Conspecific Brood Parasitism in Birds: A Life-History Perspective

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Abstract

Conspecific brood parasitism (CBP), whereby females lay eggs in the nests of other conspecifics, occurs in over 200 species of birds. As an alternative tactic to typical nesting, CBP expands and enriches the classic avian clutch size problem. It is an integral component of a flexible life-history strategy and, consequently, many intriguing aspects of this behavior—adaptive benefits to parasites, host-parasite interactions, population and evolutionary dynamics—can be understood best from a life-history perspective. Because parasite fitness depends on hosts, yet parasitism potentially reduces host fitness, CBP offers a novel opportunity to explore conflicts of interest within species. The intersection of life-history evolution, conflicts of interest, and frequency-dependent fitness provides much scope for theoretical exploration, and recent models indicate a complex range of evolutionary dynamics is possible, including consequences of CBP for population dynamics and conservation. CBP may also be a macroevolutionary stepping stone to diverse breeding systems.

INTRODUCTION

Parental care is costly (Clutton Brock 1991). It comes as little surprise, then, that various forms of reproductive parasitism have evolved that enable individuals to gain the many benefits of parental care while avoiding the substantial costs and constraints. The best-known examples of such reproductive parasites are the one hundred species of obligate interspecific avian brood parasites—birds that never have nests of their own, but instead lay eggs in the nests of individuals of other species, who then care for the parasite's eggs and young (Davies 2000, Rothstein 1990). This seemingly bizarre behavior—having one's young raised entirely by another species—has attracted the interest of naturalists and evolutionary ecologists alike for centuries (see Davies 2000) and, over the past several decades, has been the focus of much research on host-parasite coevolution, ecological specialization, mimicry, antiparasitic tactics of hosts, and conservation biology (Davies 2000, Payne 1977, Rothstein 1990).

Far less well appreciated are the conspecific brood parasites who lay eggs in the nests of other individuals of their own species, but provide no subsequent care for the eggs. Although no less puzzling than its interspecific counterpart, conspecific brood parasitism (CBP) has received much less attention, perhaps because it is more difficult to detect, and hence to study. In Yom-Tov's (1980) first review of this behavior over a quarter of a century ago, only 53 species were listed as conspecific parasites. With the advent of molecular genetic techniques, accompanied by increasingly detailed field studies, CBP has now been documented in 234 species of birds (Yom-Tov 2001), and is particularly prevalent in eight groups: grebes, waterfowl, grouse and allies, rails, estrildid finches, swallows, starlings, and weaverbirds.

A growing body of empirical and theoretical work is beginning to explore this behavior from a variety of perspectives. Who are the parasites and why do they lay parasitically? What are the consequences to hosts? What adaptations do hosts or parasites exhibit that might increase their success in their reciprocal evolutionary conflict of interest? What are the evolutionary and population dynamics of brood parasitism and typical nesting in populations? The result is a vibrant, but somewhat scattered collection of research that to date has lacked a synthetic, overarching framework. A goal of this review is to work toward such a synthesis. Indeed, an overarching framework within which to understand the evolutionary ecology of CBP already exists—simply, life-history evolution—and we hope to show that viewing CBP from within such a framework can help integrate and clarify the large body of literature that has developed.

Why is CBP so interesting? We can suggest at least four reasons. First, as a discrete alternative to the primary reproductive strategy of providing parental care, brood parasitism is one of the relatively few examples of an alternative female reproductive behavior (ARB). ARBs have been extensively studied in males, but have received much less attention in females (Henson & Warner 1997)—a female perspective will enrich, and broaden, our understanding of ARBs in general. Second, by its very nature, CBP offers challenges not posed by the study of interspecific brood parasitism. For example, host-parasite coevolution must take a very different trajectory within species, given that any genes that code for adaptive traits expressed in hosts or parasites will also find themselves expressed in the other player. Theory on intergenomic conflict (Rice & Holland 1997) may have much to teach us about how such arms races arise in the case of CBP (if they do), and their likely evolutionary dynamics. In the interim, detailed field studies have uncovered a fascinating array of host and parasite adaptations. Third, the dynamics of hosts and parasites are inherently frequency-dependent, because parasites depend on hosts of the same species, and a purely parasitic population could never persist. Parasite reproductive success depends on the availability of suitable host nests, while in turn, host success may be depressed by frequent parasitism. CBP is therefore well suited to evolutionary game theory analysis, and a veritable explosion of theoretical models has occurred. Finally, because of its potential impacts on both host and parasite fitness, CBP could have significant population consequences, and thereby implications for conservation and management.

We focus this review on birds simply because it is the group with which we are most familiar, there is an extensive recent literature on this topic in birds that has not been fully synthesized, and because life-history evolution has received far more attention in this taxonomic group than others. For the other major groups of organisms in which this behavior is prevalent, excellent reviews of CBP in insects have been published by Field (1991) and Tallamy (2005), and insight on similar behaviors (alloparental care) in fishes has been provided by Wisenden (1999).

WHY DO FEMALES LAY EGGS IN THE NESTS OF OTHERS?

Epiphenomenon or Adaptation?

Early studies of CBP focused primarily on proximate explanations for parasitic behavior (Heusmann et al. 1980). Recent studies have instead focused on the adaptive basis of CBP, typically in the context of alternative female reproductive behaviors (e.g., Andersson 1984, Eadie et al. 1988, Sorenson 1991, Yom-Tov 1980). The possibility that CBP is a nonadaptive consequence of some other behavior should always be considered (e.g., Semel & Sherman 2001, Waldeck & Andersson 2006). However, the fact that CBP occurs in a large number of species belonging to diverse taxa, and given that a growing number of studies demonstrate positive fitness consequences of CBP and sophisticated means by which birds pursue parasitic egg-laying (e.g., Ahlund 2005, Brown & Brown 1988, Weigmann & Lamprecht 1991), suggest that the epiphenomenon hypothesis cannot provide a general explanation of this behavior.

Current Hypotheses

Existing hypotheses on the adaptive benefits of CBP have typically been classified into four types (reviews in Andersson 1984, Eadie et al. 1988, Lyon 1993a, Petrie & Møller 1991, Sorenson 1991):

1. Best-of-a bad-job (BOBJ)—females lay parasitically when environmental or phenotypic factors limit the ability to breed otherwise (constraint), or when environmental conditions are unfavorable such that the prospects for successful reproduction by nesting are low (restraint). Parasitism is maintained in a population as a conditional tactic (Dawkins 1980) because, even though it yields a lower payoff than nesting, some fitness is obtained that would not otherwise be possible. Under the restraint hypothesis, it is also possible that even when nesting could be successful, parasitsim might be a preferred option if the cost of reprodution is high. Strictly speaking, this is not a BOBJ but rather an example of optimizing reprodutive effort to maximize lifetime fitness (parasitism provides an intermediate alternative to nesting or not nesting that fine tunes benefits relative to reproductive costs).
2. Nest loss—females lay parasitically after their nest is destroyed during laying. Their option is to waste partially formed eggs or lay them in another female's nest (also sometimes referred to as a BOBJ).
3. Lifelong specialist parasites—females depend entirely on other females to raise their offspring and enjoy higher lifetime fitness when rare in the population, presumably because of the advantages of emancipation from parental care and enhanced lifetime fecundity. However, because these parasites rely entirely on nesting individuals to rear their offspring, negative frequency-dependent selection stabilizes the frequencies of nesting and parasite females in the population (a mixed evolutionarily stable state).

4. Fecundity enhancement—nesting females lay eggs parasitically to bypass some of the constraints of parental care on clutch and brood size, and thereby increase fitness beyond that possible through nesting alone. This hypothesis has also been referred to as a mixed reproductive strategy, but here is intended in the sense originally implied by Trivers (1972).

The problem is that these hypotheses are potentially confounded at multiple levels, intermixing ideas on what a female does (nest, parasitize, or both) with what she gets out of her decision (fitness benefits), with the ecological factors influencing her decision (nest loss, resource limitation), and finally with the mechanisms that might maintain some frequency of CBP in combination with nonparasitic nesting [condition-dependent versus frequency-dependent evolutionarily stable strategies (ESSs)]. Moreover, many of these hypotheses are vague about the specific component of fitness that CBP benefits. We think that some insight can be gained by considering CBP more broadly in the context of a flexible life-history strategy, which entails consideration of both the developmental basis of parasitism (Sorenson 1991) and the specific fitness components that make CBP beneficial in the different ecological and social contexts in which it is used.

Conspecific Brood Parasitism and Nesting Decisions Integrate to Comprise a Flexible Avian Life History Strategy

Consider the set of reproductive options open to a female in any given year, and how CBP might fit into this scenario: she can refrain from breeding entirely, she can lay all of her eggs parasitically, she can lay all of her eggs in her own nest, or she can combine parasitism with nesting. Sorenson (1991) provided a conceptual model that nicely summarizes all four options in a single life-history framework (**Figure 1**). According to this model, the optimal level of reproductive investment of a female varies with ecological conditions, following Williams (1966). When prospects for success via nesting are low and/or costs of reproduction are high, females respond by employing strategies of low reproductive investment (nonbreeding or parasitic egg-laying). Conversely, when prospects are good, females increase their reproductive investment, perhaps above the maximum that could be invested in a single nest, leading to both nesting and laying some eggs parasitically (**Figure 1**).

Sorenson's (1991) model emphasizes two important points. First, the set of four reproductive options provides a series of decisions on a continuum from low to high reproductive investment, as well as low to high fitness returns. Depending on the life-history features of a particular species, however, not all options need be realized. For example, in some species, most or all parasitism appears to be by non-nesting females (Forslund & Larsson 1995, Sandell & Diemer 1999), whereas in other species, parasitism is almost entirely by nesting females (Brown & Brown 1998). The distinction between parasites with and without their own nests is important because these two contexts of parasitism likely involve different constraints, and different hypotheses may apply.

Second, brood parasitism is combined in various ways with typical nesting over a female's lifetime to provide a flexible life-history strategy, whereby females tailor their reproductive investment and options to prevailing ecological and social conditions (Eadie 1989, Lyon 1993a, Sorenson 1991). Key here is the idea of plasticity: The four different options (**Figure 1**) are decisions available to any female in a single breeding season, and the optimal decision for a specific female will depend on the ecological, demographic, and social context she faces in a given year. Because these factors will change across years, so too will the option chosen by a female. The focus on flexibility fits with empirical observation—there is no evidence for any species of professional life-long parasites, and the few studies that have followed banded individuals across years all

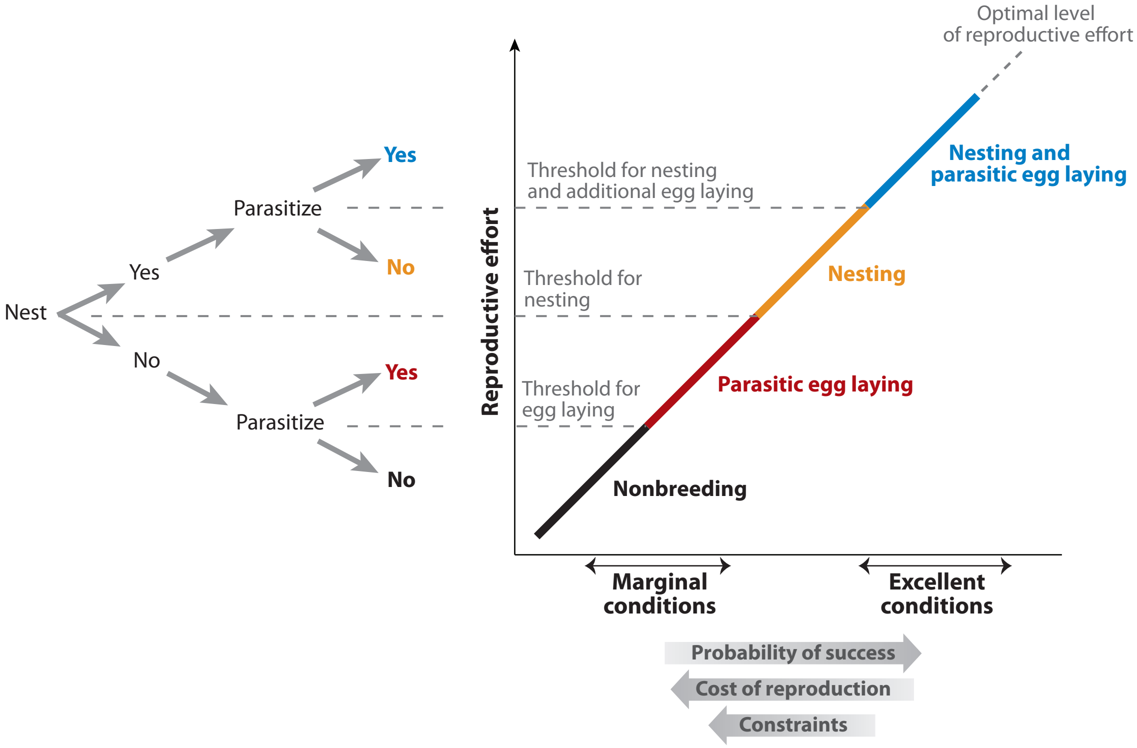

Figure 1

Sorenson's (1991) reproductive decision model. The optimal level of reproductive effort in breeding (*45° line*) varies directly with ecological and phenotypic conditions (probability of success, parental ability, costs of reproduction, ecological constraints, etc.). Nesting requires a high minimum reproductive investment (*dashed horizontal line* labeled Threshold for nesting). Egg laying also requires a minimum level of reproductive effort, but this threshold is lower than that for nesting (*dashed horizontal line* labeled Threshold for egg laying). Without the possibility of conspecific brood parasitism, females are faced with an all-or-none decision to nest or not breed. In marginal conditions (e.g., low probability of success), females would expend either much more reproductive effort (above the optimal investment) or much less (below the optimal) than conditions would warrant. Parasitic egg laying requires a lower level of effort (egg laying) and so allows a female to adjust her investment to better match the probability of success. Conversely, when conditions are excellent and the probability of success is high, females should increase their reproductive investment, possibly above the maximum that could be invested in a single nest. By laying eggs parasitically, in addition to nesting, females can adjust their investment upward when returns on investment are high. Only some females may be able to exceed a threshold where both nesting and parasitic egg laying are possible. The model shows the optimal match between reproductive effort and environmental conditions; in reality most females may not be able to invest optimally, owing to imperfect information or because the reproductive option does not permit infinite fine tuning of investment.

provide direct evidence that females switch options across years (Ahlund & Andersson 2001, Eadie 1989, Forslund & Larsson 1995, Heusmann et al. 1980, McRae 1998, Sorenson 1991). In the parlance of alternative reproductive behaviors, nesting and CBP are alternative reproductive tactics that, when combined together in all possible combinations, comprise a conditional life-history strategy (Brockmann 2001, Gross 1996). With conditional life-history strategies, fitness comparisons across tactics, or across options (e.g., parasites versus nonparasites, Brown & Brown 1998) are not informative in terms of understanding the evolution of the overall life history. Fitness of some options may be low, but the option will be favored as long as it provides higher fitness than all other options would in a given context; fitness relative to that of individuals pursuing other options is not germane (**Figure 1**).

An Alternative Classification of Hypotheses

Sorenson's framework provides a synthetic overview for how parasitism fits into an overall female reproductive strategy, but we still need to understand specifically how fitness is enhanced by engaging in CBP. We propose a modification to the current conceptual structure for hypotheses on CBP that instead focuses on the three fundamental fitness components that influence optimal reproductive investment: (*a*) current fecundity, (*b*) offspring survival, and (*c*) adult survival (and hence future fecundity). These are the same fitness components that apply to clutch-size evolution in general (Godfray et al. 1991, Martin 1987, Roff 1992, Stearns 1992). This makes sense because CBP is, in many ways, simply an extension of the classic clutch-size problem (how many eggs to lay and where to lay them?).

It is also instructive to consider fitness components separately for the two different ecological contexts—parasites without nests of their own and those with a nest—because different life-history trade-offs may be involved (**Table 1**). Effectively, there are three questions that should be

Table 1 A framework of hypotheses on the adaptive benefits of conspecific brood parasitism[a]

Context	Mechanism	Fitness component enhanced	Previous hypothesis
Non-nesting parasite	**Egg production**—females bypass the cost of nesting (incubation, brood care) and can thus allocate more effort into egg production and maximize total fecundity	Current fecundity	Not emphasized; could explain lifelong parasites
	Nest/territory limitation—females unable to obtain nest site or territory; females could invest heavily in attempting to acquire a site, but would exact a huge cost in adult survival; given that females lack critical resources for nesting, CBP increases fecundity over that obtained by non-nesting	Adult survival and/or Current fecundity	BOBJ Constraint Salvage strategy Nest limitation
	Energy/condition/experience—females in poor condition, with reduced access to energy resources or lacking experience would pay large survival costs by attempting to nest on one's own; parasitism provides a lower cost alternative	Adult survival	BOBJ Restraint Salvage strategy Energy limitation
	Quality of brood rearing—laying eggs in nests of higher quality parents or higher quality sites enhances offspring survival over what would have been possible in a nest/site of one's own	Offspring survival	Nest predation could apply
Nesting parasite	**Nest loss**—females suffering nest loss during egg-laying salvage some reproduction by laying remainder of developing clutch parasitically	Current fecundity	BOBJ Constraint Salvage trategy Nest loss
	Clutch size/brood size constraints—bypass clutch-size or brood-size constraints and increase total production of offspring via increased fecundity and/or increased offspring survival	Current fecundity and/or offspring survival	Fecundity enhancement Side-payment Dual nesting
	Cost of reproduction—reduction of clutch size in own nest (by laying some eggs parasitically) reduces costs of parental care and enhances adult survival	Adult survival	Not emphasized

[a] This framework emphasizes the distinction between hypotheses that apply to females with versus without nests, and focuses attention on the key fitness components influenced through CBP. Some hypotheses are not mutually exclusive.

answered to understand the benefit of CBP in any specific context: (*a*) does the female have a nest or not; (*b*) what fitness components and life-history trade-offs play a role in leading to increased fitness benefits via parasitism; and (*c*) what ecological, social, or physiological factors influence these trade-offs? We have attempted to recast existing hypotheses in this framework (**Table 1**). This shift in focus provides three benefits: It directs attention to the specific fitness components, which are too often implicit rather than explicit; it identifies fitness components that have not been adequately considered in existing hypotheses; and it clearly distinguishes between fitness components and the ecological factors that influence fitness components (e.g., nest site limitation, stressful conditions). Although our framework focuses on the individual fitness components that drive the benefits of CBP, we are well aware that life-history traits evolve by optimizing trade-offs between traits. Accordingly, some contexts of parasitism may involve increased fitness levels for some components, and reductions for others, relative to the alternative reproductive decisions available to the female. In addition, the adaptive explanations for parasitism (**Table 1**) are not mutually exclusive, and parasitism might increase more than one fitness component.

Given this revised framework, we now review empirical studies with respect to the different contexts of CBP, their ecological correlates, and what is known about the fitness components that CBP benefits. With respect to the question of whether or not parasites have nests of their own, individual brood parasites have now been identified in 17 species: in six species, parasitism was by both nesting and non-nesting females; in six other species, it was primarily by nesting females; and in five species, the parasites were non-nesting females. Most of these studies measured some aspects of reproductive success, but they vary tremendously in the depth at which fitness components were investigated.

Parasitism by Non-Nesting Females

As Sorenson's framework shows (**Figure 1**), parasitism by non-nesting females is bracketed by two other options—not laying any eggs at all, or laying all eggs in your own nest (**Figure 1**). Which of these other options is the main alternative to a non-nesting parasite may vary, perhaps explaining why several different ecological contexts and fitness components can all lead to parasitism by non-nesting females. One possibility is that females unable to obtain some critical resource for breeding—a nest site or territory—adopt parasitism as a BOBJ alternative to nesting, implying that the trade-off is with nesting and that fitness would be higher if they were able to have a nest. Support for this general idea comes from observations that CBP correlates with nest site availability (Eadie 1989, Lank et al. 1989, Sandell & Diemer 1999) or territory saturation (Lyon 1993a), and experiments that alter the frequency of parasitism by altering nest site availability (Eadie 1991, Gowaty & Bridges 1991).

Alternatively, laying parasitically may be a superior option even when females have the option of nesting (i.e., parasitism is driven by restraint, not constraint). Restraint can be favored owing to trade-offs involving any of the three basic fitness components, but typically these are not made explicit and instead an all-purpose "salvage strategy" is tested (a term applied to several BOBJ hypotheses). Support for the salvage strategy hypothesis is suggested by observations that non-nesting parasites are often young, inexperienced, or physiologically stressed females (Eadie 1989; Lank et al. 1989; Semel & Sherman 2001; Sorenson 1991, 1993; Weigmann & Lamprecht 1991). It would be interesting to know the degree to which these patterns reflect excessive costs of reproduction if these females were to nest, fecundities as a nesting bird that would be too low to offset fixed costs of parental care (Eadie & Lyon 1998), or insufficient parenting abilities to make nesting profitable (low offspring survival). The major difficulty in distinguishing among these alternatives is that we can only observe the fitness gained in the context actually chosen by the female, and we do not know how they would perform were they to nest. Comparisons with females that do have nests would be misleading because these are females with more to invest, and therefore with different trade-offs—the apples-to-oranges comparison problem.

An underappreciated alternative explanation for parasitism by non-nesting females is that parasitism might be driven by survival effects on offspring, rather than the adult female. If a female expects low payoffs from laying eggs in her own nest, due to poor parenting ability, low territory quality, or high risk of nest predation, then laying all eggs parasitically may yield higher fitness than if she were to nest. This "upgrade" benefit to brood parasitism could work in two ways. Females could base the decision to nest or lay parasitically on the situation at their own nests relative to the average success of parasitic eggs in the population. This would require some simple rule of thumb based on predictors of average egg success. Alternatively, parasites could assess variation among potential hosts and target nests that have higher than average survival rates, as has been shown for two species (Brown & Brown 1991, Pöysä & Pesonen 2007). Pöysä & Pesonen (2007) proposed that variation in nest site safety, coupled with an ability to selectively parasitize safe sites, might explain brood parasitism, but their model implicitly assumed that parasites are professional lifelong parasites. The hypothesis we outline here provides a broader context for this idea.

Parasitism by Nesting Brood Parasites

The Nest Loss hypothesis predicts that brood parasitism directly follows the predation or destruction of a female's nest during laying, a prediction observed in several species following either experimental (Emlen & Wrege 1986, Feare 1991, Haramis et al. 1983, Stouffer & Power 1991) or natural nest destruction (McRae 1997). However, experimentally inducing brood parasitism may not always be very informative about the overall importance of nest loss; in European starlings (*Sturnus vulgaris*), for example, parasitism was induced by two separate nest destruction experiments (Feare 1991, Stouffer & Power 1991) but nest loss rarely occurs under natural circumstances (Power 1998). Nest loss appears to be at most a minor explanation for most species, but it is an important factor in two species (Emlen & Wrege 1986, McRae 1997).

Most parasitism by nesting females involves females with their own nests who lay parasitically before they initiate their own clutches and typically parasitism is associated with an increase in total fecundity (Ahlund & Andersson 2001, Lyon 1993a, McRae 1998, Møller 1987, Sorenson 1991). However, contrary to Brown & Brown (1988), brood parasitism need not be associated with an increase in total current fecundity to increase fitness. For example, consider a bird that reduces the clutch size in her own nest by one egg to lay the egg parasitically [as Brown & Brown (1988) report for egg-transferring swallows]. Total fitness is increased as long as the net increment in fitness from the parasitic egg exceeds the fitness that would have been gained had the egg been laid in the female's own nest. This situation can occur when an egg has a very small effect on fitness when laid in the bird's own nest [as modeled by Jackson (1993)], when parasites are able to lay in nests with higher-than-average offspring survival (Brown & Brown 1991, Pöysä & Pesonen 2007), or when a clutch-size reduction significantly increases adult survival. Ultimately, because nesting females have their own nests, the key question is, Why don't they lay the parasitic eggs in their own nests? This is a clutch-size problem that can obviously involve any of the three basic fitness components. We explore this idea further in the **Supplemental Materials** (follow the **Supplemental Materials link** in the online version of this article or at **http://www.annualreviews.org**). Although it is useful to consider the potential roles of each fitness component in isolation, in reality they will often operate jointly, particularly fecundity and offspring survival (e.g., Lyon 1998).

Risk Spreading Is Not a Viable Explanation for Brood Parasitism

A persistent idea is that brood parasitism benefits females by spreading the risk of nest predation—spreading eggs among more than one nest increases a female's probability of having at least one offspring survive (Payne 1977). With both simulation and analytical models, Bulmer (1984) showed that there is little selective benefit to spatial bet-hedging in the form of laying eggs in multiple nests. Most studies of brood parasitism now reject a role for risk-spreading (Lyon 1993a, Pöysä & Pesonen 2007, Sorenson 1991), but some empirical studies continue to claim support for the idea (e.g., Alves & Bryant 1998; Brown & Brown 1988, 1989). Clearly, the idea has deep intuitive appeal, perhaps because evolutionary biologists are trained to think about individuals and sometimes lose sight of the fact that it is selection on genotypes that ultimately matters (Hopper et al. 2003). For example, selection on a trait depends on the average fitness for all individuals bearing the trait—in the case of spreading versus clumping eggs, when the average fitness is calculated for a large number of spreaders, the issue of individual variance in reproductive success vanishes. Put another way, the contribution to the overall average fitness by a clumper who loses her nest and produces zero offspring is exactly offset by a successful clumper that produces a whole brood (see also Hopper et al. 2003).

PARASITISM . . . OR NOT? THE FITNESS COSTS OF RAISING FOREIGN OFFSPRING

A fundamental issue, and one that has received surprisingly little empirical investigation, is the magnitude of the fitness costs to hosts of raising foreign young. This is a critical issue for several reasons: (*a*) if hosts suffer no fitness costs from raising foreign offspring, or even gain net benefits, then it is obviously not a parasitic interaction; (*b*) the magnitude of the costs to hosts critically influences predictions about the evolution of brood parasitism, especially the role of kin selection; and (*c*) an understanding of the costs of parasitism is essential for understanding the presence or absence of host defenses.

Brood parasitism can potentially reduce host fitness in several ways: host clutch size can be reduced by egg damage or egg removal by the parasites during the act of parasitism (Lombardo et al. 1989); enlarged parasitized clutches can suffer reduced hatching success (Eadie 1989, Semel & Sherman 2001, Weigmann & Lamprecht 1991) or take longer to incubate and suffer an increased risk of predation (Gibbons 1986, Nielsen et al. 2006a); hosts can suffer a reduction in the number of their own offspring fledged (Lyon et al. 2002); or hosts may suffer lower adult survival (Brown & Brown 1991). Although it is tempting to believe that the costs of parasitism will be highest in species that feed their offspring and where brood size is constrained by parental food (e.g., Rohwer & Freeman 1989), costs also can be high in some precocial species (e.g., Sorenson 1991).

Most evidence for a cost of brood parasitism comes from observational studies that compare the reproductive success of parasitized and nonparasitized individuals. Several such studies have shown that hosts have lower hatching or fledging success than nonparasitized individuals (Brown & Brown 1991, Lank et al. 1990, Romagnano et al. 1990, Semel & Sherman 2001, Sorenson 1991). The correlation between parasitism and adult survival has received less attention: Brown & Brown (1991) found considerably lower survival in parasitized cliff swallow individuals but Lank et al. (1990) found no pattern in a study of waterfowl. Without experiments, however, any evidence for costs is not fully convincing because differences between parasitized and nonparasitized nests could reflect the fact that lower quality birds or territories are more vulnerable to parasitism (Eadie 1989, Lank et al. 1990). Only three experimental studies of costs have been conducted—these find little evidence for costs of moderate levels of brood parasitism, perhaps not surprising because all three studies involved precocial species (Briggs 1991, Dugger & Blums 2001, Eadie 1989). Additional experiments are needed.

Depending on the specific nature of the costs, however, observational studies can provide evidence for costs of parasitism that are unlikely to be confounded by individual quality. For example, Sorenson (1997) found surprisingly high costs of parasitism in two species of waterfowl: Parasitic females displaced large numbers of host eggs from the nest during parasitism. Lyon et al. (2002) found that few American coot (*Fulica americana*) parents raised all of the chicks they hatched, due to starvation, and that each successful parasitic chick costs the host one of their own. Calculations further revealed that the overall population-level fitness costs of parasitism for coots (i.e., potential strength of selection) were as high as those reported for some of the most heavily parasitized host species of common cuckoos (*Cuculus canorus*) in Britain (Lyon 2003).

It is possible, at least in theory, that the addition of foreign young could provide a fitness benefit to hosts in some situations, a possibility most likely for precocial species that do not feed their chicks. For example, hosts might gain antipredatory benefits from larger broods, through dilution of predation risk for individual offspring, through enhanced vigilance, or because the foreign offspring are disproportionately likely to suffer predation (Andersson 1984, Eadie & Lumsden 1985, Eadie et al. 1988). These benefits could explain acceptance of parasitic eggs as well as adoption of foreign young after hatching (Eadie et al. 1988). To date, there is sparse empirical data to support this speculation. In one species, observational data suggested a benefit to larger brood sizes (Eadie 1989) but no such benefits were apparent in the same species when tested using experimental alterations of brood size (Eadie & Lyon 1998).

A Role for Kin Selection?

In some birds, such as waterfowl, natal philopatry is female-biased rather than male-biased. Andersson (1984) first suggested that, in such species, kin selection might facilitate the evolution of CBP. If hosts and parasites are close relatives, direct costs of parasitism to hosts might be offset by their inclusive fitness gains from increased reproduction of a related parasite (Andersson 1984, 2001). This idea has enjoyed wide appeal, but theoretical and empirical work languished until recently. Zink (2000) considered CBP from the perspective of reproductive skew theory and suggested that CBP and cooperative breeding might represent a continuum of parental care provided by secondary females. His ESS model predicts conditions when CBP would be favored over solitary nesting or cooperative breeding and, surprisingly, indicates that relatedness between females would make CBP less likely. However, Zink assumed that parasitism was very costly (host clutch size is reduced by the exact number of parasitic eggs added). Under this assumption, a female who parasitizes a relative could reduce her indirect fitness more than she would enhance her direct fitness. If CBP has minimal costs, this prediction reverses (Lyon & Eadie 2000). Andersson (2001) expanded Zink's model, adding the ability of hosts to discriminate among kin and nonkin, and found that his original prediction was upheld, provided that the costs of parasitism are not high. However, the accuracy of kin recognition turns out to be crucial (Lopez-Sepulcre & Kokko 2002).

Empirical studies on host-parasite relatedness have only recently been conducted, and support is mixed. A number of studies have found evidence of relatedness between host and parasites (Andersson & Ahlund 2000, Nielsen et al. 2006b, Waldeck & Andersson 2006), whereas others indicate that kinship does not play a role (Pöysä 2004, Semel & Sherman 2001). Parasitism of kin could also occur simply as an incidental byproduct of random host choice coupled with close spatial proximity in the territories of relatives (McRae & Burke 1996). However, all forms of kin-biased CBP, even those where kin recognition is lacking, have the potential to reduce the costs of brood parasitism and thus weaken selection for host defenses (Jamieson et al. 2000).

Quasi-Parasitism: Asymmetry in Costs at Host Nests

The existence of "quasi-parasitism" (QP), whereby a host male copulates with the parasitic female and sires the parasitic eggs laid in his nest (Wrege & Emlen 1987), would alter the distributions of costs of parasitism: host females, but not males, would suffer the cost of the parasitic eggs. Quasi-parasitism has been reported in about a dozen species, based entirely on genetic evidence, but in most cases, alternative explanations have not been adequately rejected (e.g., errors in parentage exclusion, rapid switching of mates; Griffith et al. 2004). QP is undoubtedly rare in nature and for the few cases that might be confirmed with more sophisticated molecular techniques, it will be essential to distinguish between QP that arises by chance, and that driven by social interactions between host males and parasitic females over access to host nests (see Griffith et al. 2004).

HOST-PARASITE INTERACTIONS: THE EVOLUTION OF HOST DEFENSES AND PARASITIC TACTICS

The fitness of each of the two participants in brood parasitism—parasite and host—can be enhanced by behaviors or traits that increase fitness gained from parasitism (parasite) or mitigate the fitness costs owing to parasitism (hosts). Such behaviors have been the focus of intensive study in interspecific brood parasitism (Davies 2000, Rothstein 1990). Most, but not all, of these same behaviors and traits could also apply to CBP and there is evidence that many of them do occur in at least a few of the species studied in detail.

Host Defenses

The intensity of natural selection for host defenses depends on population-level fitness costs of brood parasitism [average costs of parasitism per host times the frequency of parasitism in the population (Lyon 2003)], as well as the net benefit gained by the defensive trait. As with interspecific brood parasitism (Davies 2000, Rothstein 1990), the absence of particular defenses in species with CBP could reflect insufficient population costs of parasitism to select for the trait, lack of sufficient net benefit from the trait, or lack of genetic variation for the trait to evolve despite a strong selective benefit.

The simplest way to reduce the costs of brood parasitism is to prevent it from occurring—such defenses in the form of nest guarding and active repulsion of prospecting brood parasites have been observed in several colonial species (Brown & Brown 1989, Emlen & Wrege 1986, Møller 1987). Hosts can also mitigate the costs of parasitism once it has occurred by deserting the nest and starting a new nest, rejecting parasitic eggs or chicks, or by adjusting clutch size, hatching patterns or parental effort when parasitic chicks are likely to hatch along with their own. However, such defenses are only useful for the types of costs that are "recoverable" and some costs—like displacement of eggs from the host nest (Sorenson 1991)—cannot be recovered by any host defenses once the parasitism has occurred (Røskaft et al. 1990).

McRae (1995) observed desertion of early parasitized nests in moorhens (*Gallinula choropus*) and explored the demographic conditions under which such desertion, followed by renesting, would be favored. Egg rejection based on egg recognition is a widespread and effective host defense against interspecific brood parasitism (Davies 2000, Rothstein 1990) but it is notably absent in most taxa with CBP. That many taxa readily reject conspecific parasitic eggs added to their nests before the host begins to lay her own eggs, but not after (Brown & Brown 1989, McRae 1995, Stouffer et al. 1987) indicates that a lack of egg recognition, not an inability to physically reject eggs, underlies the absence of rejection based on recognition in these species. Interestingly, egg rejection based on recognition does occur widely in two taxa, both of which show considerable intraspecific variation in egg features: rails (Rallidae: Jamieson et al. 2000; Lyon 1993a, 2003) and weaverbirds (Ploceidae: Lahti & Lahti 2002, Jackson 1998), although interspecific brood parasitism cannot be ruled out as the explanation for egg recognition in weavers (Davies 2000, Lahti 2006). In both village weavers (*Ploceus cucullatus*) and American coots, egg rejection is more likely for eggs that differ in appearance from the host's eggs, indicating visual cues are used in recognition (Lahti & Lahti 2002, Lyon 2003). Experimental manipulations of egg frequencies further reveal that coots and weaverbirds know their own eggs and do not simply reject minority eggs that differ in appearance from the majority egg type (Lahti & Lahti 2002, Lyon 2007). The possibility that hosts recognize and discriminate against parasitic chicks has been examined once, in captive zebra finches (*Taeniopygia guttata*), with no evidence that hosts differentiate their own young from parasitic offspring (Fenske & Burley 1995).

Andersson & Eriksson (1982) were the first to explore the clutch-size implications of CBP and showed, with a simple model, that hosts can benefit by reducing their clutch size in response to parasitism. Subsequent theory, however, indicates that adaptive host clutch-size responses are very sensitive to variation in egg survival functions (Ruxton & Broom 2002, Yamauchi 1993). Several field studies report smaller clutch sizes in host nests (Brown & Brown 1989, Møller 1987) but experiments are needed to show (*a*) that these are facultative responses, and not simply correlates of individual quality (Eadie 1989) and (*b*) that observed reductions are adaptive and not simply inadvertent consequences of the proximate mechanisms that regulate clutch size (Lyon 2003). Power et al. (1989) modeled the conditions under which a nonfacultative evolutionary reduction in clutch size might be favored as an adaptation to CBP in species with determinate (inflexible) egg-laying patterns. However, it is virtually impossible to convincingly reject all alternative hypotheses for observed population clutch sizes that appear consistent with the model (Rothstein 1990).

Parasite Tactics

The most basic task for brood parasites is to get their eggs into a host nest. In some species, parasitic females spend considerable time monitoring and checking potential host nests and then quickly sneak in to lay eggs in unattended nests (Brown & Brown 1989, Emlen & Wrege 1986, Møller 1987). In other species, successful parasitism occurs in the presence of the host (Sorenson 1991), sometimes despite strong aggressive resistance (McRae 1996). A remarkable form of brood parasitism has been documented in two species—parasitic females physically transfer in their beaks eggs from their own nest to a host nest (Brown & Brown 1988, Jackson 1993). This behavior provides female cliff swallows (*Hirundo pyrrhonota*) with far more flexibility in both the timing of brood parasitism and choice of hosts than simply laying eggs directly in a host nest (Brown & Brown 1991).

Parasites can enhance fitness from parasitism by assessing and choosing host nests that provide the best survival options for their eggs. Randomization simulations, whereby observed patterns are compared to distributions generated by random parasitism within observed spatiotemporal patterns of host use, are particularly powerful for demonstrating nonrandom host choice (Brown & Brown 1991, Emlen & Wrege 1986, Lyon 1993b). Nonrandom host choice has been shown with respect to timing of the host's laying cycle (Brown & Brown 1989, Emlen & Wrege 1986), nest success (Brown & Brown 1991), and risk of nest predation (Pöysä 2003).

An interesting problem faced by brood parasites is how to allocate eggs optimally among several host nests (Andersson 1984, Lyon 1993b). The pattern of egg allocation by individual brood parasites has been well studied in only a few species. Parasitic European starlings almost invariably lay a single egg per host nest (Pinxten et al. 1991, Romagnano et al. 1990), perhaps owing to strong constraints on brood size (Power et al. 1989). In all other species examined, parasites often lay several eggs per host nest, although there is considerable variation among individuals (Ahlund 2005, Gibbons 1986, Lyon 1993b). In American coots, parasites were more likely to lay a single egg per host nest when many hosts were available, indicating a trade-off between host limitation and maximizing fitness per parasitic egg laid (Lyon 1993b). Single laying is beneficial in coots owing to intense sibling competition and because egg rejection rates are higher at nests receiving multiple parasitic eggs (Lyon 1993b). When parasitic females have their own nests, an added twist to egg allocation is the trade-off between eggs laid parasitically and in the parasite's own nest (Lyon 1998). Under some conditions, parasitism favors a reduction in the female's clutch size in her own nest (Lyon 1998). Nielsen et al. (2006a) examine this allocation problem in terms of trade-offs between energetic costs of incubating eggs in the parental nest versus reduced survival of chicks if eggs are laid parasitically.

Another way that parasites can increase the fitness gained from parasitic eggs would be to alter the competitive arena in the host nest, either by decreasing competition from host chicks or by increasing the competitive abilities of parasitic chicks. Removing host eggs would seem to be the easiest way to reduce competition, but it has only been documented in one species, the European starling (Lombardo et al. 1989). Starlings have also been studied to see if parasites fortify their eggs with testosterone to enhance chick competitiveness, but there was no evidence for this tactic (Pilz et al. 2005).

MODEL PARASITES

Theoretical models to explore the evolutionary dynamics of CBP have proliferated in the past decade, with the current tally at 23 (see **Supplemental Table 1**). These models focus on two primary questions: (*a*) Under what circumstances can a parasitic strategy invade a population of nonparasites, and (2) under what conditions would CBP be evolutionarily stable (i.e., an ESS)? Not surprisingly, game theory approaches have figured significantly. Most models also address fundamental life-history decisions such as how individuals should allocate resources to laying parasitic versus nonparasitic eggs, and in several models, clutch-size decisions are the main focus (**Supplemental Table 1**). Despite a rather eclectic series of approaches, a few central conclusions emerge. First, almost all of the models demonstrate that, under specific sets of conditions, CBP can invade a nonparasitic population and be evolutionarily stable (Broom & Ruxton 2002, Eadie & Fryxell 1992, May et al. 1991, Nee & May 1993, Takasu 2004, Yamauchi 1993).

Second, several models reveal regions of parameter space where CBP would be evolutionarily unstable, resulting in a variety of outcomes (e.g., Eadie & Fryxell 1992, May et al. 1991, Nee & May 1993, Robert & Sorci 2001). Moreover, some models indicate that there is not necessarily a single unique ESS. Broom & Ruxton (2004) show that it is not difficult to produce a system with "any number of specified ESSs," a result that might explain why different local populations of the same species can exhibit markedly different levels of CBP (Broom & Ruxton 2004). These results point to the need to consider not only the evolutionary stability of CBP, but also the convergence stability (i.e., the ESS is an evolutionary attractor). To do so requires that CBP be considered more fully within the framework of adaptive dynamics (McGill & Cohen 2007).

Third, for many of these models, the predicted behaviors of both hosts and parasites, and the evolutionary stability of CBP itself, depend critically on assumptions about a few key parameters, such as the number of eggs laid by parasites and nonparasites, the distribution of eggs among nests, the degree to which hosts reject parasitic eggs or repel parasitic females, and the form of the function relating egg/offspring survival to the number of eggs in the nest (**Supplemental Table 1**; Maruyama & Seno 1999, Nee & May 1993, Takasu 2004, Yamauchi 1993). In many cases, empirical data to estimate these parameters are woefully lacking.

Finally, assumptions about the context in which CBP occurs can greatly affect the predicted evolutionary and population dynamics of CBP (de Valpine & Eadie 2008, Nee & May 1993). For example, Nee & May (1993) found that the existence of one type of parasitism (parasites without nests; BOBJ) could "immunize" a population against invasion by other types of parasitism (e.g., pure "professional" parasites). Of the studies summarized in the **Supplemental Material** most consider only a single type of parasitism, focusing either on nesting parasites (14 studies) or separate parasitism (10 studies), with only a few addressing BOBJ parasitism (e.g., de Valpine & Eadie 2008, May et al. 1991). Clearly some of the disparity in key predictions among models reflects the fact that they consider parasitism in quite different contexts.

POPULATION DYNAMICS AND CONSERVATION

One of the intriguing elements of CBP is that it may have significant consequences at the population level. High frequencies of parasitism can depress average reproductive success, whereas parasitism may be favored nonetheless when critical resources for breeding are limited (Eadie et al. 1998). This can potentially lead to a variety of population trajectories, including cyclic oscillations of population size (May et al. 1991), population crashes (Eadie & Fryxell 1992), or situations in which it is impossible to have both population dynamical stability and evolutionary stability (Nee & May 1993). Moreover, the ESS parasitism rate, equilibrium population size, and population stability can differ considerably depending on the type of parasitism considered (BOBJ, nesting parasites, or specialist parasites; de Valpine & Eadie 2008).

Surprisingly few empirical studies have examined the influence of CBP on population dynamics. Of those that have, most have simply reported a correlation between the frequency of parasitism and population density (e.g., Eadie 1989, Heusmann et al. 1980, Lank et al. 1990). Noticeably missing are studies demonstrating that high levels of CBP, in turn, result in population declines. Detecting population dynamic impacts of CBP will be difficult because the frequency of CBP is likely influenced by other factors that can also impact population dynamics (e.g., food, predators, and nest sites), leading to spurious correlations. Direct experimental manipulation of population densities or the resources that influence CBP (e.g., nest sites) will likely be required.

Understanding the influence of CBP on population dynamics has practical, as well as theoretical, implications. If CBP influences population stability, and if management of resources such as food or nest sites influences the frequency of CBP, then it will be essential to understand these relationships to develop effective conservation and management strategies for species in which CBP is frequent (Eadie et al. 1998). For example, Semel & Sherman (1986, 2001) suggested that extremely high levels of CBP in some populations of wood ducks (*Aix sponsa*) resulted from the placement of large numbers of visible nest boxes in close proximity. This resulted in widespread CBP, intraspecific interference among females, and reduced egg hatching success. Failure to fully appreciate the population-level impacts of CBP may lead to well-meant but misadvised management actions (Eadie et al. 1998).

EVOLUTIONARY ROUTES AND RADIATIONS

Ecological Correlates of Conspecific Brood Parasitism Among Taxa

CBP has evolved independently in several groups of birds, and numerous ecological factors have been proposed to explain the variation observed among taxa (summarized in **Supplemental Table 2**). Comparative analyses indicate that CBP occurs more commonly in species with (*a*) precocial young (Rohwer & Freeman 1989); (*b*) cavity or colonial nest locations

(Beauchamp 1997, Eadie 1991, Eadie et al. 1988; but see Geffen & Yom-Tov 2001); and (*c*) large clutch sizes and "fast" life histories (e.g., high fecundity, high reproductive effort, early age of sexual maturity; Arnold & Owens 2002, Beauchamp 1997, Eadie 1991, Geffen & Yom-Tov 2001). The correlation with precocial young may simply reflect the very high frequency of brood parasitism in two precocial taxa, the waterfowl and grouse and their allies, which itself may be driven by the high success rate of parasitic eggs in precocial birds (Sorenson 1992). Correlations with nest site location and "fast life histories" point to two other drivers: (*a*) factors that constrain or reduce the benefits of establishing a nest, and thereby enhance the relative payoff of laying some eggs parasitically (e.g., nest site limitation), and (*b*) factors that enhance the payoffs of laying parasitically to increase total fecundity and/or survival of young and adults (e.g., availability of hosts, high potential fecundity). Both are consistent with our emerging view of CBP as a flexible life-history tactic that enables females to adjust reproductive investment to prevailing ecological, social, and physiological conditions (**Figure 1**). Indeed, given the potential benefits of parasitic egg laying, it is surprising that CBP is not more widespread. Understanding the ecological and life-history correlates that predict its absence may be as interesting as searching for correlates of its presence (Sorenson 1992).

From Conspecific Brood Parasitism to Interspecific Brood Parasitism and Beyond

The evolutionary trajectory of CBP extends beyond this behavior as a final endpoint. For example, there are indications of strong links between CBP and "posthatching brood amalgamation," and many of the life-history correlates that predict CBP also predict brood amalgamation, at least in waterfowl (Beauchamp 1997, Eadie et al. 1988). More broadly, parasitism within species has long been implicated as an evolutionary precursor to parasitism between species. Hamilton & Orians (1965) first suggested that interspecific brood parasitism (IBP) evolved through a transitional phase whereby females subject to nest loss laid eggs in a conspecific nest (see also Payne 1977); more recently the idea that CBP could serve as an evolutionary stepping stone to IBP was generalized to include mechanisms other than nest loss (Lyon & Eadie 1991). Recent comparative analyses provide mixed support for this hypothesis (Beauchamp 1998, Poiani 1998, Yom-Tov & Geffen 2006). For example, Yom-Tov & Geffen (2006) concluded that IBP in altricial birds evolved directly from a nonparasitic ancestor, rather than indirectly through some other form of parasitism. In contrast, within the Anatidae, transitions to IBP (both facultative and obligate) are significantly greater on branches of the phylogeny on which CBP occurs (Beauchamp 1998; and see Lyon & Eadie 2000, figure 1). Several analytical models provide further support for the hypothesis that CBP could be a stepping stone to the evolution of obligate IBP (Cichon 1996, Robert & Sorci 2001, Yamauchi 1995).

CBP has also been considered as a possible intermediate step in the evolution of cooperative or communal (joint) nesting (Vehrencamp & Quinn 2004). Perhaps most tantalizing is the suggestion that brood parasitism, communal breeding, and cooperative breeding are simply endpoints along a continuum that is driven by ecological constraints, opportunities, and kinship (Vehrencamp 2000, Zink 2000). Recent models by Zink (2000) and Andersson (2001) are valuable not only in exploring links between different breeding systems, but equally important, this conceptual framework indicates that CBP has the potential to explain the presence or absence of other important breeding options. For example, cooperative or communal breeding may be absent in some taxa because CBP is a more profitable option, a pattern that would be expected to be reflected by earlier female dispersal. Clearly, these links need to be considered when exploring marcoevolutionary links between different avian breeding systems.

SUMMARY POINTS

1. After two decades of research we are beginning to understand the evolution of CBP in terms of life-history evolution, but we still face many unanswered questions about this intriguing behavior.
2. Hypotheses to explain CBP have intermixed ideas on the fitness benefits, ecological drivers, and evolutionary dynamics. We propose a framework with more emphasis on the adaptive basis of CBP in terms of the key fitness components that drive life-history evolution.
3. Empirical studies indicate that CBP is an integral component of a flexible life-history strategy that allows females to adaptively adjust their reproductive investment according to prevailing (and varying) ecological, social, and physiological conditions. Different hypotheses for CBP turn out be explanations for different points along a continuum of adaptive life-history options.
4. Evolutionary conflicts of interest between hosts and parasites within the same species provide another context for intergenomic conflict. Host-parasite interactions are just beginning to be explored in this context, but recent studies reveal a remarkable variety of sophisticated host and parasite tactics.
5. The extraordinary diversity of models used to examine the evolutionary dynamics of CBP reflects the growing interest in CBP as a rich and challenging system for theoretical analysis. A concern is that many of these models, though analytically pleasing, may not adequately represent the range of flexible life histories observed in real conspecific parasites.
6. CBP could have profound impacts on population dynamics. This topic has received remarkably little attention, but should receive more given both the unique opportunity to link population and evolutionary ecology, and the potential implications for conservation biology.
7. CBP needs to be placed more fully in the context of avian breeding systems—as an important precursor to the evolution of parasitism between species, but also as an antecedent or an evolutionary alternative to other avian breeding systems such as communal or cooperative breeding.

FUTURE ISSUES

1. There is a critical need for more detailed empirical studies of the fitness consequences of CBP to both hosts and parasites, using modern molecular genetic tools and longer-term studies of known individuals.
2. Two elements—the cost of parasitism and the role of kinship—remain central to several current models and debates, and yet data are remarkably scant for either of these.
3. The cognitive mechanisms underlying CBP have been little explored. Do hosts recognize their own eggs? Do hosts and parasites count? What assessment cues and decision rules might hosts and parasites use? Does spatial memory play a role in locating host nests?

4. The endrocrinological basis for CBP is only beginning to attract attention, and maternal effects on offspring phenotype have rarely been explored. Do parasitic and nonparasitic females differ in hormonal profiles? Do parasitic females manipulate offspring phenotype (e.g., via androgens in eggs)? Do stress hormones influence parasitism or offspring phenotype or fitness?

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

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Contents

Indexes

Errata

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