



Why Do Birds Lay Eggs in Conspecifics' Nests?

6

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Abstract

Conspecific brood parasitism (CBP) resembles interspecific brood parasitism, except that parasitic females lay eggs in the nests of conspecifics. CBP is a female alternative reproductive behavior, and understanding its evolution requires a life history approach. We review studies that investigate life history aspects of CBP. One or more life history components have been examined for 56 species, 49 of which are relevant to the adaptive basis of CBP. Various approaches have been used to detect CBP, but there is increasing reliance on molecular methods. Molecular methods are not always foolproof, and false exclusions are incorrectly interpreted as CBP; future studies should employ multiple lines of evidence. Two types of parasites have been documented, often in the same species: non-nesting females without their own nest in a given year and nesting females that lay some of their eggs parasitically. There is no evidence for lifelong professional brood parasites; non-nesting females apparently adopt parasitism to make the best of a bad job, although we lack a clear understanding of the specific constraints that prevent these females from nesting or the costs that make restraint a better option. Parasitism by nesting females is common, surprisingly so in the precocial waterfowl, and is only rarely associated with breeding interruption or nest loss. Nesting females appear to use parasitism to enhance their reproductive output, but for

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most species it is not clear why females don't lay the additional eggs in their own nest. A full understanding of this form of brood parasitism will require a better understanding of clutch size constraints.

6.1 Introduction

Conspecific brood parasitism (CBP), where parasitism occurs among females of the same species, might seem to be a rather simple analog of interspecific brood parasitism (IBP). There are indeed the same potential benefits to the parasites through emancipation from parental care, similar potential costs to the host of providing parental care to foreign offspring, and possibilities of diverse parasite and host tactics to promote or avoid successful parasitism, respectively. Yet, on closer examination, it quickly becomes evident that CBP represents a unique and intriguing breeding system on its own. The critical distinction between CBP and IBP is that CBP is a facultative form of brood parasitism—since CBP involves hosts of the same species—a population of pure parasites cannot logically exist. This simple fact underpins every aspect of CBP—how the behavior is adaptive and when it is expressed in populations, the unique coevolutionary dynamics that arise because a given individual can be both parasite and host, the possibility that relatedness between host and parasite might make the behavior a form of cooperation rather than parasitism, and the potential for the behavior to influence population dynamics through density-dependent and frequency-dependent influences.

These attributes of CBP make for a rich and challenging system of considerable potential for both theoretical and empirical research. Moreover, CBP is not a rare phenomenon—it occurs most frequently in birds and has now been documented in almost 250 species (Chap. 5). However, CBP has received only a fraction of interest afforded its ecological cousin IBP. Despite its widespread occurrence, detailed demographic studies of CBP have been conducted in only a few well-studied species. In most species where CBP has been documented, it is unclear even which females are pursuing this behavior or why. The dearth of information is somewhat surprising given that CBP occurs in more species than IBP (245 vs 100 species, Davies 2000, Chap. 5) and is not that much less common than cooperative breeding (358 species of birds; Ligon and Burt 2004)—yet the past several decades have been dominated by interest in cooperative breeding and interspecific brood parasitism and a deep understanding of those breeding systems has developed. Studies of CBP offer a similar but yet untapped opportunity.

The key question, and the focus of this chapter, is why do females engage in CBP in the first place? Why would natural selection favor a female who lays some or all of her eggs (in a given year) in the nests of other conspecific females? We have argued previously that CBP should be viewed through the lens of life history theory, and indeed in many cases, we believe that CBP can be considered as a classic clutch size problem—how many eggs to lay and when and where to lay them to maximize

lifetime fitness (Lyon and Eadie 2008). At its essence, CBP represents a fundamental life history decision that allows females to diversify their reproductive options under varying ecological and physiological conditions (Lyon and Eadie 2008). For birds without CBP, there are only two options available to females that are physiologically capable of breeding: nest or refrain from nesting if the costs of nesting are high or the resources needed for nesting are limited. CBP increases the range of allocation options for females (Sorenson 1991; Lyon and Eadie 2008): rather than having to choose between all (nesting) or nothing (not breeding), CBP allows the intermediate option of laying some eggs without paying the full costs of establishing a nest, incubating the clutch, and providing care for the offspring. Similarly, nesting also comes with constraints: females in many species are capable of laying more eggs than they can raise in their own nests, and CBP allows nesting females to circumvent this constraint and increase their total production of offspring.

CBP is an intriguing life history phenomenon because it is an example of an alternative reproductive tactic (ART), and this opens the study of CBP to the well-developed conceptual framework for the evolution and ecology of alternative life histories (Field 1992; Brockmann 2001; Oliveira et al. 2008). Virtually all of the ART literature focuses on males, usually in a mating context. Female ARTs have received a small fraction of the attention lavished on their male counterparts (but see Henson and Warner 1997), possibly because female ARTs fall outside the purview of sexual selection (Lyon and Montgomerie 2012). Most female ARTs, and specifically CBP, involve allocation of eggs rather than matings and thus fall within the scope of classic life history theory (Andersson 1984; Eadie et al. 1988; Lyon 1993, 1998; Lyon and Eadie 2008; Andersson and Åhlund 2012). A balanced and richer understanding of ART evolution should include both a male and female perspective (Lyon and Montgomerie 2012).

Our goal in this chapter is to provide a comprehensive review of the empirical work conducted over the past several decades to describe and characterize CBP in birds and to provide some guidance on future research needs. In a previous review, we summarized a conceptual framework for the study of CBP (Lyon and Eadie 2008) that emphasized CBP as a life history problem. Our intent here is to summarize what we have learned in the past three decades about the adaptive basis of CBP from field studies and to determine where the gaps remain in our understanding of CBP as part of a flexible alternative female life history tactic. We focus specifically on the parasites, rather than the hosts, to gain a general understanding of why some females, sometimes, act as conspecific brood parasites and to determine what fitness gains they might obtain by doing so. This focus on parasites means that we do not cover quasi-parasitism, where host males sire the parasitic eggs in their nests, because quasi-parasitism is more of an explanation for why a host would accept parasitic eggs than why the female lays parasitically in the first place. Similarly, we do not consider the costs of parasitism, nor do we review parasite or host tactics (we consider these elsewhere). However, to fully address the question of why females lay eggs in conspecifics' nests, we do consider briefly the patterns of parasitism through females' entire lives and the role that kinship might play.

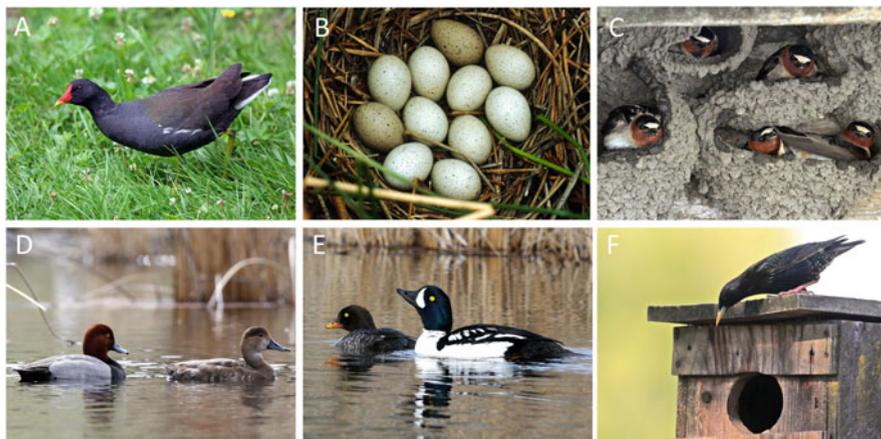


Fig. 6.1 Examples of some of the species where life history aspects of CBP have been particularly well studied. (a) Common moorhen. (b) American coot nest with two eggs (darker eggs) that have been laid by a conspecific brood parasite. (c) Colonial nesting cliff swallows, a species where parasites transfer their eggs to a host nest in their beak. (d) A study of redhead ducks, a species with both CBP and IBP, led to an influential life history framework for investigating CBP. (e) Two species of cavity-nesting ducks, Barrow's (shown here) and common goldeneyes, have been particularly well studied and motivated much of the early theory on CBP. (f) European starling, a cavity-nesting species where parasites appear to be non-nesting females unable to establish a nest of their own. All photos by Bruce Lyon

Our list of species was compiled based on our general familiarity of the field and from Web of Science searches with the following terms: conspecific brood parasitism (331 hits), intraspecific nest parasitism (422 hits), and egg dumping (175 hits). Because our focus in this chapter is on the adaptive basis of CBP for parasitic females, we included in our survey only studies that provide information relevant to life history aspects (i.e., we did not include studies that only report the frequency of parasitism). Based on our survey, information on one or more life history components of CBP is available for 56 species from 19 different families of birds. Figure 6.1 illustrates a few of the model species that have been particularly well studied. As is true of the distribution of CBP generally (Yom-Tov 2001), waterfowl are particularly well represented. Our survey is available as an online Appendix (see Lyon and Eadie 2017; posted at Figshare; DOI <https://doi.org/10.6084/m9.figshare.4787872>); here we provide summaries of the main patterns from the data compilation. We attempted to complete a thorough survey, but we acknowledge that some papers may have been overlooked. Further, our determination of whether a particular pattern or result was found in any given paper was based as closely as possible on the authors' conclusions, but occasionally our interpretation of the data differed, and we report our assessments in the online Appendix. Finally, in most cases we decided to report the results of our compilation in terms of the frequency of studies that reported a particular feature, rather than the frequency of species. We did this because in most

Table 6.1 Methods used to detect conspecific brood parasitism

Method	Count	% of methods (<i>N</i> = 197)	% of studies (<i>N</i> = 106)
Observational methods			
Laying patterns (L)	64	32	60
Clutch size (CS)	31	16	25
Direct observation (DO)	24	12	23
Egg features (EF)	21	11	20
Camera (C)	7	4	7
Genetic methods			
Microsatellite DNA (M)	19	10	18
Minisatellite DNA fingerprinting (DF)	8	4	8
Protein fingerprinting (PF)	11	6	10
Allozymes (AZ)	4	2	4
Egg white proteins (EWP)	2	1	2
Genetic polymorphism chicks (GP)	1	<1	1
Captive populations			
Semi-captive population (SCV)	1	<1	1
Captive population (CV)	4	2	4
Total	197		

Data are the frequency (number of studies) in which each method was used (*N* = 106 studies). Multiple methods may have been used in the same study. Abbreviations in parentheses refer to the codes used in the online Appendix

cases, results varied among studies, and there was no simple way to accurately represent the findings at the species level.

6.2 Methods for Detecting CBP and Why They Matter

Conspecific brood parasitism often requires different methods of detection than interspecific brood parasitism because CBP can be much more difficult to detect—distinguishing between eggs of different females of the same species can be far more challenging than distinguishing eggs of different species (Andersson 1984). Accordingly, a variety of methods have been used to detect CBP (Yom-Tov 1980; Eadie et al. 2010), including egg laying rates, eggs laid well after clutch size is complete, unusually large clutch size, egg features, and several genetic methods (Table 6.1).

Egg laying rates can be potentially powerful for detecting CBP. Females cannot lay more than one egg per day due to the physiology of egg production and laying, so the addition of two or more new eggs to a nest in 24 h is typically strong evidence that more than one female has laid eggs in a nest (Yom-Tov 1980; Brown 1984; Gibbons 1986). Egg features like egg shape and the pattern and color of markings can be reliable in systems with extreme variation among females, particularly when

combined with other information like egg laying rates (Jackson 1992; Lyon 1993; Eadie et al. 2010), and in some cases it also makes it possible to identify the parasitic females that lay the eggs (Lyon 1993). The accuracy of these field methods was confirmed by McRae and Burke's (1996) comparison of field and genetic methods for determining parasitic eggs in moorhens (*Gallinula chloropus*)—they found perfect correspondence between demographic and genetic methods.

The advent of increasingly powerful genetic techniques has revolutionized the study of CBP, and our survey shows that researchers have been quick to adopt each new method as it became available (44% of studies in the online Appendix, Table 6.1). The earliest approach—enzyme polymorphisms—allowed researchers to exclude parasitic offspring as legitimate offspring from the social parents, but not to identify the female brood parasites themselves (Gowaty and Karlin 1984) at least without additional information such as direct observation of egg laying by parasitic females (Wrege and Emlen 1987). However, as the power of the methods increased, it became possible to reliably identify the parasitic females based on genetic inference alone: e.g., minisatellite DNA (McRae and Burke 1996) and microsatellite DNA (Nielsen et al. 2006). Relatively few of the studies we reviewed used microsatellite DNA to detect CBP (18%, Table 6.1) perhaps because this method has only recently become relative easy and inexpensive. The newest addition to the genetic toolbox, protein fingerprinting based on egg albumin samples, is particularly powerful because it focuses on the maternal rather than the offspring genotype (Andersson and Åhlund 2001). Moreover, samples can be obtained from fresh eggs, and no embryonic development is needed, an important issue because parasitic eggs often fail to develop in some species, and eggs may be destroyed, rejected, or depredated before hatching, precluding typical DNA sampling methods.

Researchers working on CBP need to be vigilant not only to reduce the risk of false assignments of maternity but also the risk of false exclusions—false exclusions are interpreted as examples of CBP. It is notable that of 106 studies where one or more methods were used to detect CBP, only 18% used *both* genetic and observational methods, whereas 26% used only genetic techniques, and 56% used only observational methods. Moreover, while microsatellite DNA markers are generally reliable, given a sufficient number of variable loci (e.g., Queller et al. 1993), our own simulations suggest that risk of false exclusion and assignment may be elevated for species with a combination of high levels of female relatedness and a lack of information about sires (Thow et al., unpublished information). Unfortunately this is a situation that often applies to waterfowl, a group that accounts for a large portion of the detailed studies of CBP (26 of our 56 species). Errors in parentage assignment are a concern not only because they can provide false evidence for the occurrence of CPB but also because such errors could generate spurious life history patterns.

6.3 Frequency of CBP: Variation Between and Within Species

The frequency of parasitism reported in the studies reviewed ranged from extremely rare (e.g., 3% of pied avocet (*Recurvirostra avosetta*) nests, 1% chicks; Hötter 2000) to extremely common (100% of ostrich (*Struthio camelus*) nests; Kimwele and Graves 2003). It has long been recognized that parasitism is particularly widespread in the waterfowl in terms of occurring in many species (Yom-Tov 1980; Andersson and Eriksson 1982); our survey now indicates that parasitism also occurs at a higher frequency within species in the waterfowl than in non-waterfowl taxa (Fig. 6.2). Reviews of CBP show that it is particularly common in precocial birds (Chap. 5); in our review this pattern is dominated almost entirely by the waterfowl (only a single precocial species does not belong to Anseriformes), and so we refrain from drawing conclusions about precocial birds generally.

Many studies report parasitism only in terms of the percentage of nests that are parasitized (online Appendix, Fig. 6.2). Reporting the frequency of parasitic eggs or chicks would also be useful because it gives a more accurate representation of the frequency of the tactic and it is also useful in determining the fitness costs (to hosts) or benefits (to parasites) of the behavior (e.g., Lyon 2003). Our survey indicates clearly that the percentage of nests parasitized considerably exceeds the percentage of eggs or chicks that are actually parasitic (Fig. 6.2).

One other measure that is only rarely obtained is the frequency of females in a population that engage in parasitism. For non-nesting females, this would be virtually impossible to determine, but it has been determined for nesting females in few different species: 25% of American coots (*Fulica americana*) in a given year (Lyon 1993) and 27% of moorhens over a 3-year period (McRae 1998).

6.4 The Adaptive Basis of Parasitism: Why Do Females Lay Parasitically?

6.4.1 Review of the Hypotheses

The key life history issue for CBP is how and why laying eggs in the nests of other conspecifics enhances the fitness of the brood parasite. To answer this, we must first determine which females in the population are the brood parasites. Do they have a nest of their own or are they non-nesting females? What alternative options are available to these females, and what specific life history trade-offs favor laying eggs parasitically over the alternatives that are possible for those eggs? We provided a review of existing hypotheses previously (Lyon and Eadie 2008) and so only briefly summarize the hypotheses here.

It is important to first consider the possibility that “apparent” CBP may not be adaptive brood parasitism at all. Behaviors other than CBP can result in a pattern identical to brood parasitism—nests that contain eggs laid by more than one female but where only one female incubates. There are two possibilities: nest site competition (Semel and Sherman 2001) and nest take-over (Robertson 1998).

Two hypotheses can explain why *non-nesting females* engage in parasitism:

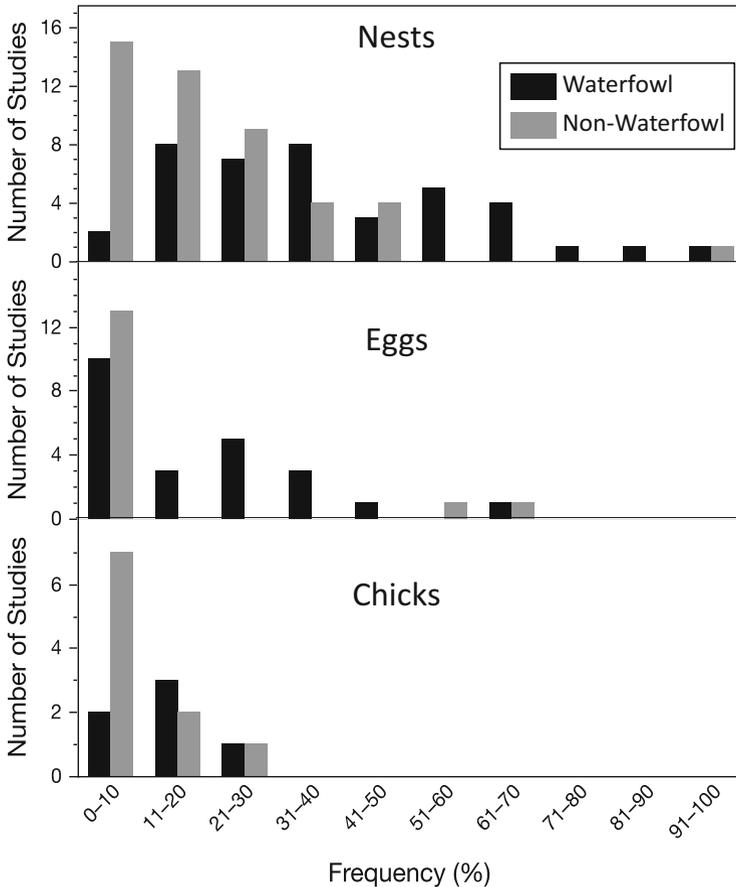


Fig. 6.2 The frequency of conspecific brood parasitism (CBP) in birds. Each bar is the number of studies that report a given frequency of CBP (arranged in ten percentiles) as measured by the percentage of nests parasitized (top), percentage of parasitic eggs detected (middle), or percentage of parasitic chicks detected (bottom). Black bars represent waterfowl; gray bars are all other bird species. In studies that report a range of frequencies, we used the minimum frequency

1. *Lifelong Specialist Parasite*—parasites never nest, and complete emancipation from nesting increases fecundity; the parasites depend completely on nonparasites for success, and frequency-dependent trade-offs lead to an equilibrium balance of professional parasites and nonparasites (Yom-Tov 1980; Eadie and Fryxell 1992).
2. *Best of a Bad Job (BOBJ)*—females lay parasitically because they are unable to nest due to limited nest sites or territories (constraint) or because their poor environmental or phenotypic situation makes parasitism a better option than nesting (restraint). Distinguishing between restraint and constraint aspects of BOBJ has proven exceptionally difficult (Lyon and Eadie 2008).

Two hypotheses can explain why *nesting females* lay some of their eggs parasitically:

1. *Breeding Interruption*—females resort to parasitism when forced to by nest predation or interference from conspecifics and salvage some fitness from reproductively committed eggs that would otherwise be wasted.
2. *Reproductive Enhancement* (or *Side Payment*)—parasitism allows a nesting female to bypass some constraint of investing parental care in offspring and thereby increase her reproductive success. The specific constraint being circumvented by parasitism could include any of the key life history variables: fecundity, offspring survival, or adult survival.

Two other hypotheses deserve mention. Pöysä (1999) suggested parasites gain by choosing nest sites safe from predation (*nest predation hypothesis*). However, because parasites are always expected to maximize fitness gained from parasitism, it is important to determine whether this factor drives parasitism or is simply an aspect of host choice by parasites. The *risk-spreading hypothesis* proposes that parasitism allows females to spread the risk of predation and increase the probability that a female will fledge some offspring (Payne 1977; Rubenstein 1982). Simulations show that the probability of fledgling at least one offspring is not important to natural selection: the mean fitness of the strategy matters, and in all but the tiniest population size, the average fitness of the two strategies is virtually identical (Bulmer 1984; Hopper et al. 2003). Andersson and Åhlund (2012) recently proposed a new, viable strategy that resembles risk spreading—parasitism reduces the time that eggs are exposed to predation and increases mean reproductive success.

6.4.2 Which Females Are the Parasites?

The identity of parasites is known for just over a third of the species in our survey (22 of 56 species, online Appendix). Most of these species ($n = 16$; 73%) have both nesting and non-nesting parasites, indicating that there will be more than one context and explanation for the CBP. For the species that have both types of females, nesting females often account for over half of the parasitic females. In five species (23%), only nesting parasites were recorded, and only one species (5%) had *only* non-nesting parasites. As we show below, in virtually all of the species with nesting parasites, nest loss is not a factor, so these females are not being forced to be parasites.

6.4.3 Why Do Female Birds Engage in CBP?

“Apparent” brood parasitism that results from competition over nest sites has only been invoked as an explanation in four studies and for only three cavity-nesting species (Table 6.1): bufflehead (*Bucephala albeola*), wood duck (*Aix sponsa*), and

Table 6.2 Support for alternative hypotheses on the adaptive basis of conspecific brood parasitism

Hypothesis	Yes	No	Total	% Yes	% of studies ($N = 43$)
Breeding interruption (BI)	10	7	17	59	13
Best of a bad job (BOBJ)	22	5	27	81	51
Nest competition (NC)	4	1	5	80	9
Reproductive enhancement (RE)	15	3	18	83	35
Risk spreading (RS)	2	2	4	50	5
Total	53	18	71		

Data are the frequency (number of studies) for which each hypothesis was claimed to be supported (yes) or refuted (no). Multiple hypotheses may have been tested in a single study. Abbreviations in parentheses refer to the codes used in the online Appendix

European starling (*Sturnus vulgaris*). Two of these studies presented limited evidence, but Semel and Sherman (2001), in particular, provided convincing evidence of nest competition in wood ducks by testing and rejecting alternative hypotheses. However, two lines of evidence can be used to reject the *nest competition hypothesis* as the primary or general explanation for CBP in a population (these tests have been applied to goldeneye ducks (*Bucephala* spp.) but not wood ducks). First, behavioral observations show clear differences in the behaviors of the females that lay in the same box, some of which indicate that only one female intends to nest (Åhlund 2005). Second, parasitic females can often be induced to lay in unoccupied nests baited with eggs, but they do not stay and care for the eggs they lay, counter to a key prediction of the *nest competition hypothesis* (Pöysä 2003; Odell and Eadie 2010).

In terms of adaptive hypotheses for CBP, at least one hypothesis has been claimed as supported for 28 species. For many of these species, more than one explanation for CBP seems to apply (Table 6.2, online Appendix). In species with non-nesting parasites, there is no evidence for specialist lifelong parasites. Twelve studies were able to follow parasites across breeding attempts, and in all cases the parasites had nests of their own at some point. In contrast, there is considerable evidence that non-nesting females resort to parasitism to make the best of a bad job: BOBJ was reported in 22 studies of 19 species, and the cases were evenly spread between waterfowl and non-waterfowl species. For most of these, it is unclear whether restraint or constraint explains the lack of nesting, but the aggregate results of our survey suggest that constraint may be more important than restraint. Nest limitation (i.e., *constraint hypothesis*) was invoked as an explanation in ten studies (Table 6.3). Experiments with cavity-nesting birds provide particularly compelling evidence that lack of a nest site forces some birds to resort to parasitism. In four species, nest boxes were added or removed to alter nest availability; all four studies altered the frequency of parasitism (Eadie 1991 (two species); Gowaty and Bridges 1991; Saitou 2001). More commonly, indirect evidence is used to infer that nest limitation is important; density is the most commonly reported correlate of parasitism (Table 6.3). However, parasitism could correlate with population density for other reasons, such as increased host availability (Rohwer and Freeman 1989). For example, parasitism correlates with colony size in cliff swallows (*Petrochelidon pyrrhonota*) (Brown 1984), but nest limitation is not an issue because they build their own nests. In the

Table 6.3 Ecological correlates associated with conspecific brood parasitism

Correlated variable	Yes	No	Total	% Yes	% of studies ($N = 63$)
Age experience of females (A)	11	6	17	65	17
Body condition of female (FC)	2	3	5	40	3
Density of nests (D)	22	6	28	79	35
Nest limitation (NL)	10	8	18	56	16
Quality of nest sites (NQ)	3	1	4	75	5
Density/availability of hosts (H)	5	2	7	71	8
Mate limitation (ML)	3	0	3	100	5
Ecological conditions—drought (ECD)	3	0	3	100	5
Ecological conditions—flooding (ECF)	1	0	1	100	2
Synchrony of nesting (S)	2	2	4	50	3
Time in season (T)	19	3	22	86	30
Total	86	32	118		

Data are the frequency (number of studies) for which each variable was claimed to be correlated (yes) or not (no) with the occurrence of CBP ($N = 63$ studies with correlates reported). Multiple correlates may have been evaluated in a single study. Abbreviations in parentheses refer to the codes used in the online Appendix

barn swallow (*Hirundo rustica*), Møller (1989) demonstrated the effect of host availability by increasing the local occurrence of parasitism rate experimentally by adding empty nests.

It is much harder to experimentally evaluate the role of restraint, although in theory food supplementation experiments could assess some aspects of restraint. Inspecting the ecological correlates associated with the studies that invoke BOBJ provides indirect evidence that restraint may be relatively uncommon (Table 6.3). Only two studies report female body condition as a correlate of parasitism, although in general discussions it is often mentioned as a possible factor influencing CBP. In contrast, female age is a frequent correlate ($n = 11$), but this could either reflect young females that choose not to breed or that are competitively inferior in competition for limited nest sites or other resources. A couple of studies do provide fairly convincing evidence for restraint—in canvasbacks (*Aythya valisineria*) and redheads (*A. americana*)—rates of parasitism increased during drought conditions when the prospects for successful nesting were low (Sorenson 1991, 1993). These ducks build nests in emergent vegetation so nest sites should not be limiting.

Our survey reveals that nesting females that engage in parasitism infrequently do so because they are forced due to breeding interruption (Table 6.2); this explanation was reported for ten species, including two for which only experimental nest loss caused parasitism (Feare 1991; Shaw and Hauber 2012). One experimental study of nest loss suggests that these experiments should be interpreted with caution: experimental destruction of European starling nests caused parasitism, but few cases of

naturally occurring parasitism are associated with nest loss because nest predation is rare (Stouffer and Power 1991).

For most nesting parasites, reproductive enhancement seems to be the mostly likely explanation for parasitism; it was reported in 15 studies of 12 species (Table 6.2). For seven species, nesting parasites lay more total eggs than nonparasitic nesting birds, indicating a fecundity enhancement. The critical question then becomes why the females do better by laying these eggs parasitically rather than in their own nests. This is essentially a clutch size question, and it is surprising how few studies of brood parasitism consider this issue. Because clutch size determination is thought to differ between birds that feed their offspring (altricial, semi-precocial) and those that do not (precocial), we consider this issue separately for these two groups of birds.

CBP as a clutch size decision has been explicitly assessed in only four species that feed their offspring. In three species, the observation that parents suffered brood reduction due to limited food suggests that brood parasitism allows nesting females to bypass parental care constraints on family size and increase total production of offspring (Jackson 1993; Lyon 1993; McRae 1996). In the cliff swallow, some nesting females transfer eggs in their beak from their own nests to host nests. Because egg transfer often occurs after the parasites have completed laying their own clutch, Brown and Brown (1988) suggested that the birds are unlikely to be increasing their fecundity (although they could have laid larger clutches in anticipation). Further investigation revealed that this form of parasitism targets host nests with above-average success rates (Brown and Brown 1991). It is also worth stressing that fitness comparisons of entire classes of eggs—parasite versus nonparasite—can be misleading, because it is the fitness gained from specific eggs that matters. Hatching success of parasitic eggs is typically lower than that of host eggs (19 of 24 studies). This does not rule out reproductive enhancement as an explanation for CBP, contrary to some suggestions. The key is how the parasitic eggs would have fared had they been laid in the parental nest; investigations from this perspective show that parasitism allows females to increase the success of marginal eggs that would have low success had they been laid at home (Jackson 1993; Lyon 1998).

One surprise from our survey is the preponderance of nesting parasites in the precocial waterfowl. Waterfowl do not feed their offspring, and it has long been assumed that their clutch size is strongly influenced by egg laying capacity rather than food for the chicks (Lack 1967; Ankney and MacInnes 1978; but see Arnold and Rohwer 1991 for a contrary perspective). The observation that female nesting parasites in several waterfowl species lay more total eggs than nonparasites (Eadie 1989; Sorenson 1991; Åhlund and Andersson 2001) suggests that some other factors must be at play in these species. Understanding CBP by nesting waterfowl is essentially a clutch size problem. However, clutch size determination in this group remains poorly understood although several factors have been identified that might play a role, including saving reserves for renesting (Milonoff 1989), decreased egg viability combined with length of nest exposure to nest predation (Arnold et al. 1987), nest exposure to predation alone (Andersson and Åhlund 2012), variability in nest predation risk (Pöysä 1999), incubation costs to the female (Hepp et al. 1990),

length of the incubation period (Rohwer 1985), hatching success (Rohwer 1985), and fledging success (Eadie and Lyon 1998).

Most of the above factors have not yet been examined in the context of CBP. Two egg removal experiments with common goldeneye suggested that females can lay more eggs than they normally do (Andersson and Eriksson 1982; Milonoff and Paananen 1993), an observation that raises the question as to why nonparasitic females do not lay these extra eggs in their own nests. However, one complication is that these studies were done in populations with CBP, and the authors were not able to distinguish between host and parasite eggs (all eggs were assumed to be nonparasitic). Odell and Eadie (2010) showed that parasitic female wood ducks are more likely to target host nests with low numbers of eggs, so we need to be sure that increases in fecundity due to experiments actually reflect the nest owner's response.

In addition to the traditional ideas on clutch size limitation in precocial birds, two new hypotheses have been proposed for brood parasites. In a hypothesis aimed specifically at the puzzle of nesting parasites, Andersson and Åhlund (2012) suggested that parasitism might allow females to maximize their annual reproductive success by reducing the length of time that eggs are exposed to the risk of parasitism. The fitness advantage to this type of risk spreading is quite modest, and an unstated assumption is that parasites must have very similar hatching success compared to nonparasitic eggs. This would require almost perfect laying synchrony with the host; otherwise the fitness loss of eggs laid too late to hatch would swamp the modest anti-predation gains. In seven of nine studies of seven waterfowl species, parasitic eggs were less successful than host eggs, mainly because the parasite eggs were laid after the host began incubation (online Appendix). However, because the hypothesis applies specifically to nesting females, it will be critical to separately assess the success of the eggs laid by nesting females. In American coots (*Fulica americana*), parasitic eggs of nesting parasites were more than twice as successful as eggs of non-nesting parasites, entirely due to better synchrony with the host's laying schedule (Lyon 1993).

A second hypothesis could explain parasitism in precocial birds. Pöysä (1999) proposed that parasites specifically target safe nest sites with high survival rates. Non-nesting parasites may benefit by laying parasitically in a high-quality host nest, rather than establishing a nest of their own in an unsafe site. Nesting females forced to occupy relatively unsafe nest sites could benefit by laying as many as their eggs as possible in hosts with safe nests and, when hosts are no longer available, lay the remainder in their own nest. This idea has only been tested so far for one species (common goldeneyes); the results suggest that parasites do target safe sites, but it is unclear which females (nesting or non-nesting parasites) do so (Pöysä 1999, 2006).

6.5 Brood Parasitism Through Life

One question that has received little attention is how brood parasitism integrates into a female's entire lifetime life history strategy. It is clear from our review of studies that followed individual females across years (or breeding attempts) that females are

flexible and change tactics across years, depending on factors such as age, population density, nest and territory availability, and ecological conditions like drought. Given this flexibility, one interesting question is what trajectories individual females follow through the course of their entire life. Do all females show similar trajectories (an age/experience-driven strategy) or do females differ in when, and how much, they invest in parasitism based on ecological or phenotypic contingencies?

In terms of the lifespan of a female, 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). Sorenson (1991) proposed one framework, based on reproductive effort, for thinking about how this socially and ecologically driven flexibility fits together in terms of a life history strategy. Alternatively, two studies illustrate how the effects of population dynamics on the resources needed for nesting, such as nest sites, might cause temporal variation in the conditions that favor nesting versus parasitism (Eadie and Fryxell 1992; Eadie et al. 1998). Finally, Jaatinen et al. (2011) use a strategy selection modeling approach to show how variation in female quality can influence the trajectory and combination of tactics adopted by females throughout life. To the extent that the drivers that favor CBP are unpredictable across time, these different models predict that we might expect considerable variation among females in their lifetime patterns of parasitism, nesting, and perhaps even sabbaticals from breeding entirely.

It is also possible that there are consistent differences among females in how they respond to the conditions that favor parasitism, either due to genetic differences or long-lasting effects from early life (ontogenetic effects). Intriguingly, two studies found that parasitism by nesting females was repeatable across breeding attempts (Møller 1987; Schielzeth and Bolund 2010). Why would females show consistent differences in when and how much they employ CBP? Two broad explanations are possible (these also apply to alternative male reproductive tactics, Brockmann 2001). First, conditions early in life could influence a female's phenotype (size, quality, etc.), which in turn affects her optimal pattern of investment in nesting versus parasitism throughout her life. Second, trade-offs between nesting and parasitism could favor the evolution of different traits that enable success at one of these tactics, but not both. In the extreme, these trade-offs might favor the evolution of lifetime specialists, as is commonly observed for male alternative tactics (Oliveira et al. 2008), but as noted above, there is no evidence for life specialist conspecific parasites. Alternatively, there may be genetic variation among females in the propensity to engage in CBP in particular contexts; a reaction norm approach could be used to examine this (Oliveira et al. 2008). This could be daunting for field studies but should be feasible for captive populations like the zebra finch (*Taeniopygia guttata*) where consistency in allocation to CBP has already been demonstrated (Schielzeth and Bolund 2010).

6.6 A Role for Kinship?

For some birds CBP might not be parasitism at all. Andersson and Eriksson (1982) were the first to note that CBP is disproportionately common in waterfowl (Anatidae), a group where natal philopatry is female-biased rather than the more usual avian pattern of male-biased natal philopatry. Andersson and Eriksson (1982) suggested that female philopatry could result in hosts and parasites being related. Andersson (1984) followed with an elegantly simple model showing how female relatedness might facilitate the evolution of CBP, a finding that prodded researchers to reconsider CBP as a kin-selected, cooperative breeding system (see Chap. 12) rather than as a parasitic interaction. This stimulated a flurry of genetic studies, although a consensus has yet to be reached, and it may be relevant mostly to the waterfowl. Nonetheless, the possibility of cooperation, potentially facilitated by kinship, blurs the distinction between CBP and cooperative breeding such that they may simply represent points along a life history continuum (Zink 2000; Zink and Lyon 2016).

An important caveat, however, is that kin-selection can facilitate host acceptance of parasitic eggs (reducing selection on host resistance), but it does not explain why the parasites lay the eggs as brood parasites in the first place. For this reason, we did not focus on the kinship aspect in this paper but recognize it as an intriguing development in understanding CBP, especially for species such as waterfowl with female-biased philopatry (several reviews and theoretical papers address this topic, including Andersson 1984; Zink 2000; Lyon and Eadie 2000; Andersson 2001; Lopez-Sepulcre and Kokko 2002; Eadie and Lyon 2011; Anderson 2017).

Concluding Remarks and Future Directions

In slightly over three decades, we have moved from simply documenting the frequency of CBP among species to exploring, in a diversity of species, the question of why females pursue this behavior and what fitness benefits might accrue. With the advent of powerful molecular genetic methods and detailed field studies of marked individuals, we have learned that CBP is not simply a rare, aberrant, or accidental behavior as some early authors proposed. Rather, it is clear that CBP represents a flexible alternative female life history tactic that allows females to adjust reproductive effort to varying ecological and physiological conditions.

We offer four take-home messages and directions for future research. First, attention to the methods and analyses used to detect CBP is critical. Care in assigning maternity must be extended to how we exclude females as possible mothers because false exclusion could lead to “apparent” support for a variety of appealing (but possibly incorrect) hypotheses. The number of markers in molecular studies is sometimes low, and conclusions should be supported

(continued)

using multiple lines of evidence, including a focus on demographic aspects like egg laying rates at focal nests.

Second, our survey reveals that there are clearly two types of CBP—by non-nesting and by nesting females. For non-nesting parasites, there is no evidence for “pure” lifelong parasites, and most researchers conclude that this type of parasitism is a best of a bad job (BOBJ), although the underlying constraints or restraints are rarely known. Parasitism by nesting females was surprisingly common. This was unexpected, especially for waterfowl. Why don’t these females lay all their eggs in their own nest rather than risk their eggs in a nest of another female? A number of hypotheses have recently been proposed, but much empirical and theoretical work remains, particularly in the context of adaptive clutch size. Most studies to date have been observational, and the clutch size aspect would clearly benefit from an experimental approach.

Third, the variation in the extent to which females pursue CBP within and among years points to a critical need to follow females over their entire lifespan. Virtually no studies have followed females throughout their life to explore the flexibility of parasitic behavior or the trade-offs that might be involved. Indeed, some females might be more specialized towards parasitism and others towards nesting, as might be expected if different skills, experience, physiological state, or personality influences a female’s reproductive trajectory.

Fourth, we highlight the value of CBP as a model system to examine an array of ecological and evolutionary dynamics. CBP is unusual in being an alternative *female* reproductive tactic; most research on ARTs has focused on males, and CBP offers an exceptional opportunity to expand this framework. Moreover, given that females are typically the sex that drives population dynamics, there is rich potential to explore the links between the behavioral dynamics, population dynamics, and evolutionary dynamics of this intriguing behavior.

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