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Original Article

The economics of nestmate killing in avian brood parasites: a provisions trade-off

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Some brood parasites kill all their host's offspring shortly after hatching, whereas others are tolerant and are reared in mixed host–parasite broods. This difference may arise because nestling parasites face a "provisions trade-off," whereby the presence of host nestlings can increase or decrease a parasite's food intake depending on whether host young cause parents to supply more extra food than they consume. We model this trade-off and show that the optimal nestmate number from a parasite's perspective depends on the interaction of 2 parameters describing a parasite's stimulative and competitive properties, relative to host young. Where these parameters differ from one host–parasite pair to the next, either nestmate killing or nestmate tolerance can be favored by natural selection for maximum intake. We show that this extends to variation between hosts of generalist parasites. In an experimental field study, we found that nestling shiny cowbirds (*Molothrus bonariensis*) reared by house wrens (*Troglodytes aedon*) had higher food intake and mass growth rate when accompanied by host young than when alone, whereas those reared by chalk-browed mockingbirds (*Mimus saturninus*) had higher food intake, mass growth, and survival when reared alone than with host young. In both hosts, total provisioning was higher when host nestlings were present, but only in house wrens did cowbirds secure a sufficient share of that extra provisioning to benefit from host nestlings' presence. Thus, a provisions trade-off might generate opposing selective forces on the evolution of nestmate killing not only between parasite species but also within parasite species using multiple hosts. *Key words:* brood parasitism, *Molothrus bonariensis*, shiny cowbird, virulence. *[Behav Ecol]*

INTRODUCTION

Obligate brood parasites lay eggs among other species' clutches and benefit from their hosts' misdirected parental effort. In many species, the young parasites attack and kill their host's offspring shortly after hatching, the fry of brood parasitic catfish eat host's eggs and fry while being brooded inside the mouth of the host Cichlidae (Sato 1986), cuckoo-wasp larva (*Chrysidinae*) devour the host larvae sharing their brood cell (Thomas 1962), and honeyguides (*Indicatoridae*) use bill hooks to mortally wound their nestmates (Ranger 1955). In the best-known example, chicks of brood parasitic cuckoos (*Cuculus* sp.) dispose of host eggs or chicks from the nest by lifting them onto their backs and tossing them out of the nest cup (Jenner 1788). Such virulent behaviors in young parasites have long been considered adaptive as they eliminate competition for food and resources; as Darwin (1859) concluded with respect to cuckoo chicks' virulent behaviors, "if it were of great importance for the young cuckoo, as is probably the case, to receive as much food as possible … those which had such habits and structure best developed would be the most securely reared."

Among the avian obligate brood parasites however, roughly one third of all extant species have either not evolved brood-killing behaviors or have secondarily lost them (Davies 2000; Kilner 2005), an absence phenomenologically referred to as host tolerance, or more accurately nestmate tolerance, on the part of the parasite. In these cases, although adult parasites may reduce host clutches (via ruin or removal of eggs), some host offspring typically survive to be reared alongside the parasite (or parasites) in the nest. As the ancestral character, nestmate tolerance might reflect the more recent origins of obligate parasitism in some lineages (i.e. evolutionary lag, Davies 2000) or be maintained by one or more constraints on the evolution of virulent behaviors in nestlings (e.g. energetic, Grim 2006; Anderson et al. 2009; Grim et al. 2009b, indirect fitness, Davies 2000, or host defenses, Broom et al. 2007; Grim et al. 2011).

A further, not mutually exclusive, explanation is that where selection favors the strategy that brings a parasite, in Darwin's words, "the most food possible," nestmate tolerance will at times be maintained. In a study of brown-headed cowbirds (*Molothrus ater*) reared in nests of the Eastern phoebe (*Sayornis phoebe*), Kilner et al. (2004) found that host parents provisioned more to nests where cowbirds shared with 2 host chicks than to nests with lone cowbirds, that cowbirds in mixed broods took the lion's share of the provisions, and that they received more food and had greater growth than cowbirds reared alone in the nest. The explanation for this result may lie in nestling begging, which has a dual effect in most altricial bird species (Rodríguez-Gironés et al. 1996, 2001): First, it stimulates host parents to increase provisioning to the nest as a whole by intensifying foraging and/or reducing their own consumption (an effect of the begging output of the whole brood), and second, it determines the partitioning of the deliveries among the nestlings (an effect of begging of individual chicks). Thus to maximize their food intake and fitness, brood parasites might in fact face a trade-off between the advantage of removing host young as competitors, and tolerating them, so as to gain the value of their assistance in stimulating host parents to work (Kilner 2003, 2004). This trade-off (hereafter: "provisions

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trade-off") could help explain the dichotomy between nestmate killers and nestmate tolerants among avian brood parasites, with differences in costs and benefits variously favoring the evolution of one strategy or the other (Kilner 2005).

In this study, we examine the provisions trade-off hypothesis both theoretically and experimentally. We first develop a model that formalizes the trade-off as the product of its component functions: the total provisioning rate stimulated by the whole brood and the share of those provisions received by a parasite nestling. The model proposes 2 qualities of a parasite nestling to be crucial in determining which scenario (host young present or absent) will optimize that parasite's intake. The first of these qualities is the relative responsiveness of host parents to own and parasite nestlings' begging. The second is the parasite's ability to compete during food allocation.

As both qualities are determined in relative terms on a host–parasite pair by pair basis, variation might exist not only between parasite species but also within generalist parasites, those that use more than one host species at an individual or population level. Here the generalist cowbirds present a conspicuous example. Large size relative to host young afforded the nestling brown-headed cowbirds of Kilner et al.'s (2004) study a significant competitive advantage in the bidding war over their diminutive phoebe nestmates. Brown-headed cowbirds, however, use a wide range of host taxa that vary in body size, incubation time, and nestling growth rates (Friedmann and Kiff 1985; Lowther 1993; Remes 2006), and thus, nestling cowbirds encounter a range of competitive brood environments (Kilner 2003; Remes 2010; Rivers et al. 2010). This raises the possibility that generalist cowbirds can encounter both scenarios in a provisions trade-off, optimizing food intake in some hosts when reared alone and in other hosts when host offspring are present. As such, these systems are of particular interest in assessing the role of a provisions trade-off in the evolution of nestling virulence. On one hand, they present a ready test of the central tenet of the trade-off, showing that a tolerant (i.e., ancestral state) parasite could face differing selection pressures depending on the dynamics of its particular host interaction. On the other hand, they raise questions about how selection for maximum food intake might be expected to act in generalists where the costs and benefits of nest sharing vary between hosts.

We perform a field experiment with a generalist nestmate tolerant parasite, the shiny cowbird (*M. bonariensis*). Like the North American brown-headed cowbird, this species is an extreme generalist, parasitizing over 200 hosts representing a wide variety of taxa, body sizes, life histories, and nesting ecologies (Lowther and Post 1999). We chose 2 representative hosts at extremes of the range of relative size: the house wren (*Troglodytes aedon,* hereafter: wren), a host smaller in body mass than cowbirds (11–14 and 40–45 g, respectively), and the chalk-browed mockingbird (*Mimus saturninus,* hereafter: mockingbird), a large-bodied host (70–75 g). Following the design of Kilner et al. (2004), we compare, in each host, food intake, growth, and survivorship of cowbirds reared in one of 2 treatment nests: a cowbird alongside host young and a cowbird alone. A previous study by Fiorini et al. (2009) found that shiny cowbirds reared in small host broods of mockingbirds had better survival and fledgling mass than those in larger broods, whereas larger host broods led to higher fledging masses for cowbirds reared by house wrens. Based on this previous study and our model, we hypothesize that nest sharing with host young is advantageous to shiny cowbird food intake and growth when parasitizing house wrens but costly when parasitizing mockingbirds.

A MODEL

We model the intake of nestling parasites as a function of brood composition. The model includes the following assumptions:

(i) Total provisioning rate to a parasitized brood (P_T, units of energy per unit time) is a function of total begging stimulation by the brood as perceived by the host parents (B_T, dimensionless). Begging stimulation here is used in its broadest sense to incorporate all stimuli provided by nestlings to elicit parental provisioning. Provisioning rate increases at a diminishing rate with increases in the brood begging stimulus, up to a maximum rate, $P_{\max}$, the maximum food per unit time the parents are capable of delivering. The following exponential function, although not unique, has the required properties:

$$P_{\mathrm{T}} = P_{\max}\left(1 - e^{-mB_{\mathrm{T}}}\right), \tag{1}$$

where m is a dimensionless positive constant that scales the response of parents to changes in begging.

(ii) Begging host and parasite chicks may not be an equally effective stimuli for parental provisioning, such that total stimuli from the begging brood, B_T, results from the summed effects (without interaction) of host and parasite chick numbers weighted by their species-specific efficiency in stimulating host parents, B_h and B_p, respectively:

$$B_{\mathrm{T}} = N_{\mathrm{h}}B_{\mathrm{h}} + N_{\mathrm{p}}B_{\mathrm{p}} \tag{2}$$

The relative value of B_h and B_p can be expressed as a parameter, β, the ratio between the strength of stimulation (provisioning increase per individual chick begging) produced by individual chicks of each species:

$$\beta = \frac{B_{\mathrm{p}}}{B_{\mathrm{h}}} \tag{3}$$

B_h and B_p are abstract and dimensionless terms that have the potential to incorporate various complexities of the begging stimulus, for example, B_h could vary with the size and/or composition of the brood (Johnstone 2004; Pagnucco et al. 2008) or according to the sexes of the feeding adults (Macgregor and Cockburn, 2002; Tanner et al. 2008) or the presence of helpers (Wright 1998). For our purposes here, however, we define a fixed B_h (=1) as the contribution to the overall begging stimulus made by one host chick. This condition allows us to express B_T in terms of the relative measure of a parasite's ability to stimulate provisions, β. Now, substituting Equation 3 into Equation 2:

$$B_{\mathrm{T}} = N_{\mathrm{h}} + N_{\mathrm{p}}\beta \tag{4}$$

Then, substituting Equation 4 into Equation 1:

$$P_{\mathrm{T}} = P_{\max}\left(1 - e^{-m\left(N_{\mathrm{h}} + N_{\mathrm{p}}\beta\right)}\right) \tag{5}$$

(iii) Once parents arrive with food at the nest, the food is distributed according to the competitive ability of each nestling. We define γ as the differential competitive ability of host (C_h) and parasite (C_p) nestlings, where competitive ability is the relative probability of consuming each food item at the time it is delivered:

$$\gamma = \frac{C_{\mathrm{p}}}{C_{\mathrm{h}}} \tag{6}$$

Competitive ability may be influenced by nestling size, positioning in the nest, begging intensity, and other variables that affect probability of feeding (Rodríquez-Gironés et al. 2001).

When $\gamma = 1$, all chicks in the nest receive an equal share of provisions. When $\gamma \neq 1$, individual parasite nestlings receive greater or fewer feeds than individual host chicks. As each competitive unit will take the same fraction of the food brought up to the nest, we can use the competitive abilities of host and parasite nestlings to calculate the rate of food intake F (units of energy per unit time) for each parasite nestling as a proportion of the total provisions to the brood (P_T):

$$F = \left(\frac{C_\mathrm{p}}{N_\mathrm{p}C_\mathrm{p} + N_\mathrm{h}C_\mathrm{h}}\right)P_\mathrm{T} = \frac{P_\mathrm{T}}{N_\mathrm{p} + \frac{C_\mathrm{h}}{C_\mathrm{p}}N_\mathrm{h}} \qquad (7)$$

Expressing the ratio C_h over C_p in terms of γ from Equation 6 gives:

$$F = \frac{P_\mathrm{T}}{\left(N_\mathrm{p} + \frac{N_\mathrm{h}}{\gamma}\right)} \qquad (8)$$

And finally, substituting P_T from Equation 5 into Equation 8 gives:

$$F = \frac{P_\mathrm{max}(1 - e^{-m(N_\mathrm{h} + N_p\beta)})}{N_\mathrm{p} + \frac{N_\mathrm{h}}{\gamma}} \qquad (9)$$

The model is described graphically in Figure 1. In this plot, m is fixed at 0.5, representing a situation whereby provisioning rate gets close to its asymptotic value (P_max) with an unparasitized brood of 5 chicks (see Supplementary Material for a sensitivity analysis of m). The plots show that when a parasite is alone in the nest ($N_\mathrm{p} = 1$, $N_\mathrm{h} = 0$), host parents provision at a rate below their maximum capability ($P_\mathrm{T} < P_\mathrm{max}$), but the parasite receives 100% of provisions. With the addition of host nestmates, the total rate of provisioning increases following a negative exponential function, whereas the share received by the parasite decreases hyperbolically. Maximum intake can occur when host nestmates are absent (Figure 1a) or present (Figure 1b) depending on the parasite–host pair's relative parameters (β and γ). Thus, the model shows that both nestmate killing and nestmate tolerant strategies could maximize food intake of the parasite. The key lies in the size and fate of the marginal increase in provisioning generated by the presence of host nestlings: If each host nestling causes a greater increase in provisioning than the amount it consumes, then the presence of host chicks would result in higher consumption for the parasite, even if a host chick takes a bigger fraction of the extra food than the parasite.

Restricting ourselves for the moment to a situation in which there is only one parasite in a nest ($N_\mathrm{p} = 1$), we can use Equation 9 to find the optimal number of host nestmates (N_opt) for the parasite, defined as the number of host nestmates ($0 \leq N_\mathrm{h} \leq 10$) for which the model predicts that the parasite will enjoy maximum intake (calculations performed in MATLAB). Figure 2 shows N_opt across the range of values (0–1) of β and γ (and $m = 0.5$). From these calculations, we can see clearly that neither stimulative nor competitive ability alone determine the outcome of the trade-off but rather that their interaction is paramount. When $\beta > \gamma$, a parasite's relative stimulative ability is greater than its relative ability to win intrabrood competition for provisions, and parasites maximize food intake when reared alone. This includes the situation where parasites are equivalent to host young in both respects, $\beta = \gamma = 1$, parameter values that also indicate the outcome for intraspecific parasites or for interspecific parasites whose only nestmates are conspecific parasites (as can occur when multiple parasitism is common). In contrast, for many (though not all) cases when $\gamma > \beta$, parasites will benefit from the survival of some host offspring and receive maximum food when sharing the nest.

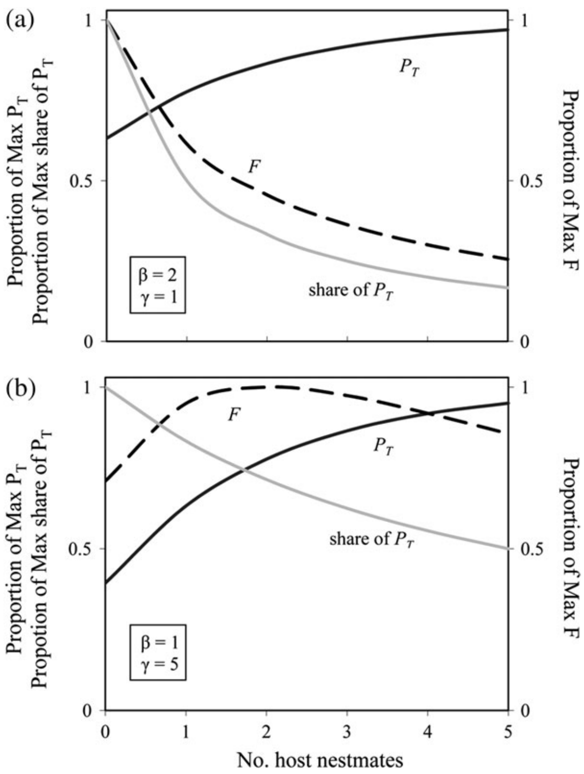

Figure 1
A model of the consequences for a brood parasite's food intake of sharing a nest with host young. Total provisioning (P_T), share of the total provisioning received by a nestling parasite (share of P_T), and thus food ingested by a nestling parasite (F) vary as a function of the number of host nestmates reared alongside the parasite. With increasing numbers of nestmates, P_T increases and share of P_T decreases (see main text for equations). Assuming that a single parasite chick is present, depending on the ability of the parasite to stimulate provisioning (β) and to compete for provisions (γ), F can be maximized either when (a) parasites are alone in the nest or (b) parasites share the nest with host young. β and γ values are inset, $m = 0.5$.

Optimal nestmate number, however, which assumes any number of nestmates is possible, may be an unlikely target for natural selection. We can in addition use the model to ask under what conditions a parasite nestling would benefit from either killing or tolerating its nestmates, where parasites are bound by a binary rule of kill all (and be reared alone) or kill none (and be reared alongside all host young that survive to hatch). Here, typical host brood sizes and the extent of host brood reduction enacted by adult parasites must play a role. Figure 3 shows these calculations for nestling parasites facing 2 illustrative host brood sizes, either 2 or 4. nestmate killing is favored over a larger range of parameters when there are more host young in the brood. For both brood sizes, however, as demonstrated in the calculation of optimal nestmate number, we find that both the presence or the absence of host nestmates can result in maximum food intake. Thus, we predict that where parasite–host pairs vary between each other in relative competitive and/or relative stimulative ability, they could be subjected to opposing selective forces on the evolution of virulent behaviors at the nestling

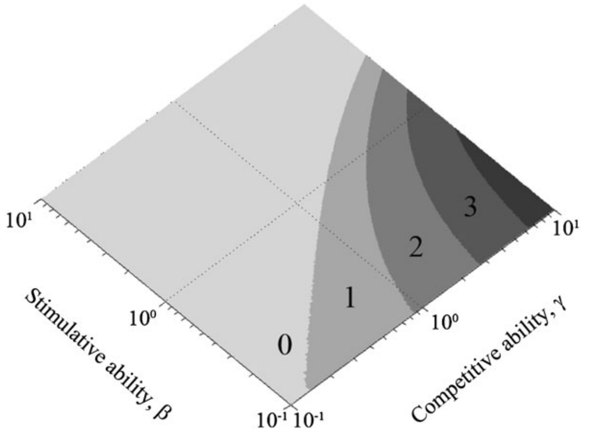

Figure 2
Optimal number of host nestmates, N_{opt} (color-coded inset numbers 0–3), for a single parasite of given relative ability to stimulate host parents to provision (β) and to win those provisions when they arrive (γ) according to a model of a provisions trade-off (see main text). Axes are logarithmic, $m = 0.5$. Dotted lines indicate $\beta = 1$ and $\gamma = 1$; thus, their intersection is the point at which parasite and host nestlings are equally matched in both begging dimensions.

stage. We now describe a field experiment designed to identify such circumstances by examining the performance of nestlings of a generalist parasite, the shiny cowbird, in nests of 2 common hosts between which the relative competitiveness of the parasites is expected to vary markedly.

METHODS

Study species and field procedures

Chalk-browed mockingbirds and house wrens are both common hosts of shiny cowbirds in southern South America. We searched for mockingbird nests in trees and shrubs of known breeding territories and checked nest-boxes erected for wren use at our field site, Reserva El Destino, an estate of approximately 600 ha (lat 35 08′S, long 57 23′W) located within the Biosphere Reserve (United Nations Educational, Scientific and Cultural Organization) Parque Costero del Sur, Buenos Aires Province, Argentina. Fieldwork took place during the breeding seasons 2008–2010. Nests were located prior to the onset of incubation. In each of the 2 host species, we created 2 treatment groups; “mixed” (a cowbird reared alongside host young) and “alone” (a cowbird reared alone).

Mockingbirds lay clutches of 4–5 eggs, but egg puncturing by adult cowbirds at or around the time of parasitism reduces clutch size for parasitized nests. At our field site, the mean number of mockingbird young in parasitized nests at hatching (± standard error) is 1.7 ± 0.2 (Fiorini 2007). Multiple parasitism is common in this host; thus, cowbirds can share the nest with other cowbirds, but our experiment focused only on the effects of host nestmates. Thus in mockingbirds, nests were manipulated to contain either 2 mockingbird eggs and 1 cowbird egg (“mixed”) or 2 “dummy” plaster-of-Paris eggs and 1 cowbird egg (“alone”); $n = 20$ per treatment (2008/2009: $n = 5$, 2009/2010: $n = 15$ per treatment). On 6 occasions, when eggs failed to hatch or were destroyed during incubation by cowbirds, we moved chicks between mockingbird nests shortly after hatching to create mixed brood treatment nests.

In wrens, the number of host young reared alongside cowbirds in natural conditions depends not only on loss from egg puncturing (initial clutch size of 4–5) but on the synchrony of parasitism with host laying; synchronous parasitism leads to cowbirds hatching earlier than host young and quickly outcompeting them to death, whereas asynchronous parasitism (when cowbirds lay after the onset of incubation) can lead to a same-age brood in which both parasite and hosts fledge (Tuero et al. 2007; Fiorini et al. 2009). In order to investigate the effect of nest sharing on the food intake of cowbirds reared in wrens, our “mixed” treatments were therefore created by simulating asynchronous laying by adding cowbird eggs to clutches of 3 or 4 host eggs 3 days after the onset of incubation such that host and parasite hatched at the same time. Nests in the “alone” treatment were handled similarly but either had all host eggs replaced by dummy eggs before incubation or (in 4 cases) host young translocated to other nests within 24 h of hatching: $n = 15$ per treatment (2008/2009: $n = 3$, 2009/2010: $n = 5$, 2010/2011: $n = 7$ per treatment).

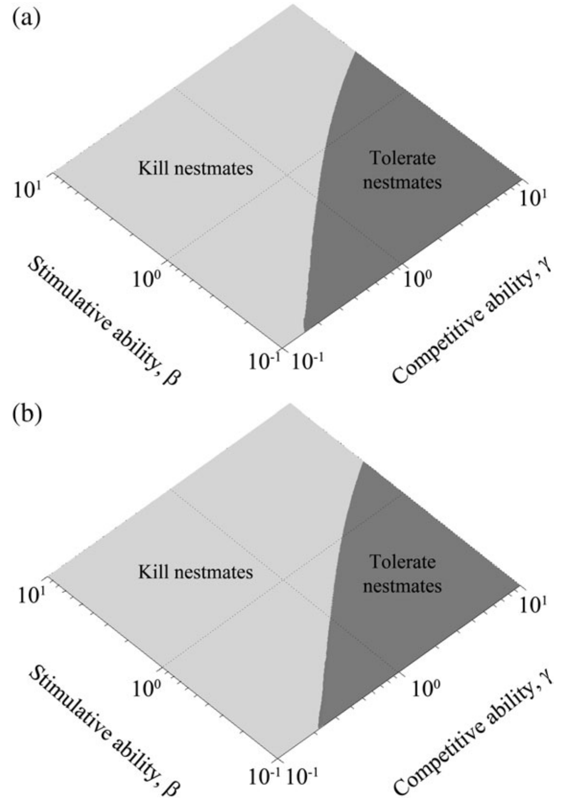

Figure 3
The adaptiveness of nestmate killing over nestmate tolerance for a single parasite chick according to a model of a provisions trade-off (see main text). The plots assume a given host brood size of either (a) 2 host chicks or (b) 4 host chicks. Dotted lines indicate $\beta = 1$ and $\gamma = 1$. The range of parameters for which nestmate tolerance maximizes food intake is larger when the number of host young in the brood is lower, though for both brood sizes, if β is low and γ high, maximum intake occurs when the single parasite chick does not kill its nestmates (dark gray), and if β is high and γ low, selection favors nestmate killing (light gray). The figure shows that typical host brood size, in addition to begging and competitive abilities, would influence the evolution of nestmate killing behavior.

Shiny cowbirds are sexually size dimorphic (Friedmann and Kiff 1985). Post-hoc molecular sexing showed that male and female cowbirds had been assigned approximately equally between treatments by chance (but see Supplementary Material for an analysis of possible sex effects).

Analysis

We filmed each nest for 2–3 h when the cowbird chick was 4 and 8 days posthatching (day of hatching = day 0) using a microcamera suspended above the nest and connected to a Digital Personal Video Recorder (Handykam: JXD990) at the base of the tree. Some nests were not recorded on one or both days due to chick death, adverse weather, or in wrens, because nests were built too close to the nest-box ceiling. All host parents resumed feeding within 30 min of placing the camera. We analyzed the final hour of each recording for 1) number of feeding visits (i.e., visits where the host parent brings food), 2) number of feeding visits in which the cowbird received food, and 3) the size of the prey (% bill width of host parent, abbreviated %BW). We used analysis of variance and nonparametric equivalents (Mann–Whitney *U* test) to test for differences in these variables between treatments.

We measured chick body mass (grams) and tarsus length (minimum tarsus, millimeters, Redfern and Clark 2001) from days 0–10 (cowbird fledging occurs day 11–12 in mockingbirds; Fiorini et al. 2009; and day 12–14 in wrens; Kattan 1996). We used chi-square tests to test for differences in chick mortality rate between treatments. Cowbird chick mortality was recorded as independent of predation when either 1) chicks were found dead in the nest ($n = 7$) or 2) they disappeared from the nest after failing to increase in weight in the 2 days prior to disappearance ($n = 3$). In the latter case, it was likely that they had died in the nest and been removed by host parents. Only chicks that survived at least 8 days were included in the growth rate analysis. To test for differences in growth rates of body mass and tarsus length between treatments (with or without hosts), we used nonlinear regression to fit growth curves of each chick to the logistic equation:

$$M_t = \frac{A}{1 + e^{-K(t - t_i)}}$$

where M is the mass (grams) or tarsus length (millimeter) of the chick at time t, A is the asymptotic mass or tarsus length, t is the time since hatching (hours, where hatching hour was designated as sunrise of day 0), t_i is the inflection point of the curve (hours), and K is the growth constant (per hour), that is, the rate constant of the logistic curve (Ricklefs 1967). A was fixed at the maximum mass or tarsus length measured to allow comparison of K values between treatments (Starck and Ricklefs 2003). We then used general linear models (GLM) for each of 4 dependent variables; growth rate of body mass and growth constant of tarsus (K for both variables), mass at 8 days posthatch, and tarsus length at 8 days posthatch. GLMs tested the effect of treatment ("mixed" vs. "alone") on each growth variable for each host (GLM univariate; type III sums of squares).

In addition, we tested for differences between hosts but within treatments to assess relative impacts of nest sharing on cowbirds in each host (including year as a factor; GLM univariate). All statistics were performed in SPSS 17.0. All errors are given as ± 1 standard error of the mean.

RESULTS

Shiny cowbirds reared by house wrens

Wrens provisioned more to broods comprising of a cowbird and their own young than to a lone cowbird at both 4 and 8 days (day 4: $F_{1,17} = 17.45$, $P = 0.001$, day 8: $F_{1,14} = 28.6$, $P = 0.009$; Figure 4). At both ages, cowbirds reared in mixed broods were larger than their nestmates (day 4: cowbirds 21 ± 1.3 g, wrens 6.5 ± 0.3 g, $t_{14} = -11.9$, $P < 0.001$, day 8: cowbirds 36.8 ± 1.3 g, wrens: 11 ± 0.3 g, $t_{11} = -18.5$, $P < 0.001$) and received a greater proportion of food deliveries than expected by chance (day 4: $\chi^2 = 63.5$, $P < 0.001$, day 8: $\chi^2 = 59.4$, $P < 0.001$; Figure 4). At 4 days, food intake for "mixed" cowbirds was not significantly different from that of lone cowbirds reared in wren nests ($F_{1,17} = 0.19$, $P = 0.61$), but by 8 days, cowbirds sharing the nest with wren chicks received significantly more food than their counterparts reared alone ($F_{1,14} = 5.85$, $P = 0.03$). Prey size did not differ significantly between treatments at either age (day 4: mixed 282 ± 5 %BW, alone 244 ± 32 %BW, $F_{1,14} = 2.46$, $P = 0.63$, day 8: mixed 363 ± 15 %BW, alone 348 ± 27 %BW, $F_{1,8} = 2.75$, $P = 0.44$).

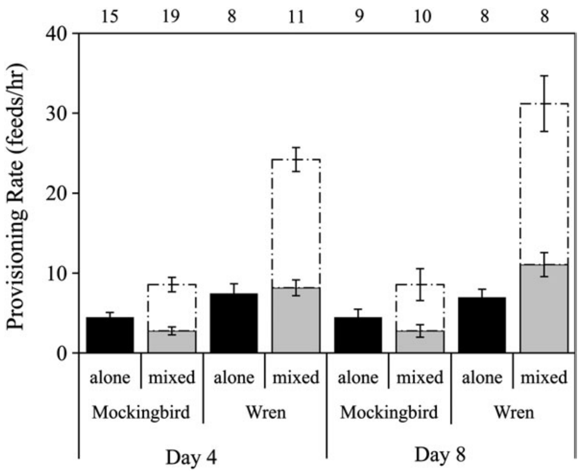

Figure 4
Provisioning rates (feeds per hour) to shiny cowbird nestlings reared alone (black bars) and reared alongside host chicks (gray bars) in either chalk-browed mockingbirds or house wrens at 4 and 8 days posthatch. Dashed bars indicate the total provisioning to the mixed broods, where host chicks received the remainder. Values are means ± standard error. Sample sizes, *n*, given above bars. See main text for statistical details.

Differences in food intake were reflected in differences in growth. Cowbirds reared alongside wren nestlings had higher rates of mass and tarsus growth (mass growth rate: mixed $K = 0.021 \pm 0.001\ \text{h}^{-1}$, alone $K = 0.016 \pm 0.001\ \text{h}^{-1}$, $F_{1,24} = 4.87$, $P = 0.037$; tarsus growth rate: mixed $K = 0.018 \pm 0.001\ \text{h}^{-1}$, alone $K = 0.016 \pm 0.001\ \text{h}^{-1}$, $F_{1,24} = 4.7$ $P = 0.04$) and reached higher day 8 body mass than those reared alone in wren nests ($F_{1,24} = 5.0$, $P = 0.035$), though we found no significant difference in tarsus length at day 8 ($F_{1,24} = 2.9$, $P = 0.13$; Figure 5). The nonpredation mortality of cowbirds reared in wren nests did not differ significantly between treatments (mixed: 2 of 16, alone: $n = 2$ of 13, $\chi^2 = 0.05$, $P = 0.82$).

Shiny cowbirds reared by mockingbirds

Mockingbirds also provisioned more to mixed broods than lone cowbird broods at 4 and 8 days posthatch (day 4: $F_{1,32} = 11.97$, $P = 0.002$, day 8: $F_{1,17} = 22.15$, $P < 0.001$; Figure 4). At 4 days, cowbirds reared alongside mockingbird young were not significantly different in mass (cowbirds 19 ± 1.7 g, mockingbirds 22 ± 1.8 g, $t_{19} = 1.54$, $P = 0.14$) nor competitiveness from their host's young (i.e., proportion of feeds secured, $\chi^2 = 0.01$, $P = 0.91$) but received significantly less food deliveries per hour than their counterparts reared alone ($F_{1,32} = 4.56$, $P = 0.04$; Figure 4). By 8 days, cowbirds cohabiting with mockingbirds weighed significantly less than their nestmates (cowbirds: 30.2 ± 2 g, mockingbirds: 42.7 ± 2 g, $t_8 = 3.84$, $P = 0.001$) and received food on fewer feeding visits than expected by chance ($\chi^2 = 10.8$, $P < 0.001$; Figure 4). Eight-day-old cowbirds alone in mockingbird nests received almost twice as many feeds per hour as those cohabiting with host young ($F_{1,17} = 4.55$, $P = 0.048$; Figure 4). Prey size did not differ significantly between treatments at either age (day 4: mixed 303 ± 21 %BW, alone

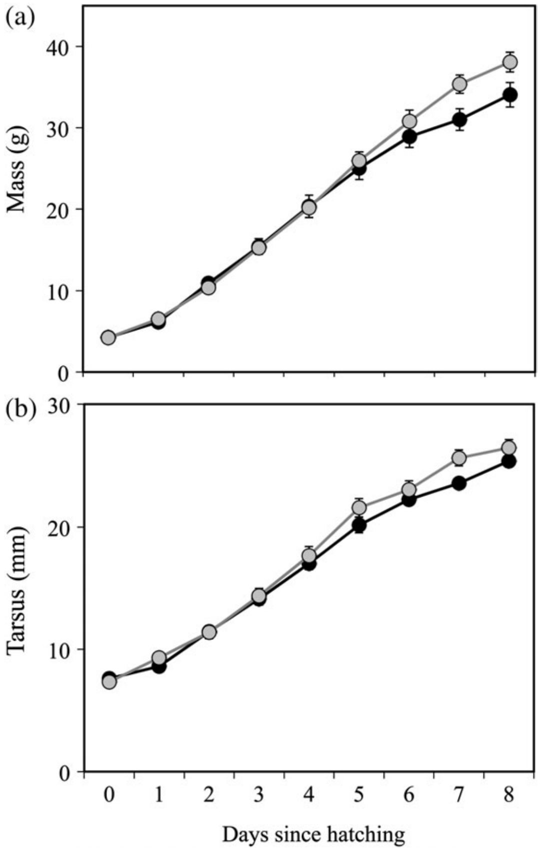

Figure 5
Growth in (a) body mass and (b) tarsus length of shiny cowbird nestlings reared alone (black circles, $n = 12$) and reared alongside 3 or 4 host chicks (gray circles, $n = 14$) in nests of house wrens. Values are means ± standard error.

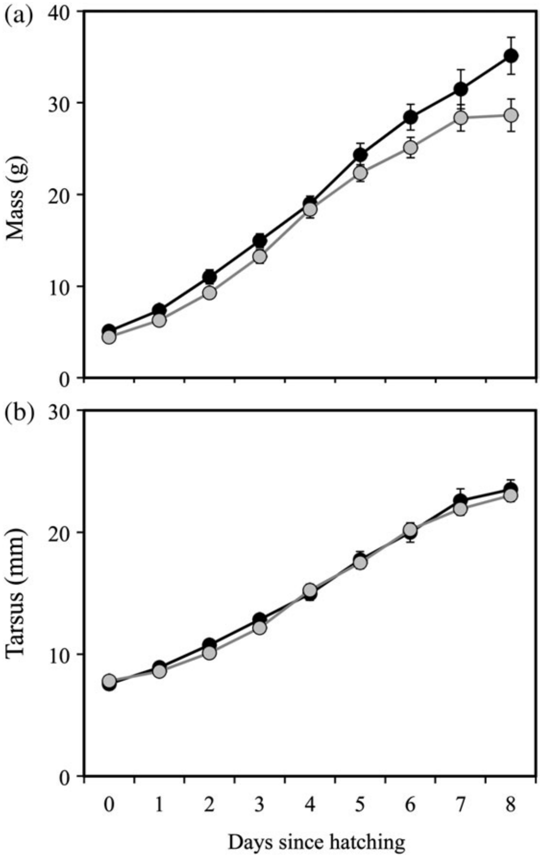

Figure 6
Growth in body (a) mass and (b) tarsus length of shiny cowbird nestlings reared alone (black circles, $n = 14$) and reared alongside 2 host chicks (gray circles, $n = 11$) in nests of chalk-browed mockingbirds. Values are means ± standard error.

302 ± 14 %BW, $Z = -0.87$, $P = 0.38$, day 8: mixed 387 ± 22 %BW, alone 413 ± 33 %BW, $Z = -5.7$, $P = 0.57$).

In mockingbird nests, cowbird nestling mortality was lower for cowbirds reared alone than for those reared alongside host chicks (excluding predation, mixed: $n = 6$ of 14, alone: $n = 0$ of 14, $\chi^2 = 7.63$, $P = 0.006$). Furthermore, cowbirds reared alone in mockingbird nests had higher body mass growth rates and reached a higher mass at 8 days than those that survived sharing the nest with mockingbird young (mass growth rate: mixed $K = 0.014 \pm 0.001$ h^{-1}, alone $K = 0.018 \pm 0.001$ h^{-1}, $F_{1,23} = 5.19$, $P = 0.032$, mass 8-days: $F_{1,23} = 5.48$, $P = 0.028$), though we found no significant difference between these treatments in growth rate of tarsus or length of tarsus (mm) at 8 days (tarsus growth rate: mixed $K = 0.014 \pm 0.001$ h^{-1}, alone $K = 0.016 \pm 0.001$ h^{-1}, $F_{1,23} = 0.002$, $P = 0.96$, tarsus 8 days: $F_{1,23} = 0.22$, $P = 0.64$; Figure 6).

Between hosts comparisons

Cowbirds reared in mixed broods in wrens had better mass and tarsus growth than those reared in mixed broods in mockingbirds (GLM, mass growth rate: $F_{4,20} = 4.2$, $P = 0.012$, tarsus growth rate: $F_{4,20} = 7.98$, $P = 0.001$) and reached greater weights and tarsus lengths by day 8 (mass: $F_{4,20} = 9.19$, $P < 0.001$, tarsus: $F_{4,20} = 10.02$, $P < 0.001$; Figures 5 and 6). There was no significant difference between cowbirds of the lone treatment in each host (GLM, mass growth rate: $F_{4,21} = 0.42$, $P = 0.79$, tarsus growth rate: $F_{4,21} = 0.45$, $P = 0.77$, mass: $F_{4,21} = 0.21$, $P = 0.92$, tarsus: $F_{4,21} = 0.86$, $P = 0.5$; Figures 5 and 6). There was no significant difference in cowbird chick survivorship between host species in either treatment (mixed: $\chi^2 = 3.5$, $P = 0.061$, alone: $\chi^2 = 2.32$, $P = 0.13$).

DISCUSSION

A provisions trade-off

Following reports that nestlings of some avian parasites experience a net growth benefit from the survival of their host's nestlings, interpreted as one side of a trade-off for maximum provisions (Kilner et al. 2004; Kilner 2005), we developed a model of the consequences to food intake that parasite nestlings might experience by sharing the nest with host offspring. The model considers that chick begging has 2 effects, one shared with the rest of the brood (increase in parental provisioning rate) and one exclusive to the begging chick (better chance of capturing food when delivered). A parasite's intake is therefore expressed as the product of total brood provisioning and the parasite's share of those provisions. Assuming selection acts to favor higher intake, our model thus helps to frame the potential routes by which nestmate killing can evolve in avian parasites.

At the crux of the model are 2 assumptions: that total provisioning is likely to be a concave function of brood size asymptoting at the maximum provisioning potential of the host parents and that food sharing is likely to be a ratio function with brood size included in the denominator. We further assumed that total provisioning depends on the number and stimulating power of the begging displays by both parasite and host nestlings and that the distribution function will depend on the competitive ability of such nestlings. All assumptions draw from empirical studies in the wider literature on avian begging (e.g., Wright and Leonard 2002), but they are of course generalizations and the extent to which they are appropriate for any one system will vary.

Our resulting model shows that either host killing or host tolerance can lead to higher parasite intake depending principally on the interaction of the parasite's competitive advantage and the effectiveness of its begging signal in stimulating host parents to work. If parasites are equivalent to host young in both competitiveness and stimulating efficiency, they receive most food when they are alone in the nest. This is also frequently true for host chicks in the absence of parasitism because parental increase in provisioning is sublinear with respect to brood size, but in the case of parasitism, there is typically no kin-mediated benefit to offset the loss of intake caused by extra nestlings. When parasites are very effective at stimulating provisioning and/or relatively ineffective in contesting the food delivered, selection for maximum intake should similarly favor nestmate killing. The opposite, however (nestmate tolerance), is expected whenever parasites have lower stimulating efficiency than host young and/or are good intrabrood competitors.

Variation in these qualities between ancestral parasitic lineages could arise simply from differences in the life histories of the species involved. Based on empirical data from both parasitic and nonparasitic systems, body size (Lichtenstein 1998; Rivers 2007; Rivers et al. 2010), egg size (Forbes and Wiebe 2010), incubation times (Ostreiher 1997; Hauber 2003), growth rates (Werschkul and Jackson 1979; Kilpatrick 2002; Remes 2010), and brood sizes (Leonard et al. 2000; Neuenschwander et al. 2003; Fiorini et al. 2009) are all likely to affect the relative competitive and signaling abilities of any one host–parasite pair. As hosts and parasites coevolve, derived traits of either party could help drive selection in one or the other direction. As such, and as is the case with any evolutionary modeling, contrasting the model's predictions with observed behavior in present-day species is not straightforward. For instance, parasites may secondarily lose or gain adaptations for begging in response to the presence/absence of host nestmates resulting from their behaviors. Also, host nestlings may evolve strategies to better compete with parasites, such as exaggerated begging (an interaction effect not included in our model, but see Pagnucco et al. 2008; Boncoraglio et al. 2009). Bearing this in mind, we nevertheless see some evidence that differences in nestling virulence of extant parasites match the model's predicted trends in chick competitive and stimulative abilities. nestmate killing common cuckoos possess begging calls capable of eliciting provisioning rates from their reed warbler hosts equivalent to a whole brood of host young (Kilner et al. 1999). Similarly, nestmate killing Horsfield's hawk-cuckoos display a wing patch to host parents to superstimulate provisioning rates (Tanaka and Ueda 2005). Also consistently with the model, common cuckoos have been shown to compete poorly when forced to share the nest with host nestmates in experimental manipulations (Martin-Galvez et al. 2005; Hauber and Moskat 2008; Grim et al. 2009a). On the other hand, several nestmate tolerant parasites compete well for food against their host nestmates; *Vidua* sp. finches are larger and hatch earlier than their host's offspring, which likely give them a competitive advantage during food allocation (Davies 2000), and the glandular markings inside the gapes of great spotted cuckoos (*Clamator glandarius*) increase their competitive ability by triggering preferential feeding from their magpie host parents (Soler et al. 1995).

Nestmate killing and the generalist's dilemma

In the case of generalist parasites, the use of multiple hosts adds interesting complications because it is obvious from the model that the relative advantages of (and hence selection for) nestmate killing and nestmate tolerance can differ between different hosts of the same parasite. In our field study, nestmate tolerant shiny cowbirds encountered both sides of a provisions trade-off depending on the host used. When reared by chalk-browed mockingbirds, nestling cowbirds had higher food consumption, mass gain, and survival when alone in the nest than when sharing with 2 mockingbird young. In contrast, cowbirds reared in the nests of house wrens had higher food intake and growth when reared alongside 3 or 4 host young than when reared alone.

Factors other than food intake may have contributed to differences in growth rates. For instance, nestlings of unparasitized broods help each other to thermoregulate, thus sometimes benefiting from larger brood sizes (e.g., Dunn 1976). However, the differences in provisioning rates we observed from video data indicate that food intake was likely the most significant driver of differential growth.

Our opposing results between the 2 host species are consistent with the predictions from a trade-off with respect to a parasite's competitive ability. In both hosts, cowbirds in mixed brood treatments elicited higher total provisioning rates than did lone cowbirds, but only in house wren nests were cowbirds able to secure a sufficiently large share of these provisions to benefit from nest sharing. Nestling size is probably key in these interactions because shiny cowbirds were considerably larger than their wren nestmates but similar in size or smaller than their nestmate mockingbirds. Other studies on cowbird begging also suggest nestling size to be important in intrabrood competition, either because host parents preferentially feed larger nestlings or because large nestlings can best jostle their nestmates out of the way when food is on offer (Dearborn 1998; Lichtenstein and Sealy 1998; Lichtenstein 2001; Kilner et al. 2004; Rivers 2007; Rivers et al. 2010). Competitive ability, however, as our model shows, is only one side of the coin; it may be that differential stimulative ability of shiny cowbird nestlings between hosts also contributed to the observed outcome in this study, if say, cowbirds are better at soliciting mockingbird parents to provision (in our model, higher β) than they are at soliciting wrens.

How then might selection for maximum provisions act in shiny cowbirds and other generalist parasites in which the optimal host nestmate number varies from host to host? One possibility is that such parasites may evolve (or retain) the behavior that achieves an overall growth advantage, given the relative incidence of host species used. Nestmate-tolerance may be better than nestmate killing in some hosts and suboptimal in others but be maintained by the average effect, weighted by relevant properties of each host species such as maximum provisioning rate, food quality and length of the nestling period (Kilpatrick 2002; Remes 2010), as well as by the prevalence of certain host defenses (Langmore et al. 2003; Broom et al. 2007; Grim et al. 2011). The frequency of multiple parasitism may also be crucial, both because it may lead to parasites sharing with siblings or half-siblings and because it changes the begging profile and competitive interactions of the brood. Multiple parasitism is common in a number of hosts of nestmate tolerant parasites (Arias de Reyna 1998; Ortega 1998), including chalk-browed mockingbirds (Fraga 1985).

A "general optimum" solution would account for the fact that the optimum in any one host is not necessarily equal to the optimum of another. We might predict, for example, that large hosts would deliver more or larger prey than smaller hosts (e.g., Grim 2006) resulting in a situation whereby a parasite had similar growth and survival in the suboptimal nestmate configuration of a large host than in the optimal one for a small host (Kilpatrick 2002). Indeed, shiny cowbirds enjoy similar fledging success in large hosts as they do in small hosts (Sackmann and Reboreda 2003; Fiorini et al. 2005), which would be consistent with this effect. In our experiment, a comparison of cowbird growth between species in fact shows the opposite trend, with both groups of cowbirds reared in wrens (mixed and alone) achieving growth rates as good or better than those observed in the highest growth (i.e., lone cowbird) treatment in mockingbirds. However, in practice, the benefits of host tolerance to wren-reared cowbirds will be considerably less because naturally occurring parasitism is often synchronous with wren laying (Fiorini et al. 2009) and results in the passive death of host young by starvation or trampling early in the nestling period (Tuero et al. 2007). Thus, within the particular pair of hosts we investigated, the host in which cowbirds most benefit from nestmates is also the host in which nestmates are least likely to be present.

A second possible solution to the generalist's dilemma of optimal nestmate number would be for parasites to adjust their virulent behaviors according to their host, either facultatively at the individual level or via the evolution of host races targeting certain hosts or host types (Gibbs et al. 2000; Mahler et al. 2007) and having host-appropriate virulent behaviors (Kilner 2005; Fiorini et al. 2009). Differential nestling virulence, where parasites kill nestmates in some hosts and not in others, is as yet unknown among today's parasites but could in theory arise if nestling aggression was triggered by host-specific stimuli or maternally inherited from host-specific females. Some evidence for host-adjusted virulent behaviors does, however, come from studies of clutch reduction by adult parasites. In cowbirds, adult females either remove or puncture host eggs at or around the time of parasitism (Ortega 1998). Fiorini et al. (2009) showed that shiny cowbirds puncture more eggs when parasitizing mockingbirds than house wrens even though the latter are easier to break. Brown-headed cowbirds have similarly been proposed to remove eggs more frequently in large hosts than in small hosts (Davies 2000). In cases where nestlings' competitive ability is predictable from host–parasite relative egg size, as it likely is in cowbirds (e.g., Rivers 2007), this differential clutch reduction by the adult parasites could arise from the parasite female's simple rule of destroying more eggs when they are larger than her own and fewer when they are smaller. Adjustable clutch reduction by adult parasites may be a way to achieve optimal brood compositions for nestling parasites in cases where partially reduced brood sizes lead to maximum intake. Our model indicates that intermediate brood sizes can indeed be optimal under some parameter values (see Figure 2). Importantly, however, although adult virulent behaviors imply greater flexibility than is possible for a nestling bound by a kill-all nor kill-none rule, clutch reduction at the egg stage is very likely to have upper limits beyond which hosts abandon their nests (Winkler 1991; Anderson et al. 2009). Also, opposing selective pressures on clutch reduction may be at play, such as optimizing incubation efficiency (McMaster and Sealy 1997). Indeed, in any host–parasite system, selection for better provisioning is unlikely to be the only factor driving the evolution of virulent behaviors; a range of other candidate costs and benefits exist (e.g., Grim 2006). Future empirical studies of nestling intake in a variety of host–parasite pairs will reveal whether, among all these potential factors, a provisions trade-off has played a primary role in the evolution of nestmate killing by parasites specifically, and brood reduction by parasites generally.

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