

PATERNITY-PARASITISM TRADE-OFFS: A MODEL AND TEST OF HOST-PARASITE COOPERATION IN AN AVIAN CONSPECIFIC BROOD PARASITE

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Abstract.—Efforts to evaluate the evolutionary and ecological dynamics of conspecific brood parasitism in birds and other animals have focused on the fitness costs of parasitism to hosts and fitness benefits to parasites. However, it has been speculated recently that, in species with biparental care, host males might cooperate with parasitic females by allowing access to the host nest in exchange for copulations. We develop a cost-benefit model to explore the conditions under which such host-parasite cooperation might occur. When the brood parasite does not have a nest of her own, the only benefit to the host male is siring some of the parasitic eggs (quasi-parasitism). Cooperation with the parasite is favored when the ratio of host male paternity of his own eggs relative to his paternity of parasitic eggs exceeds the cost of parasitism. When the brood parasite has a nest of her own, a host male can gain additional, potentially more important benefits by siring the high-value, low-cost eggs laid by the parasite in her own nest. Under these conditions, host males should be even more likely to accept parasitic eggs in return for copulations with the parasitic female. We tested these predictions for American coots (*Fulica americana*), a species with a high frequency of conspecific brood parasitism. Multilocus DNA profiling indicated that host males did not sire any of the parasitic eggs laid in host nests, nor did they sire eggs laid by the parasite in her own nest. We used field estimates of the model parameters from a four-year study of coots to predict the minimum levels of paternity required for the costs of parasitism to be offset by the benefits of mating with brood parasites. Observed levels of paternity were significantly lower than those predicted under a variety of assumptions, and we reject the hypothesis that host males cooperated with parasitic females. Our model clarifies the specific costs and benefits that influence host-parasite cooperation and, more generally, yields precise predictions about expected levels of host male paternity. These predictions will enable a more rigorous assessment of field studies designed to test adaptive hypotheses of host-parasite cooperation.

Key words.—Brood parasitism, egg-trading games, *Fulica americana*, host-parasite cooperation, paternity trade-offs, quasi-parasitism.

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Alternative reproductive behaviors allow individuals to circumvent ecological or social constraints on reproduction (Trivers 1972; Dunbar 1983; Andersson 1984; Austad 1984; Dominey 1984). Although both sexes adopt alternative behaviors, the nature of the tactics they employ differs due to sexual differences in reproductive constraints. Male reproductive success is typically limited by access to mates, and consequently male alternative reproductive tactics concern increased mating opportunities (Alcock et al. 1977; Dunbar 1983; Dominey 1984; Gross 1985). In contrast, female reproductive success is often limited by resources available for reproduction (Bateman 1948; Williams 1966; Trivers 1972) and hence females adopt alternative tactics to bypass reproductive constraints imposed by resource limitation. In several species of birds and insects, for example, females lay eggs in the clutches or nests of other conspecifics but do not assist in caring for the offspring (Brockman et al. 1979; Yom Tov 1980; Andersson 1984; Tallamy 1985; Eadie 1991).

Recently it has been suggested that the alternative reproductive tactics of the sexes may be linked in some species (Petrie 1986; Emlen and Wrege 1986; McRae and Burke 1996; Alves and Bryant 1998). For example, in species with biparental care, host males might cooperate with parasitic females by allowing access to the nest in exchange for copulations. Several studies have investigated such a paternity-parasitism trade-off, mainly by focusing on quasi-parasitism (sensu Emlen and Wrege 1986) in which host males sire eggs

the brood parasites lay in host nests. Such quasi-parasitism has been documented in a number of species (Emlen and Wrege 1986; Birkhead et al. 1990; Alves and Bryant 1998), although typically at low frequencies. Other studies, however, failed to find evidence that host males sire any parasitic eggs (McRae and Burke 1996). These discrepancies raise two important questions. First, are there benefits to host males other than quasi-parasitism that would also provide evidence for a parasitism-paternity trade-off? Quite possibly, the focus on quasi-parasitism has led researchers to miss additional, potentially more important benefits host males gain by cooperating with parasite females. Second, how large do these benefits have to be to offset the costs of parasitism and thus yield a net benefit to host males? When the costs of parasitism are small, the minimum required benefits would also be small, and large-scale studies would be required to rule out host-parasite cooperation.

To address these questions, we need to identify all of the fitness costs and benefits that shape cooperation by each of the two participants, the parasitic female and the host male. The key issue for the brood parasites in this context is not parasitism per se, but why they should cooperate with host males to lay parasitically. One obvious benefit is that such cooperation increases access to host nests, often a limiting resource for brood parasites (Eadie 1989; Rohwer and Freeman 1989), but females could also gain genetic benefits if

host males are high-quality individuals (Alves and Bryant 1998).

For host males, the benefits are less clear. Some benefits that could affect host-parasite cooperation have been considered previously, but all of the costs and benefits have not been integrated into a cohesive or synthetic framework. Moreover, most of the attention has focused narrowly on one benefit (quasi-parasitism, in which host males sire parasitic eggs), while other potential benefits to host males have been almost completely ignored (but see McRae and Burke 1996). For example, in species whose parasites have nests of their own (Brown and Brown 1988; Gibbons 1986; Jackson 1993; Lyon 1993a), host males may sire some of the eggs the parasites lay in their own nests (McRae and Burke 1996). Clearly, factors other than quasi-parasitism need to be considered to fully determine whether host males should accept parasitic eggs in exchange for mating with parasitic females.

Here, we explore the costs and benefits of a parasitism-paternity trade-off for host males, using both theoretical models and empirical field studies. We first develop a cost-benefit model to explore the conditions under which a host male could increase his fitness by accepting parasitic eggs in exchange for copulations with the parasitic female. Based on parameters that are readily measured in the field, the model provides a general framework for investigating host-parasite cooperation and highlights important components of fitness that have been ignored by most previous studies. We then provide an empirical test of this model, combining genetic paternity data with detailed demographic data for American coots (*Fulica americana*), a species with a high frequency of conspecific brood parasitism (Lyon 1993a).

PATERNITY-PARASITISM TRADE-OFFS FOR HOST MALES: A COST-BENEFIT MODEL

Our focus in this paper is on the fitness trade-offs for host males. We recognize that cooperation between parasites and host females can also occur, but the factors involved are fundamentally different from the factors we consider here (Andersson 1984, 2001; Lyon and Eadie 2000). Our model considers species with biparental care in which the male plays some role in defending a territory or guarding access to the nest (as for many species of birds, fishes, and some insects). In such species, brood parasitism can occur in a several contexts for females, each of which has different trade-offs for host males. We consider these in turn, starting with the simplest case and adding complexity as the parasitic context requires.

We begin by examining the situation in which brood parasites are nonnesting females who lay eggs in only one host nest. Here, the trade-off for host males involves only the eggs in the host nest, and the sole benefit to the host male is siring some of the parasitic eggs laid in his nest (pure quasi-parasitism). We next consider briefly the trade-offs when a parasitic female lays eggs in several host nests, adding the possibility that host males might also sire parasitic eggs laid in other host nests. Finally, we consider the situation in which the parasites have nests of their own, such that a host male can benefit further by siring eggs in the parasite's nest. In all cases, we consider fitness benefits only in terms of the

number of offspring produced, and we do not consider the genetic quality of the offspring (i.e., benefits from good genes or genetic diversity).

Pure Quasi-Parasitism

When the parasite is a nonnesting female who parasitizes a single host, the only benefit to the host male is the possibility of siring some of the parasitic eggs. This benefit, accrued whenever the male sires a parasitic egg (probability P_p), is traded against the cost of parasitism, C , which is the impact of a parasitic chick on host chicks. This cost C differs from the net cost of parasitism to the host male, which is the balance of both the fitness costs and benefits of parasitism to the host male. By siring the parasitic egg, the male can mitigate some of the fitness costs of parasitism, but the impact on the host female fitness will always be C . We assume that unsuccessful parasitic eggs (i.e., eggs that fail to produce chicks that survive to independence) affect neither the costs nor the benefits to host males. With this assumption, the trade-off of quasi-parasitism can be explored by focusing only on nests with successful parasitic eggs.

The cost of parasitism, C , is the amount by which a successful parasitic egg reduces the survival of host chicks; the value of C depends on the degree to which parental care is limiting. When parental care is completely unshareable (sensu Wittenberger 1981) each successful parasitic egg survives at the expense of one host chick, a one-for-one replacement (i.e., $C = 1$). When parental care is completely shareable, a successful parasitic chick has no effect on the number of host chicks produced (i.e., $C = 0$). When parental care is partially shareable (i.e., $0 < C < 1$), each successful parasitic chick reduces the average number of host chicks produced by a proportion C of a chick. Note that when $C < 1$, the total production of offspring, host plus parasite, is increased by $1 - C$ chicks above what an unparasitized nest would produce, because we only consider nests where the parasitic chick survives; the net impact of the parasitic chick on total chicks produced is the one surviving parasitic chick minus the impact on host chicks (i.e., $1 - C$). This increase in total chick production is one benefit host males can gain by siring parasitic eggs.

Host male paternity of his own eggs (P_H , proportion of host eggs sired) also affects the costs and benefits of parasitism because the cost of parasitism is borne only when a parasitic chick harms a host chick that has been sired by the host male (P_H). When host males do not have full paternity of their own eggs (i.e., $P_H < 1$), the cost of accepting a parasitic egg thus becomes CP_H (i.e., the cost adjusted by the probability that it impacts a chick sired by the host male). With less than full paternity of host eggs (i.e., $P_H < 1$), a host male's fitness is further increased when a parasitic egg he sires survives at the expense of an extrapair chick he has not sired.

The trade-offs of quasi-parasitism thus involve one benefit and one cost. At nests where one parasitic chick survives, the number of surviving host chicks is reduced by C (on average). The expected cost to the host male of this reduction is the loss of host chicks times the probability that he sired the chicks: $C \times P_H$. The host male's expected gain is the

probability of siring the parasitic chick: $1 \times P_p$. Thus, the benefits of accepting parasitic eggs exceed the costs when:

$$P_p > CP_H. \quad (1)$$

A host male therefore gains a net benefit from accepting a parasitic egg when his probability of fertilizing the egg exceeds the loss in host young he has sired. Put another way, host males benefit when the ratio of their paternity of parasitic eggs to host eggs exceeds the cost of parasitism:

$$P_p/P_H > C. \quad (2)$$

Thus, three factors promote cooperation between host males and nonnesting parasitic females: low cost of parasitism, low host male paternity of host eggs, and high host paternity of parasitic eggs.

Paternity in Other Host Nests

In some cases, parasitic females may lay eggs in several host nests (Gibbons 1986; Lyon 1993a) and a focal host male could gain the additional benefit of siring eggs that the parasite lays in other host nests. As before, only successful parasitic eggs affect host male fitness. We assume further that parasitic eggs will have the same success in all host nests (on average). With these assumptions, the new trade-off for host males becomes the simplest case (eq. 2) plus the probability of siring parasitic eggs in other host nests. If P_K is the average probability of siring a parasitic egg that is laid in a different host nest, per parasitic egg accepted, then host males should accept a parasitic egg in his nest when:

$$P_p + P_K > CP_H. \quad (3)$$

Obviously, whether a specific host male will gain fitness from parasitic eggs laid in other host nests depends on whether his nest is the last in the sequence of nests the parasite visits. The model, however, deals with average fitness payoffs all host males can expect, not the fitness from a specific encounter, so any nest order effects are included in the average. We also assume that, on average, each host nest receives the same number of parasitic eggs; thus, number of parasitic eggs laid can be ignored. For simplicity, we do not consider this benefit further in this analysis, but it would be straightforward to do so for systems in which it appears to be important.

Host Male Paternity in Parasitic Female's Own Nest

In many birds, parasitic females have nests of their own and they begin laying their own clutches after they lay parasitic eggs, usually without skipping laying (Gibbons 1986; Lyon 1993a; McRae and Burke 1996). In these species, an added benefit to accepting parasitic eggs is the possibility of siring eggs the parasite lays in her own nest (McRae and Burke 1996). Parasitic eggs are normally less successful than parental eggs (Emlen and Wrege 1986; Gibbons 1986; Eadie 1989; Lank et al. 1989; Sorenson 1991; McRae 1995) sometimes several fold (Lyon 1993a, 1998). Host males might therefore trade the risk of accepting low-cost parasitic eggs against the benefit of siring high-value eggs in the parasite's own nest.

We can combine this new benefit with the simple quasi-

parasitism trade-off in equation (1). This is a more complex trade-off that involves eggs in two nests—the host's and the parasite's—and so our focus is no longer on single eggs, but on the total number of chicks gained or lost per nest. Accordingly, we must now consider all parasitized nests, not just host nests with successful parasitic chicks. To do so we need to incorporate the differences in survival rates and numbers of eggs laid by the parasitic female in both nests.

For this trade-off we compute three values: (1) the total number of host chicks sired by the host male that were lost due to parasitism (the cost); (2) the total number of surviving parasitic chicks in the host nest that are sired by the host male (the quasi-parasitism benefit); and (3) the total number of surviving chicks in the parasite's own nest that are sired by the host male (the second benefit). Considering the cost first, the expected number of host chicks sired by the host male that are lost due to parasitism is $N_p S_p C P_H$. This is obtained by multiplying the cost to the host male of a surviving parasitic chick ($C P_H$; right side of eq. 1) times the number of parasitic eggs laid in the host nest (N_p) and the survival rate of those eggs (S_p). (Note that a parameter for host chick survival is not needed because the cost parameter C includes the component of host chick survival relevant to host-parasite cooperation, namely the impact of parasitic chicks on the survival of host chicks.) Second, the total number of surviving parasitic chicks sired by the host male (quasi-parasitism benefit) is obtained by multiplying the probability of siring a parasitic egg (left side of eq. 1) by the number and survival rate of parasitic eggs: $N_p S_p P_p$. Finally, the expected number of surviving chicks sired by the host male in the parasite's own nest (the second benefit) is $N_O S_O P_O$, where S_O is the survival rate of the parasite's own eggs, P_O is the probability that the host male sires each egg in the parasite's nest (or proportion of eggs sired), and N_O is the parasite's own clutch size. Comparing the two benefits with the cost, a host male should accept parasitic eggs in exchange for copulations when:

$$N_O S_O P_O + N_p S_p P_p > N_p S_p C P_H. \quad (4)$$

That is, the number of surviving chicks sired in parasitic female's nest and via quasi-parasitism must exceed the number of sired host chicks lost due to parasitism. The acceptance of parasitic eggs can also be driven entirely by the gain the host male makes in the parasite's own nest, without any quasi-parasitism (i.e., $P_p = 0$). In the absence of quasi-parasitism the trade-off becomes:

$$N_O S_O P_O > N_p S_p C P_H. \quad (5)$$

METHODS

Study Area and Animal

We studied brood parasitism and paternity in a population of American coots breeding on several wetlands near Riske Creek, British Columbia, Canada (Lyon 1993a,b). Coots are socially monogamous and males participate in all aspects of nesting, including incubation, feeding the mobile chicks, and defending territory borders (Gullion 1954). Territories share borders with two to six other territories and intense fights between neighbors over territorial borders are frequent

throughout the breeding season. The adults and chicks remain within the territorial boundaries for at least a month after hatching. Conspecific brood parasitism is common. Over 40% of all pairs are parasitized in this population, and most parasitism is by nesting females (Lyon 1993a). One-quarter of all nesting females laid some of their eggs parasitically (Lyon 1993a). They usually laid their parasitic eggs immediately before initiating their own nests, without skipping laying, and most parasitized immediate neighbors (Lyon 1993b). Egg laying takes place at night, when males are incubating (Gullion 1954; B. E. Lyon, unpubl. data), so males are in a position to allow parasites access to their nests.

Field Methods

We used a combination of several standard techniques to determine the occurrence of brood parasitism: the appearance of more than one new egg in a nest within a 24-h period; the appearance of new eggs after clutch completion; and, rarely, unique egg features (for full details see Lyon 1993a). Brood parasites were identified by visually comparing eggs among nests. The reliability of this method was confirmed by discriminant function analysis based on egg features (Lyon 1993b) and now by the genetic analyses of the present study (see below).

Demographic information was collected from 1987 to 1990, and the samples for genetic analysis were obtained in 1990. To determine the survival of different classes of eggs, and thus the costs and benefits associated with different categories of eggs, all eggs in each nest were individually marked with indelible markers and chicks were individually marked upon hatching with nape tags (Foley 1956) containing unique combinations of colored seed beads. Nests were typically checked daily during the hatching period (three to eight days). At nests where parasite and host chicks were due to hatch on the same day, chicks were pip-marked in the egg (Alliston 1975; nail on middle claw clipped) so that chicks could be matched to the egg from which they hatched. At some nests, host chicks were marked, at others, parasites were marked. We censused post-hatching survival from mobile, floating blinds to determine which chicks survived and, at focal broods, the timing and probable causes of death. Chicks were considered independent if they survived to 30 days, because very little mortality occurs between this point and actual independence at about 50 days.

To collect blood samples for genetic analysis, we trapped adults on their nests during incubation and captured chicks at nests on the day they hatched. Approximately 50–100 μ l of blood was collected by tarsal venipuncture from both adults and chicks, immediately transferred to microcentrifuge tubes containing 1.0 ml Queen's lysis buffer (Seutin et al. 1991), and refrigerated until extraction. We obtained blood samples from 11 parasitic chicks from eggs laid by three parasites in four host nests (four, three, two, and two eggs, respectively). We obtained blood samples from 26 eggs laid by seven brood parasites in their own nests. For 20 of these, we had blood samples for both the parasitic female's mate and the host male(s) at the nests she parasitized; for six additional chicks in the nest of one parasitic female, we only

had a blood sample from the parasite's mate, not the host male.

For eggs in the parasitic females' own nests, we focused our sampling on chicks that hatched earlier in the hatching order (i.e., no later than sixth) for two reasons. First, parasitic females typically lay in host nests (i.e., parasitically) before laying in their own nest (Lyon 1993b); hence host males that copulate with parasitic females during parasitism are most likely to fertilize the early eggs in the parasite's nest. Second, early-laid eggs hatch synchronously, and we could minimize our visits to the nests and disturbance to the chicks.

DNA Fingerprinting, Analysis of DNA Profiles, and Assessing Paternity

Blood samples (50 μ l brought up to 2 ml with 1 \times lysis buffer; Applied Biosystems, Foster City, CA) were incubated at 37°C for 17–24 h with 350 μ l of proteinase K (Boehringer Mannheim, Indianapolis, IN). Genomic DNA was extracted and purified using one phenol:chloroform:isoamyl alcohol (25:24:1) extraction and one chloroform:isoamyl alcohol (24:1) extraction. DNA was precipitated using 1/10 (v/v) volume of 3 M sodium acetate and 2 volumes of chilled (–20°C) 95% ethanol. Samples were kept at –20°C for at least 2 h and then centrifuged at 7000 rpm for 10 min. The DNA pellet was rinsed in 70% ethanol, air dried, and resuspended in 100 μ l Tris-EDTA buffer (10 mM Tris, 1 mM EDTA; pH 7.6). Restriction digest of 10 μ g of each DNA sample was conducted using *Hae*III (New England Biolabs, Beverly, MA; 40 units/digest for 6 h). DNA was precipitated and resuspended in 100 μ l of Tris-EDTA. DNA concentration was estimated by electrophoresis of 1 μ l of each sample with known quantities of standard DNA.

A total of 3 μ g of DNA from each sample, each with 5 μ l of loading buffer (0.25% bromophenol blue, 15% Ficoll, 0.05 M EDTA), was transferred to an Eppendorf tube and brought to an equal volume with double distilled water. Samples were heated to 65°C for 10 min and then quick chilled before loading onto a 0.8% TBE agarose gel. Electrophoresis was carried out at 30 V for 42 h in a refrigerated electrophoresis tank with recirculating 1 \times TBE running buffer (0.09 M Tris-borate, 0.002 M EDTA). The buffer was replaced after 20 h.

Samples from specific host-parasite combinations, for both the relevant adults and chicks, were run on the same gels to minimize among-gel sources of error. All gels also contained one lane of DNA from a reference standard coot and an in-lane DNA size ladder (*Hind*III and *Eco*R1 double-digested lambda phage) in each sample. After electrophoresis, DNA was transferred to an Immobilon-N membrane (Millipore, Bedford, MA) by Southern blotting. Gels were deproteinized in 0.25 M HCl for 15 min, denatured in 0.4 M NaOH and 1.5 M NaCl for 75 min, and neutralized in 0.5 M Tris-HCl (pH = 7.5) and 1.5 M NaCl for 60 min. Southern transfer was carried out using 10 \times SSC (1.5 M NaCl, 0.15 M sodium citrate) for at least 16 h. The blot was then rinsed in 6 \times SSC, air dried for 1 h, and fixed to the membrane by baking at 80°C for 2 h.

Blots were prehybridized in 15 ml of hybridization solution (7% SDS, 1 mM EDTA pH 8.0, 0.263 M Na₂HPO₄, 1% BSA) for 3 h at 65°C in a hybridization oven. Each blot was then

probed with Jeffreys 33.15 (Jeffreys et al. 1985) to detect minisatellite fragments. A final hybridization using bacteriophage lambda DNA probe was conducted to visualize in-lane molecular weight standards. Probes were labeled (random primer labeling) with dCTP using an oligolabeling kit (Pharmacia, Peapack, NJ). Blots were hybridized in 15 ml hybridization solution containing 3×10^6 CPM/ml of labeled probe at 58°C for at least 16–24 h. Membranes were washed twice for 15 min at room temperature, followed by two 30-min washes at 48°C. All blots were rinsed in $1 \times$ SSC, wrapped in plastic wrap, and exposed to X-ray film (Kodak XAR, Kodak, Rochester, NY) between 2 Kodak intensifying screens for 24 h at -70°C . Based on this preliminary evaluation, each membrane was then exposed to X-ray film without intensifying screens for up to two weeks. Following autoradiography, membranes were stripped with $0.1 \times$ SSC, 0.1% SDS, and 1 mM EDTA and preheated to 90°C for two 15-min washes. Stripped blots were then rehybridized with the bacteriophage lambda DNA probe. Autoradiograms were digitized with a flatbed scanner (using Ofoto 1.1 software, Light Source Computer Images, San Rafael, CA); Gelreader software (ver. 2.05, National Center for Supplementing Applications, Champaign, IL) was used to identify and determine the molecular size of bands in the range 1.9 to 21.0 Kb.

We used two criteria to assign paternity: (1) the number of unique bands in an offspring that could not be attributed to bands in either of the putative parents; and (2) band-sharing coefficients (Wetton et al. 1987). For each fingerprint, we calculated band-sharing coefficients as $2n_{AB}/(n_A + n_B)$, where n_A and n_B are the number of bands in the fingerprints of individuals A and B and n_{AB} is the number of bands shared by A and B (Wetton et al. 1987). Band-sharing was calculated only for individuals on the same gel.

Band fragment lengths have associated measurement errors and a cutoff point in fragment length difference is therefore needed to distinguish identical bands that differ in estimated size due to measurement error from those that are actually different bands. We used a 2% size overlap cutoff to identify separate bands. Using this criterion, a pair of putative parents yielded no more than a single unique band in a focal chick, whereas all other combinations of putative parents could be excluded as parents on the basis of several unique bands in the chick. We used the presence of one or zero unique bands as definitive evidence that we had identified both genetic parents; the presence of two or more unique fragments was evidence that one of the putative parents was not the genetic parent of the offspring.

We used band-sharing coefficients to further validate our paternity assignments. These coefficients show considerable variation and are thus less definitive than number of unique bands as paternity indicators. We scored an average of 15.3 bands per individual (range = 7–19). Background band-sharing coefficients for a sample of adults in the breeding population (i.e., for pairs of nonfocal adults run on the same gel) averaged 0.352 (median = 0.353; bootstrapped 95% CI = 0.325–0.381). Given that adult philopatry is virtually nonexistent in the study population (B. E. Lyon, unpubl. data), we assume that the individuals used to assess background band-sharing levels were not related to each other. Because

band-sharing coefficients violate assumptions of statistical independence, we used randomization techniques (Simon 1998; Blank et al. 1999) to calculate confidence intervals and to test for significant differences among categories of interest (e.g., host or parasite males and females). We calculated the sum of absolute differences (SB statistic: group mean x_i – grand mean \bar{x} , $\Sigma(|x_i - \bar{x}|)$; Simon 1998; Blank et al. 1999) as a measure of differences among groups. To determine the significance level of an observed result, we randomly reshuffled the elements of the matrix of band-sharing coefficients values (keeping sample sizes the same for each group) and recalculated the SB statistic; we repeated this 10,000 times.

Comparisons of band-sharing coefficients and unique fragments for adult-young pairs validate our criterion of more than one unique fragment to indicate that a putative male or female was not the parent of a given offspring. Band-sharing coefficients were high and not statistically different for adult-young pairs with no or one unique fragment in the offspring (SB statistic = 0.004, $P > 0.90$). However, band-sharing coefficients were significantly lower for all adult-young pairs with more than one unique fragment (all $P < 0.016$). There were no significant differences among pairs with two or more unique fragments (all $P > 0.33$). Thus, offspring that exhibit fewer than two unique fragments with a given adult also share significantly higher band-sharing coefficients. This pattern is consistent with other studies; comparisons between offspring and their genetic parents rarely yield more than one unique band in an offspring or band-sharing coefficients lower than 0.35 (Lijfeld et al. 1993; Hill et al. 1994; McRae and Burke 1996).

Statistical Comparison of Observed and Expected Paternity Frequencies

A chi-square test was used to test the observed and expected paternity levels for pure quasi-parasitism. For host paternity in parasitic females' nests, we used randomization tests to determine the probabilities of obtaining the paternity levels we observed in the field had our sample had been drawn from a population with average paternity frequencies equal to those predicted by the model. In each randomization, we first created a sample of eggs equal in number to the sample of real eggs we analyzed in parasitic females' own nests. Then, the paternity of each egg was assigned to one of two outcomes—the host sired the egg or he did not sire the egg—based on the predicted paternity frequencies from the model. This was done by generating a random number between zero and one; values equal to or lower than the predicted paternity threshold were scored as sired by the host, whereas values above the threshold were scored as not being sired by the host. We then tallied the total number of eggs in the sample sired by the hosts. Repeating this procedure 10,000 times yielded a distribution from which we determined the one-tailed probability of obtaining, by chance, the observed number of eggs sired by host males in the field study. Note that this approach tests average population levels of paternity (number of eggs in parasite's nests sired by any host male) and does not focus on specific host-parasite nest-for-nest comparisons.

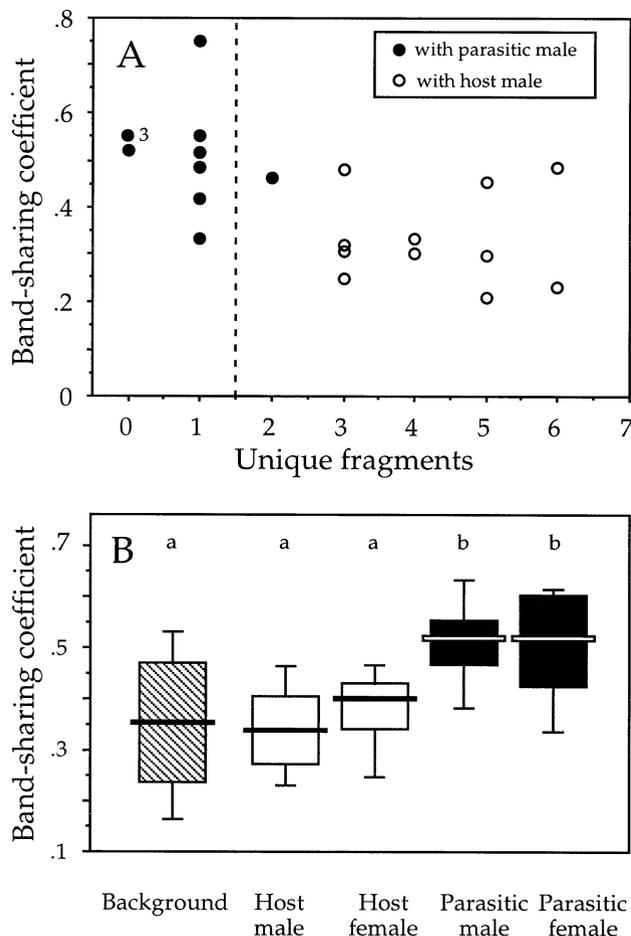


FIG. 1. (A) Band-sharing coefficients and the number of unique bands for parasitic chicks in host nests when compared with the parasitic female and either the parasitic male (filled circles) or the host male (open circles). Numbers beside points indicate multiple samples. The dashed vertical line separates comparisons with a number of unique bands within the level expected if both genetic parents have been identified (left side) from comparisons with too many unique bands for both putative parents to be genetic parents (right side). (B) Box-plots (median, horizontal line; 25–75th percentiles, box; and 10–90th percentiles, vertical line) of band-sharing coefficients for parasitic chicks in host nests with nonfocal individuals (background), host males and females, and parasite males and females, respectively. Different letters above boxes indicate comparisons that differ significantly (10,000 randomization tests).

RESULTS

Genetic Analysis of Paternity and Parasitism

Quasi-parasitism

None of the 11 parasitic eggs were sired by the host males at the parasitized nests. All chicks had at least three unique fragments that could not be accounted for by the host male and the parasitic female (Fig. 1A). This pattern alone allows us to reject the host male as a parent for all 11 parasitic eggs. For 10 of the 11 parasitic chicks, the number of unique bands not accounted for by the parasitic male and female was within the limit expected for true genetic parents (≤ 1 unique band; Fig. 1A). One chick contained two unique fragments when compared to the parasitic female and her mate (Fig. 1A).

Estimated mutation rates for our sample, assuming that single unique bands arise only from mutation, are 0.258 fragments/individual (following Westneat 1993). Accordingly, we would expect two unique bands to arise by mutation alone in 0.73 of 11 individuals ($0.258^2 \times 11$). Thus, it is not unreasonable that the parasitic male was the genetic parent of this chick. Other studies have likewise found that offspring of true genetic parents may, on rare occasions, have two unique fragments (e.g., Lifjeld et al. 1993). Moreover, comparison of the host male with that chick yielded six unique fragments; the probability that this many unique fragments would arise by mutation alone is less than 0.0003 (0.258^6), clearly ruling out the host male as the genetic father. We conclude that no parasitic chicks were sired by the host male and that the parasitic male was the sire in all cases.

Analyses of band-sharing coefficients were consistent with the results from unique fragments. Most band-sharing coefficients with host males were below the range expected for a genetic parent (Fig. 1B), whereas band-sharing coefficients between parasitic chicks and the parasite's own mate were within the range typically expected for a parent (Fig. 1B). Band-sharing coefficients of host males with parasitic chicks did not differ significantly from background band-sharing (10,000 randomization tests; host male-chicks vs. background, SB statistic = 0.048, $P = 0.40$). In contrast, band-sharing coefficients of parasite males with parasitic chicks were significantly greater than those of host males-parasitic chicks and background band-sharing, respectively (SB = 0.174, $P < 0.008$; SB = 0.164, $P < 0.001$).

Host paternity in the parasite's own nest

We found no evidence that host males sired chicks in the parasites' own nests. In all of the 26 chicks sampled, the parasitic female and her mate could account for all of the bands in the chicks (within the limit of one unique fragment) and most band-sharing coefficients were in the range expected for a parent (Fig. 2A,B). In contrast, host males could be rejected as the father of the chicks in all of the 20 comparisons in which we had samples from host males (Fig. 2A). All chicks had more than one unique fragment that could not be attributed to either the parasitic female or the host male, and most chicks had three or more unique bands (Fig. 2A). Thus, all chicks can be attributed to the parasitic male, and we have no evidence that host males sire eggs in the nests of the brood parasites that had earlier parasitized them.

In agreement with this conclusion, most band-sharing coefficients of the parasite's chicks with the host male were below the range of values expected for a parent-offspring comparison and did not differ significantly from background band-sharing (10,000 randomization tests, SB statistic = 0.055, $P > 0.13$; Fig. 2B). In contrast, band-sharing coefficients of the parasite's chicks with the parasite male were significantly greater than background band-sharing (SB statistic = 0.161, $P < 0.0001$) and greater than those of the host male (SB statistic = 0.216, $P < 0.0001$; Fig. 2B). The six samples for which we had blood samples from only the parasitic male all had a low number of unique bands and a high band-sharing coefficient with the parasitic male (Fig. 2A; squares) and were not ambiguous. Taken together, our

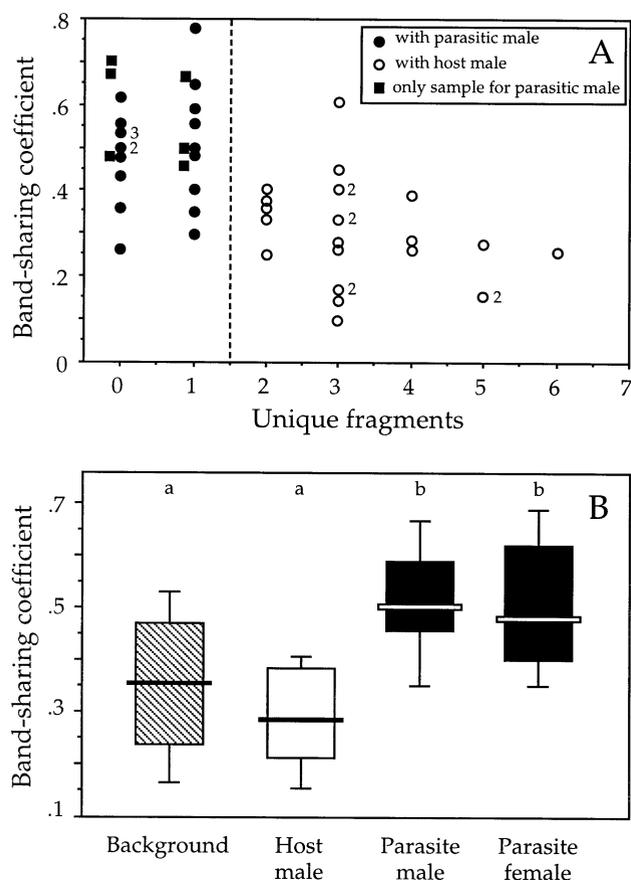


FIG. 2. (A) Band-sharing coefficients and the number of unique bands for chicks in the brood parasites' own nests when compared with the parasitic female and the parasitic mate (filled circles and squares) or the parasitic female and host male (open circles). Squares denote chicks for which blood samples were available for the parasitic male but not for the host male. Numbers beside points indicate multiple samples. The dashed vertical line separates comparisons with a number of unique bands within the level expected if both genetic parents have been identified (left side) from comparisons with too many unique bands for both putative parents to be genetic parents (right side). (B) Box-plots (median, horizontal line; 25–75th percentiles, box; and 10–90th percentiles, vertical lines) of band-sharing coefficients for chicks in the parasite's nests with nonfocal individuals (background), host males, and parasite males and females, respectively. Different letters above boxes indicate comparisons that differ significantly (10,000 randomization tests).

analyses do not support the hypothesis that parasitism involves paternity trade-offs for host male American coots.

Using the Cost-Benefit Model to Assess the Power of Our Comparisons

Before paternity-parasitism trade-offs can be rejected with confidence, we need first to determine the levels of paternity that might be expected. If expected paternity levels are high, our genetic analysis would be informative; however, if expected levels are low, a larger-scale study might be required for an adequate test. We used data from a four-year study of brood parasitism in American coots (Lyon 1993a,b, 1998) to estimate all of the parameters in our model (other than pa-

ternity). On the basis of these estimates, we can predict the minimum levels of host male paternity that would be required for the acceptance of parasitic eggs to be adaptive for host male coots; the predicted and observed levels of paternity can then be compared directly. This provides, in essence, the first attempt to evaluate the statistical power of paternity analyses to reject the hypothesis of adaptive host acceptance of parasitic eggs.

Field Estimates of Model Parameters

Cost of parasitism (C)

We wish to estimate the impact of each successful parasitic chick on the number of host chicks produced. The observation that brood reduction was pronounced in most broods indicates that parental care is limiting in American coots. Only 3% of pairs ($n = 151$) that hatched chicks raised all of their eggs to independence and, on average, only 51% of the chicks in each successful clutch ($n = 1211$ eggs) survived to independence (this total does not include parasitic eggs, which were far less successful than nonparasitic eggs; Lyon 1993a). Observations of focal broods revealed that most of this mortality was due to starvation (Lyon 1993a). Given that pairs cannot even raise all of their own chicks, parasitism should be very costly in terms of impact on host chicks.

The extra young added to broods through brood parasitism provide a natural experiment to estimate the magnitude of the cost parameter C more precisely. The total number of chicks hatched at a nest, host plus parasite, increased with the number of parasitic chicks hatched (Fig. 3A). The slope for this relationship, 0.90 (95% CI = 0.64–1.15), is very close to a slope of one, the slope expected if each parasitic chick added to a brood increased the total number of hatchlings by one chick. The number of parasitic chicks hatching did not affect the number of host chicks hatching; parasitic females do not remove host eggs (Lyon 1993b), and parasitism has only a slight effect on host clutch size (Lyon 1998). However, these additional chicks added to broods through parasitism had no effect on the total number of chicks that survived to independence (Fig. 3B). The slope for this relation, -0.01 (95% CI = -0.33 – 0.31), is essentially zero, indicating that compensatory mortality was complete. This mortality involved both host and parasitic chicks and both types of chicks had equal post-hatching survival rates when hatching order was accounted for statistically (Lyon 1992). With complete compensatory mortality, each parasitic chick survives at the expense of a host chick. For the purpose of evaluating the model, we therefore use the values $C = 1.0$ and $1 - C = 0$.

Survival of parasitic eggs (S_p)

The survival rate for parasitic eggs laid in host nests (proportion of all eggs laid that survived to independent chicks) was 0.086 chicks/egg ($n = 268$ eggs; Lyon 1993a).

Survival of eggs in the parasites' own nests (S_0)

The survival rate S_0 has two components: survival from laying to hatching and survival from hatching to independence. We partition S_0 into these two components because

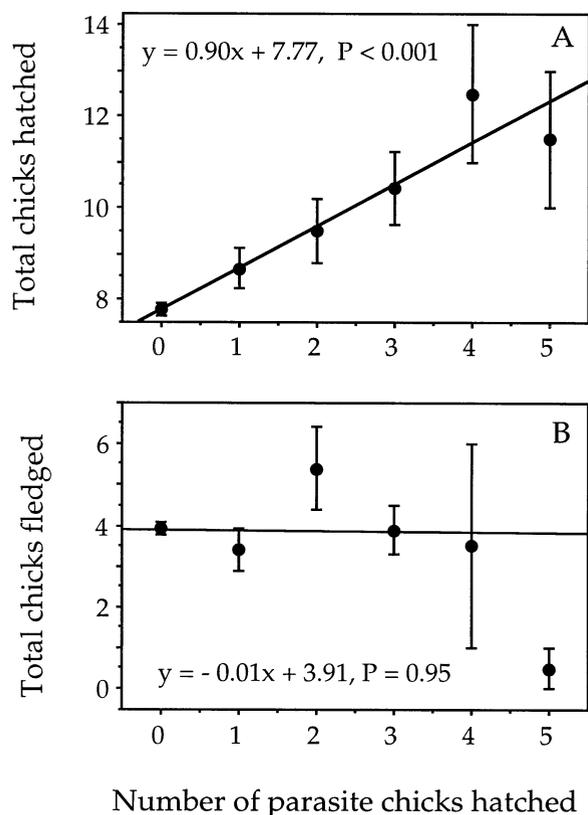


FIG. 3. Assessing the cost of parasitism by the effect of chicks added to broods through brood parasitism. (A) Relation between the number of parasitic chicks hatching at a host nest and the total number of chicks (host plus parasite) hatching. (B) Relation between the number of parasitic chicks hatching at a host nest and the total number chicks surviving to independence. Lines are simple linear regression lines; values shown are means and standard errors.

our paternity samples of chicks in parasitic females' own nests were collected at hatching, not independence, and by necessity, only included nests that hatched successfully (i.e., no samples were obtained from nests that failed to hatch). Predicted levels of paternity, based on the model, must be adjusted to take this sampling regime into account (see below). Eighty-five of 96 parasitic female nests (0.885) successfully reached hatching. The survival rate after hatching was 0.484 chicks/egg (187 chicks survived to independence from 386 eggs in 51 nests of brood parasites). Multiplying

these two survival rates yields the overall survival rate from laying to independence (0.424).

Number of parasitic eggs (N_p)

As presented above, the model focuses on the perspective of a single host male. However, parasitic females often lay in several host nests (Lyon 1993b). If these females mate with each of the host males they parasitize, their own nests may have chicks sired by more than one host male. To take this into account, we ask how many chicks should be sired in each parasite's nest by host males in general, irrespective of specific host identity. To predict this number, one needs the average number of parasitic eggs laid by a parasitic female in all of her host nests combined. On average, each brood parasite laid a total of 3.50 parasitic eggs (± 0.39 eggs, $n = 98$ parasitic females with own nests; Lyon 1993a).

Number of eggs in parasitic female's own nest (N_o)

Parasitic females laid an average of 7.69 eggs in their own nests (± 0.22 eggs, $n = 58$ nests, sample includes only nests that hatched successfully).

Comparison of Observed Versus Predicted Paternity Levels

The above parameter estimates are summarized in Table 1. We can now use these estimates to predict the minimum levels of host paternity required for the benefits of accepting parasitic eggs to exceed the costs.

Pure quasi-parasitism

With a maximum cost of parasitism, as found ($C = 1$), equation (1) indicates that host paternity of parasitic eggs must equal paternity of his own eggs just to break even (i.e., $P_p = P_H$). Starting with the assumption that host males have full paternity of the host eggs ($P_H = 1$), accepting parasitic eggs would be maladaptive for the host male with anything less than full paternity of the parasitic eggs. The observed level of host paternity of parasitic eggs (zero of 11 eggs sired) is obviously lower than the predicted full paternity (siring all 11 eggs; $\chi^2 = 18.1$, one-tailed $P < 0.0001$).

We did not assess the paternity of the host eggs in the parasitized nests we sampled, but we can nonetheless establish the threshold level of P_H above which our sample of zero eggs sired differs significantly from the predicted pa-

TABLE 1. Summary of model parameters, descriptions, and their estimated values for American coots.

Parameter	Description	Estimated value
C	cost of each parasitic egg	1.00
$1 - C$	benefit of each parasitic egg	0
N_o	parasites' own clutch sizes	7.69
N_p	number parasitic eggs laid by parasitic females	3.50
S_o	survival of parasitic females' own eggs	0.424
S_p	survival of parasitic eggs in host nests	0.086
P_p	probability that host males sire parasitic eggs	0
P_o	probability that host males sire eggs parasites lay in their own nests	0
P_H	probability that host males sire host eggs in own nest	not estimated
P_K	probability that host males sire host eggs in other host nests	not estimated

ternity levels. As P_H decreases, so does the paternity of parasitic eggs required for host males to benefit from cooperation with parasites (because when $C = 1$, P_P must exceed P_H for the host to benefit; eq. 1). Thus, we can use the confidence limits for P_P to determine how far P_H could be reduced before our sample would no longer differ from predicted levels. The one-tailed 95% confidence limits for our estimate of P_P (0% of 11 parasitic eggs sired by host males) are 0–20% (Sokal and Rohlf 1981). Thus, the observed lack of paternity of parasitic eggs would differ significantly from predicted levels as long as hosts sire more than 20% of their own eggs (i.e., $P_H > 0.2$). A recent review of extrapair paternity levels in birds found no examples in which average paternity levels for the nest-tending males were as low as 20%, and few cases with less than 40% (Petrie and Kempenaers 1998). We are therefore confident that quasi-parasitism does not account for the acceptance of parasitic eggs by host males, even if host males are less than certain of the paternity of their own eggs. Note that had extrapair paternity occurred even at moderate levels in our population of coots, we should have detected cases in our analysis of the paternity of eggs laid in parasite's own nests. All 26 eggs were attributed to the social mates of the brood parasites and we detected no cases of extrapair paternity in this sample (Fig. 2).

Host paternity in the parasite's own nest

Given that we found no evidence for quasi-parasitism, we can now use the model to predict the minimum levels of host male paternity in the parasitic female's own nest (P_O) required for acceptance of parasitic eggs to be beneficial without quasi-parasitism (eq. 5). Again, we begin by assuming that hosts have full paternity of their own eggs (i.e., $P_H = 1$), but later relax this assumption. Because we now compare different classes of nests and egg types, we need to consider egg survival rates and numbers when estimating paternity levels.

For host males, the cost of accepting each parasitic egg is 0.086 chicks (the probability that a parasitic egg survives times the cost of a surviving parasitic chick, $S_P C$). Parasitic females often parasitize more than one host nest, and we are interested in predicting the total number of chicks in each parasitic female's nest sired by all of the hosts she parasitizes, not just a specific host. We therefore multiply the cost of accepting each egg by the average number of parasitic eggs laid by each parasite (3.5) to predict the total cost to hosts from each parasitic female (i.e., the number of host chicks that were lost due to parasitism). This cost, 0.301 chicks/parasitic female, indicates the minimum number of surviving chicks in each parasitic female's nest that must be sired by host males for the acceptance of parasitic eggs to be adaptive.

The sampling regime we used requires that we make a number of corrections to the above paternity prediction before we can compare it with the observed pattern of host paternity. First, we obtained our blood samples from nests at hatching, not independence, so we must divide the predicted value by the survival rate from hatching to independence (0.484). Second, the predicted value is for all nests, including unsuccessful nests, because parasites whose own nests failed still imposed a cost on their hosts. By necessity, however, we

obtained samples only from nests that hatched successfully. To convert the predicted value to levels predicted for successful nests, we divide by the survival rate from laying to hatching (0.885). Finally, the predicted value is a per nest value, but the randomization tests assign paternity on a per chick basis, so we divide the predicted value by the average number of eggs in parasitic female nests (i.e., $N_O = 7.69$ eggs) to obtain the predicted host paternity per chick. With these adjustments, the expected host paternity per chick sampled at hatching is 0.0913 and the expected total number of extrapair chicks sired by hosts in our sample of 26 chicks is 2.38 chicks. Based on the randomization test, the probability of obtaining a sample of zero of 26 chicks sired by host males from a population that actually has host paternity as predicted (0.0913 per egg) is $P = 0.081$.

Female coots lay parasitically before they initiate their own clutches (Lyon 1993b), so copulations with host males would likely occur before the parasite begins her own clutch. Depending on the patterns of sperm storage and precedence, host paternity might be concentrated in the first few eggs that the parasite lays in her own nest (e.g., Briskie et al. 1998). To assess how laying order effects might influence the outcome of our statistical test, we repeated the analysis by restricting expected paternity to early-laid eggs. (Hatching order is very tightly linked to laying order; B. E. Lyon, unpubl. data.) To calculate expected paternity per early-laid egg, we divided the paternity estimate per nest by the number of eggs included in the pool of early-laid eggs, instead of dividing by the entire clutch size. With the assumption that only the first four eggs laid could be fertilized by the host male (roughly the first half of the parasite's clutch), our observed lack of paternity in the sample of chicks from eggs laid no later than fourth was significantly different from the model's prediction ($n = 21$ chicks, $P = 0.016$). Limiting host fertilization to the first five eggs laid also yielded a significant difference ($n = 24$ chicks, $P = 0.029$).

The above analyses assume that host males sire all of their own eggs ($P_H = 1$). If paternity of these eggs decreases ($P_H < 1$), so does the minimum levels of paternity in the parasite's nest (P_O) needed to recoup the costs of parasitism (eq. 5); all else being equal, larger samples would be required to test the model. To evaluate this fully, we conducted randomization tests with two different levels of host egg paternity ($P_H = 0.9$ and $P_H = 0.8$), restricting host paternity (P_O) to the first four eggs laid. To calculate the predicted host paternity per egg in the parasites' nests when $P_H < 1$, we multiply the value obtained with full paternity ($P_H = 1$) times the new value of P_H . With 90% host egg paternity ($P_H = 0.9$), our sample of zero host-sired chicks in a sample of 21 chicks differs from levels predicted by the model (predict 3.35 sired chicks, $P = 0.026$). With 80% host egg paternity ($P_H = 0.8$), our sample of zero host-sired chicks also differs from levels predicted by the model (predicted 2.98 sired chicks, $P = 0.041$).

Collectively, these comparisons suggest that the trade-off between paternity and parasitism is unlikely to be an important factor favoring host male acceptance of parasitic eggs in American coots. Under all but the most limiting assumptions (i.e., host males have complete paternity of their own eggs and can sire any egg in the parasite's nest, regardless

of copulation order or laying order), our sample, albeit small, was sufficient to reject the hypothesis that host males cooperate with parasite females in exchange for copulations. In sum, parasitism appears to be as costly for host males as it is for host females in the population we studied.

DISCUSSION

We did not find any evidence for a paternity-parasitism trade-off for male American coots. Our results are consistent with those from several other species (e.g., Birkhead et al. 1990; McRae and Burke 1996), although two previous studies did find evidence for such a trade-off for host males, based on the occurrence of quasi-parasitism (McKittrick 1990; Alves and Bryant 1998). In eastern kingbirds (*Tyrannus tyrannus*), electrophoretic data indicated that at least one putative parent could be excluded for 30% of all offspring (McKittrick 1990), but the patterns were consistent with either regular brood parasitism or quasi-parasitism. These levels are high for either type of parasitism, and it would be worth repeating this study with more powerful genetic techniques that can distinguish between the two types. In sand martins (*Riparia riparia*), Alves and Bryant (1998) found that quasi-parasitism occurred in 9% of broods and involved 2.4% of all chicks. However, it was not determined how host males benefited from mating with the brood parasites or whether those benefits outweighed the costs of parasitism.

In fact, aside from reporting the occurrence (or absence) of quasi-parasitism, very few studies have considered directly the costs and benefits that determine whether host males should allow parasitic females to lay eggs in their nests in exchange for copulations. A central focus of our study was to develop a model that explicitly clarifies these trade-offs for host males, and the model serves two important functions. First, it clarifies *all* of the costs and benefits that are likely to affect host male cooperation with parasites, not just quasi-parasitism. Second, these costs and benefits are readily measured demographic and paternity parameters that can be determined with field studies, as we demonstrated with American coots. Using this approach, we were able to determine that we have sufficient statistical power to reject the hypothesis that host males cooperate with parasitic females.

Recent authors have stressed the need to consider biological effects (effect size) when power analyses are conducted (Steidl et al. 1997; Thomas 1997), but in practice it can be difficult to establish biologically meaningful values of effect size. Of the recent series of papers testing for quasi-parasitism, sample sizes are rather small, and no study prior to ours has considered what levels of paternity would be required for quasi-parasitism to be adaptive for host males. If parasitism has little impact on the survival of host chicks, as appears to be the case in several species, very low paternity levels would be sufficient to favor host-parasite cooperation; thus, very large sample sizes would be required to detect this phenomenon. One reason why our study had the statistical power to fully examine host-parasite cooperation is because parasitism so strongly impacts host chicks (Fig. 3). Thus, extreme levels of paternity are needed to favor cooperation, and smaller sample sizes are sufficient to provide an adequate test. Considerations like this underscore the utility of the

theoretical approach we present. By establishing minimum host paternity levels based on biological parameters, our model allows researchers to determine meaningful effect size for use in power analysis. This will be particularly valuable for studies that find either very low or no paternity evidence for a paternity-parasitism trade-off (e.g., Birkhead et al. 1990; McRae and Burke 1996).

Cooperative interactions between host males and brood parasites require benefits to both parties. In their study of one aspect of this trade-off, quasi-parasitism, Alves and Bryant (1998) focus much of their attention on the female perspective. In our study, we focused on the costs and benefits to host males. We did this because we believe that it is ultimately the costs and benefits to host males that will determine whether the interaction is cooperative or parasitic. Parasites can benefit from laying parasitically whether or not they mate with the host (Yom Tov 1980; Gibbons 1986; Eadie et al. 1988; Eadie 1989; Jackson 1993; Lyon 1993a, 1998). However, the converse is not true; host males can only benefit from parasitism by mating with the parasite and siring some of her eggs. In addition, there are a variety of ways females can gain access to host nests when parasitism is harmful to host males, such as sneak visits to unattended nests (Emlen and Wrege 1986) or forced access to attended nests (McRae 1996), but host males cannot force females to lay in their nest if the parasite does not benefit from doing so.

The benefit that males gain from accepting parasitic eggs in exchange for copulations with parasites clearly depends on the context in which females lay parasitically. Host males are likely to gain more by cooperating with nesting parasitic females than with nonnesting brood parasites because they have more potential sources to benefit from, namely parasitic eggs in host nests and eggs in the parasitic female's nest. We consider each of these two contexts in more detail.

Quasi-Parasitism: When Benefits and Costs Are Limited to the Host's Nest

The model predicts that the magnitude of the cost of parasitism to host chicks should have an important influence on the evolution of host-parasite cooperation in cases where the only benefit to host males is siring some of the parasitic eggs laid in his nest. Under the assumption that only successful parasitic chicks impose a cost on hosts, the magnitude of the cost parameter C indicates both a cost and potential benefit of parasitism. When the cost of parasitism is partial ($C < 1$), each surviving parasitic chick increases the total number of chicks produced in host broods by $1 - C$ total chicks, and host male net fitness can be increased by siring the parasitic chick. Biological reasons for why parasitism might increase total clutch size and number of chicks produced are essentially clutch size issues and include: (1) host clutch size is limited by the egg-laying capacity of the host female and not post-hatching food resources (Ar and Yom Tov 1978); (2) parasitism has selected for an obligate adaptive reduction in clutch size for all nesting females irrespective of whether they are parasitized (Power et al. 1989); and (3) host females have a smaller optimal clutch size than the optimum for the male due to sexual conflict over clutch size (Slagsvold and Lifjeld 1989).

Clearly, an understanding of the specific, quantitative costs of brood parasitism is essential to properly assess the scope for host-parasite cooperation. Surprisingly, the costs of conspecific brood parasitism have not received much previous empirical attention (but see Andersson 1984; Eadie 1989), and our precise fitness estimates for these costs appear to be unique. Our model assumes that hosts only suffer a cost of parasitism if parasitic chicks survive, but some costs may be borne irrespective of the survival of parasitic chicks. Possibilities include: (1) host females facultatively reduce their clutch size in response to parasitism (Andersson and Erickson 1982; Lyon 1998); (2) parasitic females remove host eggs when laying parasitically (Lombardo et al. 1989); (3) hosts incorrectly reject their own eggs instead of the parasitic eggs in species with egg rejection (Lyon 1992); (4) host females desert their nests in response to parasitism (McRae 1995); or (5) parasitic chicks that ultimately perish survive long enough to impact the survival of host chicks. In American coots, fitness costs due to these reasons are either absent or minor. A few host females reduce their clutch size in response to parasitism (Lyon 1998), but the adjustment is small because the response period occurs over a very narrow period during laying (only parasitic eggs laid during the host's first three days of laying impact clutch size; Lyon 1992). In addition, because most chick mortality occurs shortly after hatching and is strongly dependent on hatching order (Lyon 1993a), parasitic chicks either perish quickly, with little apparent impact on host chicks, or survive to independence and have a strong impact on host chicks. In other species, however, unsuccessful parasitic eggs or chicks may inflict costs on host reproductive success. If so, a different approach to modeling the costs and benefits of parasitism would be required, because the two parameters we used in our model (i.e., C vs. $1 - C$) are only applicable when the costs of parasitism are limited to host nests where parasitic chicks survive.

A second important assumption of our model is that the fitness costs of parasitic chicks are independent of the number of parasitic chicks in the host nest. This assumption appears valid for American coots because only successful chicks impose costs on the hosts. Accordingly, it does not matter if a successful parasitic chick survives at the expense of another parasitic chick; the unsuccessful chick never enters in the equation. Moreover, parasitic chicks have low survival relative to host chicks (Lyon 1993a), and few host nests ever raise more than one parasitic chick. In species in which unsuccessful chicks do affect host fitness and parasitic chicks do compete with each other, it would be necessary to include a function that scales the cost of parasitic chicks relative to their number.

Host paternity of their own eggs (P_H) also affects the net impact of parasitism on host male fitness. Decreased host paternity of host eggs decreases the net fitness cost of parasitism. Variation in host paternity could play a role at the species level, whereby species with low average levels of P_H are more likely to give rise to a parasitism-paternity trade-off. Alternatively, variation within populations could also be important, whereby only individual males with low P_H benefit from trading eggs for copulations with parasitic females. Alves and Bryant (1998) found that extrapair paternity in the

sand martin appeared to be more frequent than expected in nests that also had quasi-parasitism. They suggested that this pattern could reflect a cost of quasi-parasitism to host males; seeking matings with parasitic females may increase host male susceptibility to cuckoldry. However, this pattern also could reflect a cause of quasi-parasitism, not a consequence, whereby males with low expected paternity in their own nests would be more likely to gain from cooperating with a brood parasite. These two alternatives could be distinguished by experimentally lowering male confidence of paternity (e.g., by temporary removal of the male or the female at a stage of the nesting cycle that affects confidence of paternity but not brood parasitism). If such removals increased the frequencies of quasi-parasitism or host-sired eggs in the parasites' nests, it would indicate that low host paternity is a cause, not a consequence, of a paternity-parasitism trade-off.

The Neglected Benefit: Cooperation When Parasites Are Nesting Females

In species in which parasites are nesting females, the benefits that a host male gains from a parasitic female's own nest may be far more important in favoring host-parasite cooperation than any benefits gained from quasi-parasitism. For example, parasitic eggs typically have lower survival rates than eggs that females lay in their own nest, due to mismatched timing of laying in the host's cycle or egg-rejection (Gibbons 1986; Sorenson 1991; Lyon 1992, 1993a; McRae 1995); therefore they are less valuable. Parasitic eggs laid by American coots have one-fifth the survival rate of the eggs the parasites lay in their own nests (0.086 vs. 0.42 surviving chicks per egg laid). In addition, parasitic eggs compete with host chicks, but eggs sired in the parasite's own nest do not. Thus, all chicks sired in the parasite's own nest increase host male fitness, but not all sired parasitic chicks do so. Finally, nesting parasites typically lay parasitically just prior to nesting (Gibbons 1986; Eadie 1991; Lyon 1993b; McRae 1995), a pattern that makes it more likely that the host male will sire eggs in the parasite's nest than parasitic eggs laid in the host nest. For example, if copulations occur on the same night as parasitic egg-laying, host males will not sire the first parasitic egg laid. However, copulations on the night the last parasitic egg is laid could fertilize eggs the parasite later lays in her own nest. For host males, then, eggs in parasites' nests are probably more valuable, less costly, and more likely to be sired than are parasitic eggs. Clearly, investigating cooperation between host males and parasitic females solely by assessing the occurrence of quasi-parasitism—an approach adopted by most earlier studies—could miss the most important evidence for cooperation. This potential source of additional fitness gains for host males should be considered when high frequencies of regular brood parasitism, but low frequencies of quasi-parasitism, are observed. This situation is unlikely to apply in Alves and Bryant's (1998) study of sand martins because regular brood parasitism (two broods) was even less frequent than quasi-parasitism (four broods); a focus on quasi-parasitism was sufficient to accurately estimate the potential importance of host-parasite cooperation.

McRae and Burke (1996) realized the potential for hosts

to gain paternity in the parasite's own nest and included this important fitness component in their analysis of brood parasitism in the moorhen (*Gallinula chloropus*), a close relative of coots. Their results are very similar to ours in that they found no evidence for quasi-parasitism and no evidence that host males sire eggs in the nests of parasitic females. They did not estimate the specific costs of parasitism or predict the minimum levels of paternity required for host-parasite cooperation. They did, however, propose that parasitism may be facilitated by what appear to be low costs of parasitism to hosts, coupled with a moderate chance that one of the hosts (male or female) and the parasite are close relatives. In our study, the lack of philopatry by adult coots (B. E. Lyon, unpubl. data) likely precludes any role for kin selection.

Other Players That Could Influence Cooperation: Host Females and Parasitic Males

Our analysis focused on the two participants who would benefit from host-parasite cooperation, the host male and the parasitic female. Such cooperation, however, would negatively impact the fitness of the host female and the parasite's mate, and the absence of such cooperation could reflect their defensive tactics. For example, host females might be able to intervene and prevent the parasitic female from laying in the host nest. Likewise, males mated to parasitic females could mate-guard the parasitic female and thereby prevent sufficient paternity for cooperation to benefit the host male.

Host-parasite cooperation is not a prerequisite for successful parasitism of host nests because brood parasitism was frequent in our population in the absence of cooperation. Thus, parasitic females are able to gain access to host nests without assistance from host males and, when parasitism is successful, both the host male and female suffer the costs of parasitism. Thus, host males and females have similar fitness interests with respect to brood parasitism. Accordingly, selection is predicted to favor defenses by both sexes of hosts to mitigate the occurrence and/or costs of brood parasitism. Similarly, the observation that parasitic males sired the parasitic eggs laid by their mates (Fig. 1) indicates that both sexes gain fitness benefits from parasitizing other pairs. Thus, in our population the fitness interests of host males and parasitic males, respectively, are congruent with those of their mates—the potential for conflict over parasitism lies among pairs, rather than within.

Other Trading Games between Care-Giving Males and Care-Seeking Females

We examined the conditions under which host males benefit from accepting parasitic eggs in exchange for copulations. These trade-offs show close parallels with those in a variety of other breeding systems involving care-giving males and care-seeking females. Thus, variants of our model could be useful in understanding some of the dynamics of these other breeding systems.

For example, female burying beetles in the genus *Necrophorus* lay eggs on animal carcasses, and these eggs are tended by one or both sexes in various species. Brood parasitism has been reported in some species, whereas a breeding system

similar to quasi-parasitism has been reported in others (Müller et al. 1990; Eggert and Sakaluk 1995). Our model could provide a useful framework for exploring the relationship between these two social systems. Similarly, in a variety of birds, insects, and fish, males alone care for eggs laid by one or more females (e.g., Bruning 1974; Perrone and Zaret 1979; Smith 1980; Birks 1997; Emlen et al. 1998). When individual females lay eggs for more than one male, some males may not have full paternity of the eggs and offspring they tend, but they may also sire eggs laid in the nests of other males (Oring et al. 1992). Instances in which males care for offspring sired by other males amount to reproductive parasitism by the care-seeking females. A complete understanding of the dynamics of such breeding systems may require not only an analysis of the paternity of the eggs tended by males but also the degree to which males benefit from eggs they sire in the nests of other males. Clearly, trading games between care-giving males and care-seeking females occur in a variety of social contexts other than brood parasitism, and the cost-benefit approach we have developed may be a useful starting point for understanding the factors that shape male-female cooperation in general.

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