviors (e.g., feeding, nest attendance, vigilance) at parasitized *vs.* non-parasitized nests (Uyehara & Narins, 1995; Dearborn et al., 1998, but see Clotfelter, 1997). An explanation to this paradox was recently proposed by Hauber (2001, 2002)

Table 1. Summary information on video-recordings at nests of eastern phoebes near Ithaca, NY, during the summer of 2000. Data for non-parasitized nests are based on 16 first nesting attempts. Data for parasitized nests are based on 14 total nesting attempts that include 8 first clutches from nesting sites that were only parasitized once per season and 2 clutches each from 3 additional sites that were parasitized on both nesting attempts. Age of oldest nestling represents the number of days after the hatching of either phoebe or cowbird nestlings in non-parasitized and parasitized nests, respectively.

Category (mean ± s.e.)	Non-parasitized nests	Parasitized nests
Nesting attempts	16	14
Recording sessions	25	36
Recording durations (min.)	82 ± 2.0	78 ± 3.5
Recording times (military hr.)	12 ± 0.49	12 ± 0.46
Age of oldest nestling (days)	9.6 ± 0.79	7.9 ± 0.47
Total recording duration (hr.)	34	47

who found that the absolute residual reproductive output (i.e., clutch size of second breeding attempts) of eastern phoebes (*Sayornis phoebe*) was not different between parasitized and non-parasitized hosts. However, when he calculated a relative measure of residual reproductive output (i.e., one that took into consideration the correlation between the clutch sizes of first and second broods within females), residual reproductive effort was indeed negatively related to both the overall brood size and the proportion of cowbird nestlings raised in parasitized broods (Hauber 2002).

In our study, using videotapes of parental activities at naturally parasitized and non-parasitized nests of eastern phoebes in Central New York, we sought to examine whether brood parasitism by brown-headed cowbirds was related to aspects of the reproductive behaviors of foster parents. Previous studies on phoebes demonstrated a large cost to parasitized hosts per reproductive bout: parasitized nests fledge about one phoebe nestlings compared to four phoebes in non-parasitized nests (Klaas, 1975; Hauber, 2001). Although cowbird eggs with their brown-speckles are clearly different in appearance from the almost clear white phoebe eggs (i.e., no mimicry, Weeks, 1994), phoebes do not appear to have evolved rejection of parasitic eggs (Rothstein, 1986; Hosoi & Rothstein, 2000). Currently, it is not clear whether and how phoebes modify different aspects of their parental behaviors in response to cowbird parasitism (Heinrich, 2000).

Methods

Study species

Brown-headed cowbirds (hereafter simply 'cowbirds') are the most numerous and widespread interspecific brood parasites in North America (Lowther, 1993). Cowbirds breed between late April and mid July in Ithaca, NY, and locally parasitize a wide variety of species, including flycatchers, thrushes, warblers, and sparrows (Hauber & Russo, 2000). One of their earliest hosts locally is the eastern phoebe (hereafter simply 'phoebe'), a species that has become a commensalist of human settlements and frequently nests on or near human-made structures, such

as under eaves and bridges (Weeks, 1994). We only studied nests placed on artificial substrates (Hauber, 2001). Near Ithaca, NY, cowbirds parasitize 37% of the phoebes' first nesting attempts (n=110, 1999-2000 combined). For a more detailed description of the study site and general methods, see Hauber (2001).

Breeding parameters

We estimated the clutch size in each nest for each breeding attempt by adding the total number of phoebe and cowbird eggs per clutch because we assumed that each cowbird egg was laid in lieu of a removed phoebe egg (Klaas, 1975; Hauber, 2002). For this portion of the study, we included data from both videotaped and non-videotaped nests (see below) that were monitored in our study population during 2001. We calculated clutch completion dates by monitoring clutch size during the laying period once every <5 days and assuming a rate of a single egg laid per day (Weeks, 1994; Hauber, 2001). 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±S.E: 0.95±0.067 eggs/day, one-sample t test, P>0.47, n=15 daily visits by MEH). For first nesting attempts we also determined brood sizes by establishing the number of cowbird and phoebe chicks that survived to 5 days of age after their respective hatching dates (Table 2). We used the number of 5 day old nestlings to estimate brood size because cowbirds both hatch and fledge at approximately 5 days earlier than phoebes (Lowther, 1993, Weeks, 1994), and so surviving host nestlings would be about 5 days old when parasitic chicks leave the nest (Hauber, 2001, 2002). Also, in our study populations, the number of 5 day old phoebe nestlings closely matched the number of 10 day and 15 day old phoebe nestlings in ($r_{Spearman}$=0.88, P<0.0001, n=29, and $r_{Spearman}$=0.72, P=0.023, n=11 breeding attempts, respectively). We calculated parasite load as the proportion of cowbird nestlings per brood size 5 days after the predicted hatching date of host eggs.

Video recordings

To examine parental behaviors of eastern phoebes during

Table 2. Comparison of breeding parameters of observed non-parasitized and parasitized eastern phoebe nesting attempts near Ithaca, NY, during the breeding season of 2000.

	Non-parasitized first clutches	Parasitized first clutches	t-statistic	P[1]
Count of active nests	31	14		
Clutch completion dates (May 1, 2000 = day 1)	9.5 ± 1.5	10 ± 2.6	0.33	0.75
Clutch sizes (total eggs)	4.8 ± 0.13	5.1 ± 0.23	1.2	0.23
Cowbirds eggs	0	1.6 ± 0.23		
Brood size (total nestlings)[1]	4.6 ± 0.17	2.4 ± 0.20	7.8	< 0.0001
Cowbird nestlings	0	1.4 ± 0.25		

[1] Probability remains below α-level even after Bonferroni corrections ($\alpha_{corrected} = 0.01$)

the nestling stage, we made video-recordings of a subset of all known nesting attempts within our study site: 16 non-parasitized and 11 parasitized phoebe nest sites were observed at least once during the nestling stage (Table 1). Nests choice for monitoring was haphazard because we were limited by the number of concurrently available video recorders and the duration of battery power. On average, more recording sessions were conducted at parasitized (2.6) than non-parasitized (1.6) nests (Table 1). We made recordings during only first breeding attempts for all non-parasitized nests and during the first breeding attempts for 8 parasitized nests which were not parasitized during their second breeding attempts. We also made recordings during both first and second breeding attempts for 3 additional nest sites that were parasitized repeatedly (Table 1). We assumed that our methods did not introduce a bias into our observations in a consistent manner regarding our hypotheses because the same opportunistic criterion (i.e., the shortest driving distance to an active phoebe nest located on private property) was used to select the time and the location of both parasitized and non-parasitized nests for monitoring. We also tested for potential confounds (e.g., the variability in total duration of recordings per site, seasonality, time of day) in our statistical analyses (see below).

During the nestling stage of each observed nest we recorded footage with a view of >1 m radius surrounding the nest structure using Panasonic VHS-C video cameras, placed on a tripod without camouflage at ~5 m from parasitized phoebe nests. After a recording session was terminated, we inspected the nests' contents and counted the number of cowbird and phoebe nestlings that were alive at that time. We also noted the developmental stage of each brood by calculating nestling age as the number of days after the hatching of the first hatched nestlings (these were always the cowbirds in parasitized nests). Recordings were taken throughout daylight hours and lasted until the battery or the film ran out (<1.5 hrs). Because of the proximity of all monitored nests to human activities, we assumed that the presence of video cameras did not represent a significant disturbance. Indeed, examination of the footage showed that phoebe parents typically resumed their feeding trips within 5 min. of set-up. There was neither statistical evidence of consistent time of day or seasonality effects on quantified parental behaviors (all P>0.2, see below) nor an effect of increased nest abandonment, predation, or parasitism following recording sessions (personal observations).

Behavioral data from videotapes

Video tapes were viewed at regular speed >5 months following the breeding season while using an event logger program. We were unable to discriminate between male and female phoebes and therefore recorded combined biparental behavior measures. Even though parental care by phoebes is provided in a sexually dimorphic manner (i.e., nest building, incubating, and most of the feeding are done by females, Conrad & Robertson, 1993a; Weeks, 1994), previous research using brood manipulations showed that augmentation of a brood's neediness resulted in similar proportional increases of parental care provided by mothers and fathers (Conrad & Robertson, 1993b). In our study, we calculated 'nest attendance rate' as the number of parental arrivals per observation time in hours and 'brooding' time as the proportion of observation time spent by a parent positioned directly over (i.e., not on the edge of) the nestcup. Although these two behavioral measures are clearly not biologically independent of each other because they are measurements on the same breeding pair at each site, we analyzed them separately as potential indicators of different but both costly (Heaney & Monaghan, 1996; Veasey et al., 2001; Chastel & Kersten, 2002) aspects of the adult hosts' parental behaviors.

Statistical analyses

To compare reproductive variables between non-parasitized and parasitized nests we used two-tailed unpaired t-tests for continuous variables.

We utilized the SAS System for Windows, Version 8.01, using mixed model repeated measures ANOVA to analyze the relationship between parental care measures from our video recordings and nestling age, brood size, and parasite load. Proportional variables were log-transformed [log(X+1)] to remove heteroscedasticity from the data; log transformed data were normally distributed. SAS mixed model ANOVAs typically use the containment method to calculate the denominator degrees of freedom (ddf). Since the containment method does not perform well
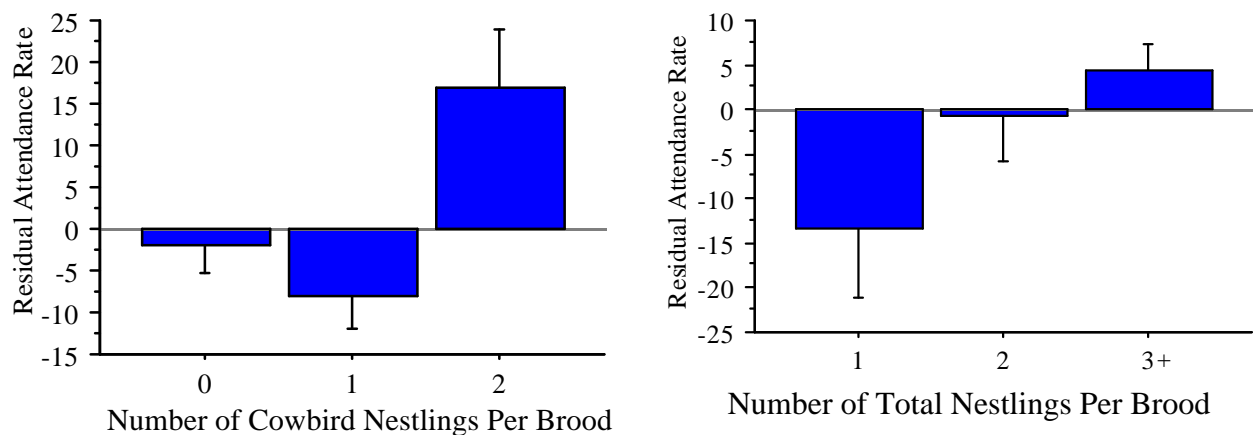
Figure 1. Illustrations of the qualitative relationship between parental attendance rate measure and the number of brown-headed cowbird nestlings (A) raised in broods or the total brood size (B) of Eastern phoebes. Residual attendance rate is calculated from partial regressions with parasite load or brood size (3+: 3, 4 or 5 nestlings), respectively. For this calculation and the illustration, each video-recording session was considered a single data point, but note that we used repeated measures ANOVA in the Results to avoid pseudoreplication (see Methods). Mean ± S.E.

with unbalanced data sets, we used the Satterwaithe method instead, which performs well under these conditions (Littell et al., 1996). The Satterwaithe method provides a numerical approximation of ddf, so the reported ddf for each ANOVA (F$_{ddf}$) are not necessarily whole numbers. We considered each breeding attempt to be independent in these analyses. This was a fair assumption because most videotaped breeding attempts (89%) were from different nests on separate breeding territories and, hence, were attended by different pairs of phoebe parents. Post-hoc statistical tests showed no effect of nest site (i.e., the repeated measure) per se in our measurements and the exclusion of second clutches (n=3 parasitized sites) did not change our statistical conclusions.

All measurements are reported as mean ± standard error and α was set at <0.05 unless otherwise noted for Bonferroni corrected tests. For illustrations in figures, non-transformed data are presented.

Results

Behavioral data from videotapes

We obtained a total of 81 hours of video recordings with averages of 2.1 hrs/nest and 3.3 hrs/nest for non-parasitized and parasitized phoebe nests respectively (Table 1). On the one hand, repeated measures ANOVA analyses that included brood size and parasite load as independent variables showed that our different measures of parental behaviors were not statistically associated with the repeated measure factor (i.e., nest site: both P>0.2). Nest attendance rate was positively related to increases in the proportion of cowbird nestlings per brood (F$_{55.3}$=5.7, P=0.023; Fig. 1A) and to total brood size (F$_{45.4}$=5.7, P=0.021; Fig. 1B) but not to nestling age (F$_{56.2}$=0.08, P=0.78), while brooding was not related to either brood size (F$_{43}$=1.5, P=0.23) or

proportion of cowbirds (F$_{53.4}$=1.9, P=0.18) but was negatively related to nestling age (F$_{55.7}$=39, P<0.0001; Fig. 2). On the other hand, reperated measures ANOVA analyses that included only whether or not a phoebe nest was parasitized (yes/no), and did not include brood size and parasite load, showed that neither measure of parental behavior (i.e., attendance rate: F$_{31.7}$=0.01, P=0.94; brooding: F$_{31.4}$=49, P=0.49) was related to whether broods were parasitized per se by cowbirds when controlled for nestling age (attendance rate: age effect, F$_{59.4}$<0.01, P=0.99; brooding: age effect, F$_{59.3}$=44, P<0.0001).

Breeding parameters

Comparing first broods only (both videotaped and non-videotaped nests from our study population combined), we found that non-parasitized phoebes raised a greater number of nestlings than did parasitized phoebes (Table 2). Phoebe clutch completion dates and clutch sizes were similar between non-parasitized and parasitized nests for first breeding attempts (Table 2). Clutch sizes of first breeding attempts were not related to their respective clutch completion dates (P$_{first clutches}$=0.67, Spearman rank test).

Discussion

Our comparison of behavioral measures of adult eastern phoebes, attending nests that were or were not naturally parasitized by brown-headed cowbirds, indicates that differences between costly aspects of parental effort in this host species are associated with brood size, parasite load, and/or age of nestlings but not to parasitism status per se. Nest attendance rates by both phoebe parents combined were positively related to the total number of nestlings (also see Conrad & Robertson, 1992, 1993b) and the proportion cowbirds raised per brood (also see
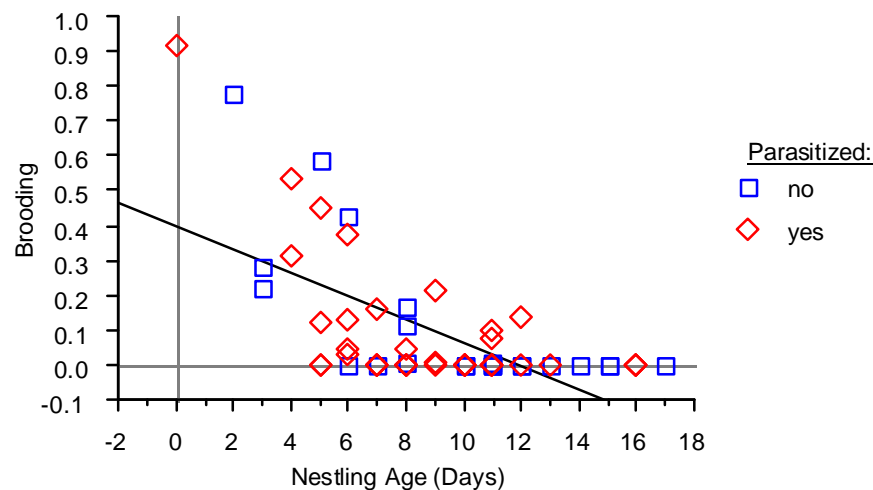
Figure 2. Relationship between brooding and the age of the oldest nestling during parasitized and non-parasitized breeding attempts of Eastern phoebes. For this illustration, each video-recording session is represented by a single data point, but note that we used repeated measures ANOVA to avoid pseudoreplication (see Methods).

Dearborn et al., 1998), while the proportion of time spent brooding covaried with the age but not the size or the composition of the brood.

That the signs of both correlation coefficients of nest attendance rates with parasite load and brood size were positive (see Fig. 1A,B) suggests that an increase of the proportion of parasitic nestling per brood has an effect on feeding rates that is similar to the effect of an increase of the brood size and, presumably, the overall need of the brood on parental provisioning rates (Conrad & Robertson, 1992). Although our video recordings did not allow the determination of individual feeding events for each nestling on every tape, nest attendance (i.e., visitation) rates appeared to be appropriate to approximate feeding rates in our analyses because, for those recordings where feeding events were identifiable, attendance rates were positively related to feeding rates ($r_{Spearman}$=0.29, P=0.023, n=63 recording sessions, KM unpublished data). This suggests that cowbird nestlings represent a greater burden for, and elicit more feeding by foster parents, than do numerically equivalent phoebe nestlings. The differentially greater level of parental response of phoebe parents to cowbird nestlings also implies that foster parents of this host species do not discriminate against parasitic nestlings in their broods (Clotfelter, 1997), perhaps because their behaviors reflect feeding decision rules that are only dependent on nestling size and begging intensity but not on species identity (Kilner et al., 1999). This is not surprising for a species like the Eastern phoebe that has probably only recently become a frequent cowbird host (i.e., after becoming a human commensalist, nesting on buildings) and does not exhibit egg-rejection of parasitic eggs (Rothstein, 1986; Hosoi & Rothstein, 2000; Rothstein et al., 2002).

In drawing our conclusions we must recognize both the correlational nature of our analyses and the relatively small proportions of the variances explained by some of the reported statistical relationships ($R^2<0.3$). Nonetheless,

the directions of the trends from our findings are in agreement with the conclusions from other studies of cowbird taxa and their host species (Kattan, 1996; Dearborn, 1998; Sedgewick & Iko, 1999).

Greater need by parasitic chicks may result from developmental aspects of cowbirds' life history that are associated with brood parasitism. Accordingly, cowbirds typically have faster growth rates and shorter nestling periods and fledge at greater weights than do host nestmates (Lowther, 1993; Lichtenstein & Sealy, 1998; Kilpatrick, 2002). Cowbirds, as interspecific parasites, are also not restrained by potential kin-selected benefits from sharing parentally provided resources with nestmates that are full or half sibs (Briskie et al., 1994). Therefore, brood parasitic nestlings may adaptively manipulate their foster parents by more intensive begging to deliver more food compared to host nestmates (Woodward, 1983; Kilner & Davies, 1999; Dearborn & Lichtenstein, 2002; Hauber, 2003). Indeed, cowbird nestlings raise their heads higher (Fig. 3) and beg more frequently in response to auditory stimuli (Hauber, 2003) than do similar aged phoebe nestlings, although it remains to be studied whether phoebe parents preferentially allocate food to begging nestlings that reach higher (see evidence for this Dearborn, 1998; Lichtenstein & Sealy, 1998 in other species).

Interestingly, nest attendance rates were related to both brood size (Conrad & Robertson, 1993b) and parasite load (Fig. 1) while brooding by adult phoebes was only related to the age of the oldest hatchling in the nest (Fig. 2). Even though both feeding and brooding are energetically expensive components of parental care (Heaney & Monaghan, 1996), especially for female parents during the early stages of the nestling period (Chastel & Kersten, 2002), the lack of differential brooding between smaller, parasitized broods and larger, non-parasitized broods, did not counterbalance the putative relationship of the increased costs of parental care for larger broods and proportionally more cowbirds.

Figure 3. Nestling cowbirds may be able to have disproportionately greater access to parental provisioning by begging more intensively and raising their heads higher compared to host easter phoebe nest mates. Photo: R. Safran.

Overall, it appears that raising cowbirds rather than phoebes represents an additional burden to the hosts' parental provisioning for its parasitized brood. Using regression equations based on our results we calculated that exchanging a cowbird chick for a phoebe chick in a brood of 4 represented ~3.6 times a greater burden of feeding by phoebe parents (Fig. 1) than adding an additional host chick. This value is somewhat higher than the "nestling equivalents" measure (1.5; based on relative peak daily metabolizable energy of cowbird vs. host nestlings) calculated by Kilpatrick (2002) for a phoebe-sized host rearing a cowbird vs. own young. This value is also larger than the magnitude of proportional difference in weight (a possible surrogate measure for a chick's energetic need) between a 10 day old cowbird vs. phoebe nestling (~1.8) (data from Lowther, 1993; Weeks, 1994). Although similar in overall dimensions, the disparity between our and the other two values could be a result of the divergent origins of these estimates. Our first calculation used parental behaviors to predict the additional burden represented by cowbird nestlings while Kilpatrick's (2002) and our second values were derived from measures of the nestlings' growth rates and relative sizes. The disparity, therefore, may be due to the differential efficiency with which parentally delivered resources (i.e., food) are processed and applied towards growth by nestling cowbird and hosts (Budden & Wright, 2001). Unfortunately, currently there are no comparative data on the digestive and metabolic physiology of cowbirds vs. phoebes.

Phoebe foster parents appear to pay disproportionately greater costs for raising a parasitic cowbird nestling when compared to raising one of their own offspring (Hauber, 2002). Our data suggests that this reduction in residual fitness could be related to increased nest attendance and feeding rates at broods with greater parasite loads (Fig. 1). We propose that parasitic cowbird chicks can manipulate adult phoebes in similar ways to how they affect foster parents in many of their other small-to-medium sized host species (Hauber in press), where foster parents increase their parental efforts in response to the proportion of parasites in their current broods (Woodward, 1983; Kattan, 1996; Dearborn et al., 1998; Sedgewick & Iko, 1999; Dearborn & Lichtenstein, 2002). Regarding the extent of the costs of cowbird parasitism on parental efforts, however, parasitized phoebe pairs raise overall fewer nestlings per brood than do non-parasitized pairs (Klaas, 1975). Perhaps as a combined result of these opposing influences (i.e., increased parasite load vs. decreased brood size), cowbird parasitism per se is not significantly related to the overall parental effort of Eastern phoebes. It still remains to be elucidated whether cowbird parasitism influences other traits of residual fitness in adult phoebes (Lorenzana & Sealy, 1999). Nonetheless, our results imply that previous studies about the selective forces favoring the evolution of parasite-rejection by Eastern phoebes (Klaas, 1975; Rothstein, 1986; Lorenzana & Sealy, 1999) did not necessarily underestimate the overall cost of brown-headed cowbird parasitism by not accounting in their calculations for differential parental effort between parasitized and non-parasitized hosts.

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