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Evolution of Conspecific Brood Parasitism versus Cooperative Breeding as Alternative Reproductive Tactics

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ABSTRACT: Cooperative breeding and conspecific brood parasitism can both be favored by ecological saturation of breeding territories or nest sites. Here, we develop a model that links these alternative reproductive tactics by focusing on nonnesting females (S) that either breed cooperatively with a nesting female (N) or parasitize a third, outside host female (H). We find that cooperative breeding is more likely to evolve with increasing relatedness of cooperating females (S or N) to the outside host female (H) and with increasing costs to the hosts for receiving parasitic eggs. Conversely, cooperation is less likely with increasing kinship between the two potentially cooperative nesters (S and N). This is because even the nesting female gains higher inclusive fitness as long as the number of parasitic eggs (of her otherwise potentially cooperating partner) is sufficiently high. We find the relationship between kinship and reproductive skew within cooperative nests can be either positive or negative depending on the fecundity of parasites versus nesting females. We also find that either of the cooperatively nesting females is more likely to tolerate a smaller fraction of group reproduction as kinship with the host female increases and as the host reproduces more (relative to the parasite) in outside nests. Finally, our model predicts that, as the outside option of conspecific brood parasitism becomes more profitable, helping behavior (zero reproduction by one female) is less likely to evolve in cooperatively breeding groups.

Keywords: brood parasitism, cooperative breeding, reproductive skew, kin selection.

Introduction

Parental care is widespread in animals and is usually central to the evolution of cooperation and conflict within animal breeding systems. In many societies, cooperation involves alloparental care, defined as providing care to offspring other than one's own biological offspring (Hamilton 1964; Wilson 1975; Andersson 1984a; Cockburn 1998; Clutton-Brock 2002). Alloparental care occurs in communal breeding (termed "cooperative breeding" in avian systems; Cockburn 2004), where offspring from more than one female are raised in the same nest and receive parental care from all breeding adults, including those that are not their biological parents (Eberhard 1986; Zink 2000; Vehrencamp and Quinn 2004). Alloparental care also occurs in systems with helpers (male or female), where nonreproductive individuals help raise the offspring of others, typically those of close kin (Wilson 1975; Andersson 1984b; Brown 1987; Cockburn 1998; Clutton-Brock 2002; Koenig and Dickenson 2004). Although the term cooperative breeding is sometimes applied to the specific form of alloparental care involving nonreproductive helpers, in this article, we adopt the broader use of the term, which includes all forms of cooperative and communal breeding with respect to joint-nesting females that may or may not reproduce themselves (e.g., Cockburn 2004).

In cooperatively breeding societies, there are potential conflicts of interest over how much each individual within the social group should invest in offspring care (Cant and Johnstone 1999; Johnstone and Cant 1999; Zink 2000, 2001; Zink and Reeve 2005; Shen et al. 2011), as well as conflicts over how the reproductive output should be shared among females (Vehrencamp 1983a, 1983b; Emlen et al. 1998; Reeve and Keller 2001; Loeb and Zink 2006; Buston and Zink 2009). These conflicts over costs of parental care and benefits of reproductive skew are often considered in isolation, but simultaneous conflict over parental care and reproductive skew is present in a variety of cooperatively breeding societies. This dual form of conflict includes societies with reproductive sharing as well as those with helpers (i.e., nonreproducing individuals that contribute to offspring care) and has been observed in birds, amphibians, fish, reptiles, and insects (Wilson 1975; Brown 1987; Cockburn 1998; Clutton-Brock 2002; Zink 2003; Taborsky 2009; Doody et al. 2009).

Conflict and cooperation over offspring care can also occur in a very different sort of social interaction, termed conspecific brood parasitism (CBP; Andersson 1984a; Davies 2000; Yom Tov 2001; Lyon and Eadie 2008). Conspecific brood parasites lay eggs in the nests of a conspecific female and then leave all of the subsequent parental care to the host female

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that they have parasitized. Brood parasitism has traditionally been viewed as fundamentally distinct from cooperatively breeding systems. Because the parasite gains all of the benefits of reproduction without paying for any of the costs of parental care, CBP is often considered a parasitic ecological interaction (Andersson 1984*a*; Petrie and Moller 1991; Davies 2000; Lyon and Eadie 2008). This approach places CBP as a within-species counterpart to the well-known interspecific brood parasitism that is shown by cowbirds, cuckoos, and a variety of social insects (Davies 2000; Brandt et al. 2005; Kilner and Langmore 2011).

Recent empirical findings, plus insights from theory, have begun to blur this traditional distinction between CBP and cooperatively breeding societies. Kin selection is thought to be an important driver of cooperative breeding, and recent models of CBP also suggest an important role for kin selection in some taxa. For example, CBP is particularly common in waterfowl, a group where high rates of female natal philopatry could lead to kin-structured populations and relatedness between host and parasites (Andersson and Eriksson 1982; Eadie et al. 1988). Evidence is now mounting that parasites and hosts are often genetically related and that kin recognition may be involved in some aspects of brood parasitism (McRae and Burke 1996; Andersson and Ahlund 2000; Jaatinen 2009, 2011*a*; Tiedemann et al. 2011; Poysa et al. 2014; Andersson et al. 2015; summarized in Eadie and Lyon 2011). When a female parasitizes relatives, any costs of brood parasitism to hosts (e.g., fewer host offspring) could be offset by the inclusive fitness benefits the host gains through the parasite's reproduction (Andersson 2001; Lopez-Supulcre and Kokko 2002). However, this scenario assumes that alternative (unrelated) host nests are in short supply and/or that parasites cannot gain access to the nests of unrelated females due to host defenses (Zink 2000; Andersson 2001; Eadie and Lyon 2011).

Vehrencamp and Quinn (2004) suggested that CBP could be an evolutionary precursor to cooperative breeding by providing a behavioral mechanism by which cooperatively breeding groups initially form. Zink's (2000) model showed that brood parasitism and cooperative breeding can be considered extremes on a continuum of parental care by a secondary female; CBP is simply the end of the continuum, where a female provides zero parental care to eggs she has laid in a communal nest. Andersson (2001) developed a similar model tailored specifically for understanding the evolution of brood parasitism and cooperation in waterfowl. Both models make important, although divergent, predictions regarding the relationship between kinship and CBP; this is due to the initial assumptions regarding the inclusive fitness costs and benefits to hosts (Lyon and Eadie 2008). Interestingly, taken together, these two models span both vertebrates and invertebrates, systems in which the costs and benefits of CBP are often quite different.

In this article, we build on these earlier models by focusing on the relationship between CBP and cooperative breeding in birds. CBP occurs in two fundamentally different life-history contexts in birds, each with very different trade-offs (Emlen and Wrege 1986; Eadie 1989; Sorenson 1991; Lyon 1993; Brown and Brown 1998; McRae 1998; Andersson and Ahlund 2001; Lyon and Eadie 2008). First, some brood parasites are females that retain the capacity to initiate their own nests within the same year, distributing eggs across host nests and their own nests. Second, other brood parasites are nonnesting females (floaters) that do not have the capacity to establish their own nests in the same year that they lay eggs parasitically. Females in these two contexts face very different trade-offs and constraints with respect to the evolutionary tactic of laying eggs parasitically (Lyon 1993; Lyon and Eadie 2008). Previous models of CBP have explored the first context, where brood parasites can pursue the alternative of establishing their own solitary nests in addition to laying eggs parasitically (Zink 2000; Andersson 2001; Broom and Ruxton 2002; de Valpine and Eadie 2009).

Here, we explore the second context, where the only alternative option available to brood parasites is cooperative breeding. We assume that solitary nesting does not occur in potential brood parasites, either because it is not possible, due to nest site or territory limitation, or because it is suboptimal due to female condition or life-history trade-offs (Lyon and Eadie 2008). The context of CBP by nonnesting females is particularly relevant to the evolution of some forms of cooperative breeding, because theory suggests that both helping and CBP can be promoted by the same basic ecological constraint—habitat saturation that largely precludes opportunities for independent breeding (Brown 1969; Koenig and Pitelka 1981; Andersson 1984*b*; Koenig and Dickenson 2004; Lyon and Eadie 2008). However, the broader perspective considered by Emlen (1992), whereby females may expect a low payoff from independent breeding for any reason, could also apply. Thus, it is reasonable to consider CBP and cooperative breeding as two distinct reproductive alternatives available to females that are unable to nest independently due to any constraints that make normal nesting suboptimal. Our approach is to integrate both these alternatives (CBP and cooperative breeding) into a single evolutionary framework to understand the factors that might influence whether females will evolve to be parasitic or cooperative.

Specifically, we examine how outside options for the CBP alternative (targeting of a host female by a nonnesting female) affect the stability of cooperative breeding as well as the division of reproduction (skew) within these cooperative nests. Our model can apply to two contexts: first, species that show both CBP and cooperative breeding, and second, understanding macroevolutionary patterns in terms of

whether CBP or cooperative breeding is favored as a fixed strategy within a species. Examples of species that include both CBP and cooperative breeding include white-fronted bee-eaters (*Merops bullockoides*; Emlen and Wrege 1988), anis (Vehrencamp 1978; Riehl 2010), magpie geese (*Anseranas semipalmata*; Whitehead and Tschirner 1991), and common moorhens (*Gallinula chloropus*; McRae and Burke 1996). The model we present is also highly relevant for several families of birds where both tactics co-occur (such as ratites, waterfowl, rails, starlings, weavers, and woodpeckers; Lyon and Eadie 2008); here, our model provides insights into understanding within-clade patterns of expression of the two alternative tactics. Our model is specific to birds because, although CBP is common in some insect groups (Tallamy and Horton 1990; Field 1992; Loeb 2003; Zink 2003), most cases involve brood parasites that also pursue solitary nesting, and nonnesting parasites are extremely rare (reviewed in Tallamy 2005).

Model

In this model, we use a specific nomenclature for two potentially cooperative breeders, where one female is designated as the "nesting" (primary) female and another female is designated as the "secondary" female (Zink 2000). We assume that secondary females (S) do not have the alternative option of nesting solitarily; rather, they can either (1) join with the nesting female (N) via cooperative breeding or (2) target an alternative host female (H) via brood parasitism. This new perspective incorporates a third player in the model, the potential external "host" female that may receive parasitic eggs. With three players, we must consider genetic relatedness between three dyad combinations (host-secondary females, host-primary females, and primary-secondary females) in an approach that is similar to the three-breeder skew model of Johnstone et al. (1999). We use the framework of previous reproductive skew models that explore the conditions under which a secondary female's "outside option" (here, CBP) affects the solutions for reproductive skew within a cooperatively breeding pair as well as the overall stability of such paired breeding groups (Johnstone 2000; Reeve and Shen 2006; Buston and Zink 2009; Johnstone and Cant 2009). The nesting female (N) is presented with the alternative tactics of (1) accepting female S ("secondary female") to join her in a cooperative nest or (2) rejecting female S to maintain her own solitary nest. This rejection of female S can be termed the "outside option" that is available to female N.

Following Buston and Zink (2009), we define p_n or p_s as the specific fraction of group reproduction (G) in the communal nest that females N and S will require (respectively) based on the outside options described above. We use Hamilton's rule (1964) to determine the behavioral tactics favored by natural selection. Three individuals potentially interact in our model (females N, S, and H), which requires three relatedness measures. For an individual X, an action i is favored over an action j if $X_i + (r_{xy})Y_i + (r_{xz})Z_i > X_j + (r_{xy})Y_j + (r_{xz})Z_j$, where X_i (or X_j) is the focal individual's reproductive output associated with the ith (or jth) action, whereas Y_i (or Y_j) and Z_i (or Z_j) are the reproductive outputs of the other two individuals associated with the focal individual pursuing the ith (or jth) action.

Turning to the specific individual players in our model, three possible relatedness values are designated as r_{ns}, r_{nh}, and r_{sh}. Note that, whereas female N does not interact directly with female H, her decision to reject female S will also affect the inclusive fitness of female H by increasing the probability of brood parasitism (assuming that these additional eggs have a fitness impact on the host). It is possible to consider r_{nh} and r_{sh} as average genetic relatedness in the population, due to random mixing, under the absence of kin recognition. However, when secondary females employ kin recognition, such as the active avoidance of kin for CBP or the active recruitment of kin for cooperative breeding, r_{sh} represents the result of active decision making by the secondary female to target hosts that are less related to them than the background hosts available in the population. Similarly, r_{nh} may represent a similar phenotype that female S is attracted to across both nesting and host females.

Our general modeling approach involves five major steps, corresponding to the behavioral tactics of potentially cooperating females. First, we consider the fitness of the nesting female N, solving for the minimum reproductive shares (p_n) from the communal nest that she requires to refrain from pursuing her outside option of rejecting the secondary female. Second, we consider the fitness of the secondary female S, solving for the minimum reproductive shares (p_s) from the communal nest that she requires to refrain from pursuing her outside option of brood parasitism. To determine whether these minimum requirements are mutually met for both females, we need to evaluate whether female N's minimum share requirements can be met, given female S's minimum share requirements (step 3) and vice versa (step 4). Both of these conditions must be met for cooperative breeding to be evolutionarily stable. Finally, for the fifth step, we solve for the window of acceptable reproductive sharing within the nest, given that S is accepted by N and that S subsequently stays to cooperatively breed with N. This window of reproductive sharing represents the region of "group stability" for cooperative breeding; when this window encompasses complete reproductive skew (i.e., $p_s = 0$), helping behavior is also evolutionarily stable. Definitions of the parameter values used in the model can be found in table 1.

Parameter	Definition
N	Nesting female
S	Secondary female
H	Host female
V_n	Offspring by nesting female when solitary
V_s	Offspring by secondary female via parasitism
V_h	Offspring by host female without parasitism
E_s	Eggs laid by secondary female via parasitism
E_h	Eggs laid by host female
F	Survival rate of eggs in a host female's nest
k	Relative impact of parasitic offspring on host offspring
G	Offspring in a cooperative group (nesting and secondary)
p_n	Fraction of group reproduction G attributed to female N
p_s	Fraction of group reproduction G attributed to female S
r_{nh}	Genetic relatedness between females N and H
r_{ns}	Genetic relatedness between females N and S
r_{sh}	Genetic relatedness between females S and H

Defining the Outside Options Available to Nesting and Secondary Females

Before describing the five major components of our model, it is crucial to define the fitness payoffs of the outside options available to females N and S. The solitary breeding success of female N, after female S either leaves voluntarily or is ejected, is V_n (total surviving offspring). Similarly, V_s is the total number of surviving offspring that the secondary female (female S) produces via the alternative tactic of conspecific brood parasitism. When females N and S breed cooperatively, the average number of surviving offspring for female H (the outside, unparasitized host female) is V_h. When female S pursues brood parasitism, however, female H's fitness is necessarily reduced in a density-dependent fashion, based on the number of parasitic eggs laid. The survival of parasitic eggs laid by female S is also affected by the same density-dependent survival rates.

Details of the cost functions for alternative tactics are critical to the predictions of cooperation models. Previous models of CBP collapse the survival costs of parasitic eggs into just one parameter to achieve mathematical simplicity, whereas we develop cost parameters that encapsulate biologically meaningful aspects of offspring mortality while, at the same time, allowing for a continuous range of costs. We assume that any density-dependent survival cost of an enlarged host clutch is spread equally across all eggs (host and parasite). If we express the direct host fitness as $V_h = F \times E_h$, where F is the intrinsic survival rate of host eggs

(with no parasitic eggs) and E_h is host clutch size, we can define the survival rate after receiving parasitic eggs as

$$F' = F \times \frac{E_h}{E_h + E_s \times k}. \tag{1}$$

Here, F' is the new survival rate that is assumed to be spread across all eggs in the nest equally (host and parasite). Variable k represents the per-egg impact (typically ranging from 0 to 1) of parasitic eggs E_s on the enlarged clutch ($E_h + E_s$). When $k = 0$, additional eggs have no effect on overall egg survival rate, and $F' = F$. However, when $k = 1$, the maternal care destined for E_h eggs is now spread fully over $E_h + E_s$ eggs and $F' < F$. Note that it is also possible for k to be negative, such that parasitic eggs increase survival of the host eggs, in which case parasitism is directly beneficial to the host (appendix C in Zink 2000; Andersson 2001; Loeb 2003; Loeb and Zink 2006).

Substituting the original definition $F = V_h/E_h$ into equation (1) allows us to define a new expression for host fitness after parasitism (assuming that the original host clutch size E_h is not affected by the presence of parasitic eggs):

$$V_h' = E_h \times F' = \frac{E_h \times V_h}{E_h + E_s \times k}. \tag{2}$$

Because we assume that the survival rate F' per egg is the same for host and parasite, the direct fitness of the parasite in a host nest can be expressed as

$$V_s = E_s \times F' = \frac{E_s \times V_h}{(E_h + E_s \times k)}. \tag{3}$$

We assume that, if parasitic eggs are laid across multiple host nests or a host nest receives eggs from multiple parasitic females, the incremental survival effect (k) and host-parasite relatedness (r_{sh}) represent average values. In our model, we do not directly address the possibility of host nests being targeted by multiple parasites at the same time. This is because we are interested in the invasion criteria for when parasitism is an evolutionarily stable strategy for secondary females relative to cooperative breeding. With a low initial frequency, double parasitism will be very unlikely and thus not affect the invasion criteria, at least while parasitism remains rare in the population. We discuss this assumption further in the "Discussion" section.

Solving for the Minimum Shares Required by the Nesting Female

We first consider the minimum reproductive share of total reproduction by the cooperatively breeding group (G) that female N must obtain so that she does not pursue an evic-

tion of female *S*. By applying Hamilton's rule to the nesting female *N*'s decision to eject the secondary female *S* or demand a share p_n of total reproduction *G*, we obtain

$$p_n G + r_{ns}(1 - p_n)G + r_{nh}V_h > V_n + r_{ns}V_s + r_{nh}V_h'. \quad (4)$$

Note that female *N*'s decision to eject female *S* potentially has two inclusive fitness consequences: the effect on female *S*'s reproduction (given that *N* and *S* are related) and the effect of female *S*'s subsequent brood parasitism on the host female *H*'s fitness (given that *N* and *H* are related). Thus, by preventing female *S* from sharing a cooperative nest, female *N* experiences a reduction in inclusive fitness if female *S* instead lays parasitic eggs in the nest of female *H*, a relative of female *N*.

Converting the inequality into an equality and solving for p_n yields the minimum share of reproduction that female *N* must obtain to refrain from dissolving the group and ejecting female *S*:

$$p_n = \frac{V_n - r_{ns}(G - V_s) - r_{nh}(V_h - V_h')}{G(1 - r_{ns})}. \quad (5)$$

Substituting in equations (2) and (3) reveals the following:

$$p_n = \frac{V_n - r_{ns}G + [E_s V_h(r_{ns} - kr_{nh})/(E_h + kE_s)]}{G(1 - r_{ns})}. \quad (6)$$

This is the minimum share that female *N* requires (of total group reproduction *G*) to avoid pursuing group dissolution through an ejection of female *S*.

This minimum share of reproduction (p_n) required by the nesting female to pursue communal nesting with the secondary female always decreases with decreases in V_n (solitary nesting female clutch size) and any increases in *k* (costs of parasitic eggs). Thus, as the outside options for both females decrease, the nesting female is willing to tolerate a smaller fraction of group reproduction. Under the general condition $kr_{nh} < r_{ns}$, the minimum required share p_n decreases with any decreases in V_h or E_s. This condition ($kr_{nh} < r_{ns}$) is always satisfied when there is both a cost of parasitism and when a nesting female is not more related to the outside host female than to the secondary female. Under this likely scenario, the nesting female will also tolerate a smaller fraction of group reproduction with increases in overall group reproduction or size of a solitary host clutch (*G* or E_h).

Based on the results above, the female *N* is expected to tolerate a smaller fraction of group reproduction with an increase in the ratio of host eggs (E_h) to parasite eggs (E_s) in the outside nest. This result suggests that reproductive skew

in a host-parasite nest can indirectly influence reproductive skew in a cooperatively breeding nest. As reproduction is skewed toward female *H*, relative to female *S* in the host nest, the nesting female *N* is more likely to tolerate a smaller fraction of group reproduction, presumably to prevent the host female from incurring the costs of parasitism. Correspondingly, p_n always decreases with increasing relatedness between female *N* and female *H* (nesting females will tolerate a smaller fraction of group reproduction when relatedness to outside hosts, r_{nh}, increases). In addition, p_n decreases with increases in r_{ns} (relatedness between female *N* and female *S*) under the complex condition $E_s[V_h - k(G + r_{nh}V_h - V_n)] < E_h(G - V_n)$. However, p_n increases with increases in r_{ns} when the opposite is true. Note that, when relatedness between female *N* and the outside host female *H* is zero, this condition collapses to $V_h/(G - V_n) < k + (E_h/E_s)$.

Solving for the Minimum Shares Required by the Secondary Female

Next, we consider the minimum reproductive share that female *S* requires of total reproduction by the cooperatively breeding group (*G*) to keep from voluntarily leaving the group to pursue brood parasitism. By applying Hamilton's rule to female *S*'s decision to leave the group or demand a share p_s, we can solve for the minimum p_s that is required to keep female *S* at the nest:

$$p_s G + r_{ns}(1 - p_s)G + r_{sh}V_h > V_s + r_{ns}V_n + r_{sh}V_h'. \quad (7)$$

Converting the inequality into an equality and solving for p_s yields the minimum share of reproduction that female *S* must obtain to refrain from leaving the group:

$$p_s = \frac{V_s - r_{ns}(G - V_n) - r_{sh}(V_h - V_h')}{G(1 - r_{ns})}. \quad (8)$$

Substituting in for equations (2) and (3) reveals

$$p_s = \frac{E_h r_{ns}(V_n - G) + E_s[kr_{ns}(V_n - G) + V_h(1 - kr_{sh})]}{G(E_h + kE_s)(1 - r_{ns})}. \quad (9)$$

This is the minimum share that female *S* requires (of total group reproduction *G* from a communal nest with female *N*) to avoid pursuing the outside tactic of brood parasitism. This minimum share of group reproduction (p_s) always decreases with decreases in V_n (clutch size of nesting female) and increases in *k* (cost of parasitic eggs). Thus, as the outside options for both females decrease, female *S* is willing to tolerate a smaller fraction of *G*. In addition, the minimum share p_s always decreases with decreases in V_h (clutch

size of host female without parasitism) or E_s (number of parasitic eggs), again representing less profitable outside options for female S. Alternatively, the minimum required share p_s always decreases with increases in G or E_h (clutch size of host female when parasitic eggs are present). Therefore, similar to the results for p_n, female S is willing to tolerate a smaller fraction of G as the ratio of E_h to E_s increases (i.e., reproductive skew in the host-parasite nest).

In terms of the relatedness values, p_s always decreases with increases in r_{sh}; female S tolerates a smaller fraction of group reproduction, rather than parasitizing a host female that is kin. In addition, p_s decreases with increases in r_{ns} when $E_s[V_h - k(G + r_{sh}V_h - V_n)] < E_h(G - V_n)$. However, p_s increases with increases in r_{ns} when the opposite is true. Note that, when relatedness between female S and the outside host female H is zero, this condition collapses to $V_h/(G - V_n) < k + (E_h/E_s)$. The relationship between p and r has received much attention in earlier skew models. Restraint models of reproductive skew (e.g., Cant and Johnstone 1999) predict a positive relationship between p and r, whereas concessions skew models (e.g., Reeve and Ratnieks 1993) predict a negative relationship between p and r. Our model predicts that, for both females (N and S), the p versus r relationship can be either negative or positive depending on the above conditions.

Conditions under Which a Nesting Female May Accept the Secondary Female

Next, we must determine the conditions under which cooperative breeding is evolutionarily stable from the perspective of female N, given the minimum reproductive share that female S demands. We contrast the inclusive fitness of female N when she complies with female S's minimum required share versus when she refuses to concede the minimum share that female S requires. We assume that the nesting female is in complete control of group membership and that female S does not challenge her during ejection for sole ownership of the nest (because as a nonnester she cannot, by definition, successfully nest on her own).

The inclusive fitness for female N when she breeds cooperatively will be greater than that if she pursues the alternative of ejecting female S under the following condition:

$$(1 - p_s)G + r_{ns}(p_s)G + r_{nh}V_h > V_n + r_{ns}V_s + r_{nh}(V_h - V_h'). \tag{10}$$

Solving for G gives

$$G > \frac{V_n + r_{ns}V_s - r_{nh}V_h'}{1 - p_s(1 - r_{ns})}. \tag{11}$$

Substituting in for p_s and solving again for G yields

$$G > \frac{(r_{sh} - r_{nh})V_h' - r_{sh}V_h}{1 + r_{ns}} + V_n + V_s. \tag{12}$$

Substituting in equations (2) and (3) reveals

$$G > V_n + \frac{V_h[E_s(1 - kr_{sh} + r_{ns}) - E_h r_{nh}]}{(E_h + E_s k)(1 + r_{ns})}. \tag{13}$$

This is the general condition for cooperative breeding being favored from the perspective of female N when female S is demanding her minimum required reproductive share of group reproduction G.

Conditions under Which a Secondary Female May Breed Cooperatively with the Nesting Female

Next, we determine the conditions under which cooperative breeding is evolutionarily stable from the perspective of the secondary female, given that female N favors cooperation (i.e., eq. [13] has been satisfied) and given that female N requires a minimum fraction p_n of G. When female S forms a cooperatively breeding group under these conditions, her inclusive fitness will be greater than if she had left the group to pursue brood parasitism when:

$$(1 - p_n)G + r_{ns}(p_n)G + r_{sh}V_h > V_s + r_{ns}V_n + r_{sh}(V_h - V_h'). \tag{14}$$

Solving for G reveals the following inequality:

$$G > \frac{r_{ns}V_n + V_s - r_{sh}V_h'}{1 - p_n(1 - r_{ns})}. \tag{15}$$

Substituting in for p_n and solving again for G yields

$$G > \frac{(r_{nh} - r_{sh})V_h' - r_{nh}V_h}{(1 + r_{ns})} + V_n + V_s. \tag{16}$$

Substituting in equations (2) and (3) reveals

$$G > V_n + \frac{V_h[E_s(1 - kr_{nh} + r_{ns}) - E_h r_{sh}]}{(E_h + E_s k)(1 + r_{ns})}. \tag{17}$$

This is the general condition under which cooperative breeding is favored from the perspective of female S when female N is demanding her minimum required reproductive share of group reproduction G. Note that the minimum conditions for group stability are almost exactly the same for both females, because equation (17) is identical to equation (13) except that r_{sh} and r_{nh} are reversed. This means that

the minimum conditions favoring cooperative breeding are just slightly more easily satisfied for the female (N or S) that is most related to the outside host female H. However, for figures 1–5, we assume that $r_{sh} = r_{nh}$, which is the general condition where equations (13) and (17) are exactly equal.

We have derived a general solution for the value of group reproduction above which there will be some region of group stability (i.e., some possible division of group reproduction that satisfies both females). This result (eq. [13] and eq. [17]) effectively solves for the point where p_s is just equal to $1 - p_n$ (i.e., the amount left over from the nesting female's share is just enough to satisfy the secondary female). This is the threshold group productivity where the minimum requirements for cooperative breeding are just satisfied; below this threshold, female S will always pursue the brood parasitic tactic. By taking the first derivative of this threshold condition of group stability, we find that cooperatively breeding groups will become more likely with increases in E_h and decreases in E_s. Thus, as reproductive skew in host-parasite nests moves toward the host, due to lower parasite fecundity and/or higher host fecundity, cooperative breeding is more likely. Cooperatively breeding groups are also more likely as the cost of parasitism k increases, as well as when r_{nh} and r_{sh} (relatedness to host) increase.

We can graphically depict how different parameter values shift the probability that the threshold of cooperative breed-
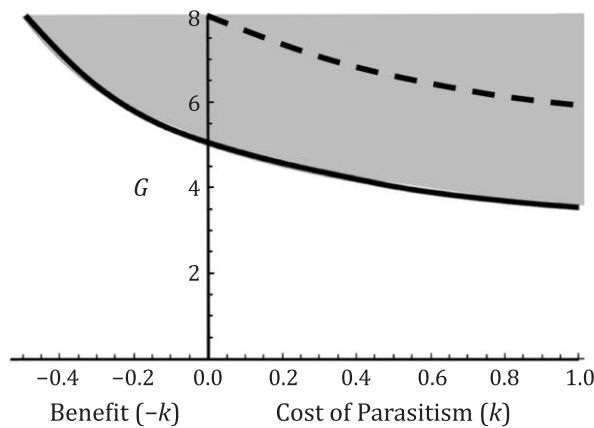

Figure 1: Threshold values of group productivity (G) required for cooperation to be favored over brood parasitism across different costs or benefits of parasitic eggs (k). Other variables are fixed: $V_h = 3$, $V_n = E_h = E_s = 5$, and $r_{nh} = r_{sh} = r_{ns} = 0.5$. Note that, even when there is no cost ($k = 0$), cooperation is the stable strategy when group productivity is equal to or greater than the original V_n. This threshold value of G increases steadily as parasitic eggs actually increase survival of host clutch (for negative values of k). The shaded region depicts when cooperation is favored over parasitism between first-order relatives, and dashed line represents when kin are avoided by parasites, which raises the threshold of cooperation as parasitism no longer imposes costs on kin ($r_{sh} = r_{nh} = 0$); all other parameters stay the same. See table 1 for definitions of the parameter values used in the model.

ing will be satisfied. Figure 1 shows that increasing the costs of parasitism (k) makes cooperation more likely (i.e., a larger gray region). Figure 2 shows that cooperation becomes less likely with increases in the number of parasitic eggs laid by female S and increases in r_{ns}. In both figures, the decreased likelihood of groups forming when primary and secondary female kinship increases is a unique outcome of this model, relative to reproductive skew theory generally, where kinship drops out of the stability conditions entirely (Reeve and Ratnieks 1993; Johnstone 2000; Buston and Zink 2009). This is because even the nesting female gains higher inclusive fitness (and secondary female direct fitness) as long as the number of parasitic eggs E_s is sufficiently high. However, the magnitude of this effect of kinship on group stability is diminished as the relatedness to host females decreases (fig. 3).

Solving for the Window of Reproductive Sharing (Conditions under Which Females Are Expected to Breed Communally)

For the region of parameter space past the threshold condition for group stability (i.e., where eq. [13] and eq. [17] are satisfied and $p_s + p_n \ll 1$), we can determine the exact size of the "window of reproductive sharing." This window represents the range of all possible combinations of reproductive shares where both N and S achieve at least their minimum requirement for cooperation (similar to the "window of group stability" in Buston and Zink 2009 and the "window of selfishness" in Reeve 2000 or "tug-of-war zone" in Reeve and Shen 2006). We derive the maximum allowed values of p_n and p_s that satisfy the conditions for cooperation by simply substituting in $(1 - p_n)$ for p_s (in eq. [9]) and $(1 - p_s)$ for p_n (in eq. [6]). For cooperative breeding to be stable, each female cannot take any more reproduction than would leave enough to satisfy the other female's minimum requirement. Therefore, the window of reproductive sharing is where female N's shares range from p_n to $(1 - p_s)$ and female S's shares range from p_s to $(1 - p_n)$. The exact values of reproductive sharing within this window are likely to be determined by competition over the remaining group reproduction (after the minimum required shares are satisfied; see "Discussion" for implications and mechanisms).

Figure 4 illustrates the window of reproductive sharing for a specific set of parameters. The value of G where the two lines cross in figure 4 is the threshold value of G where cooperative breeding becomes stable (i.e., where $p_s = (1 - p_n)$, or where there is just enough group reproduction for both female's minimum requirements to be satisfied). The shaded region represents the "window of reproductive sharing," which is the range of parameter space where cooperation is stable. Note that, as the width of the window increases, cooperation is stable over a broader range of parameter
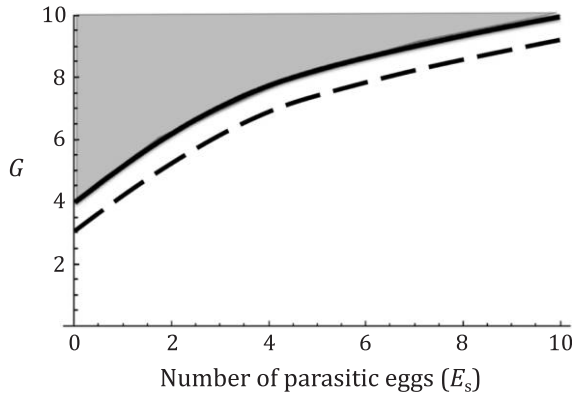
Figure 2: Solid line represents the threshold values of group productivity (G) required for cooperation to be favored over brood parasitism across different numbers of parasitic eggs (E_s). Here $k = 0.3$, $V_h = 3$, $V_n = 4$, $E_h = 2$, $r_{nh} = r_{sh} = 0$, and $r_{ns} = 0.5$. The shaded region depicts when cooperation is favored over parasitism when nesting females are not related to outside host females (e.g., active avoidance of kin as potential hosts). The dashed line represents the threshold condition for cooperation where females are full siblings, which lowers the threshold of cooperation as parasitism imposes costs on kin ($r_{ns} = r_{nh} = r_{sh} = 0.5$); all other parameters remain the same. See table 1 for definitions of the parameter values used in the model.

values. It is possible to derive a general solution for the width of the window of reproductive sharing by solving for the fraction of leftover reproduction that is not claimed by each female's minimum required share:

$$(1 - p_s - p_n) = \{E_h(1 + r_{ns})(G - V_n) + E_s[Gk(1 + r_{ns})$$
$$- V_h(1 + r_{ns} - k(r_{nh} + r_{sh})) - V_n k(1 + r_{ns})]\}$$
$$/G(E_h + E_s k)(1 - r_{ns}). \tag{18}$$

Taking the first derivative of equation (18) with respect to each parameter allows us to determine how the size of this window of reproductive sharing may change. The window size always increases with decreases in V_n, V_h (solitary clutch sizes of nesting and host females) or E_s (number of parasitic eggs). The window size also increases with increases in k, G, or E_h. In terms of the relatedness values, the size of this window of reproductive sharing always increases with increases in r_{sh} or r_{nh}. The window also increases with increases in r_{ns} when the inequality $E_s[V_h - k(G + r_{(s,n)h}V_h - V_n)] < E_h(G - V_n)$ is satisfied (the same inequality that defines a positive or negative relationship between p and r_{ns}).

Predicting the Case Where Secondary Reproduction Is Zero (Helping Behavior)

The evolution of helping behavior (when one female or male gives up reproduction entirely to focus solely on increasing group productivity G) is a major question in the

evolution of cooperation (Alexander 1974; Stiver et al. 2005). Therefore, it is useful to consider the most extreme case in which female S is willing to give up all reproduction rather than leave voluntarily to pursue brood parasitism. This is the situation where the window of reproductive sharing includes complete skew ($p_n = 1$ and $p_s = 0$). By applying Hamilton's rule to the secondary female's decision to leave the group or stay and help when $p_s = 0$, we obtain

$$r_{ns}G + r_{sh}V_h > V_s + r_{ns}V_n + r_{sh}V_h'. \tag{19}$$

Converting the inequality into an equality and solving for G yields the minimum additional reproduction that female N must produce ($G - V_n$) with the help of female S to keep female S from leaving the group:

$$G - V_n > \frac{V_s + r_{sh}(V_h' - V_h)}{r_{ns}}. \tag{20}$$

Substituting in equations (2) and (3) reveals

$$G - V_n > \frac{E_s V_h(1 - k r_{sh})}{r_{ns}(E_h + k E_s)}. \tag{21}$$

The left-hand portion of equation (21) represents the minimum increase in offspring production by female N (above and beyond her solitary productivity V_n) that is necessary
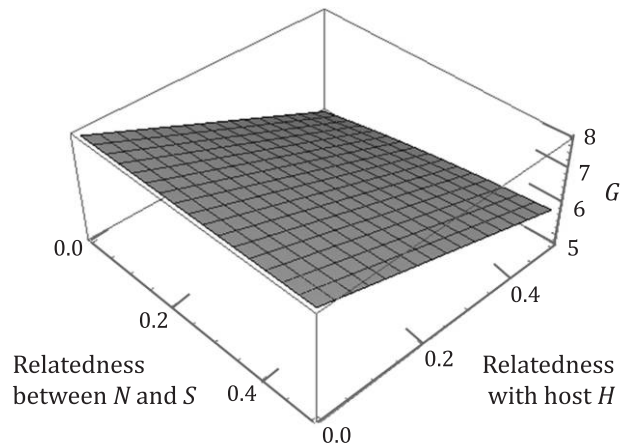

Figure 3: Relationship between the minimum conditions for group stability (expressed as a threshold of group productivity [G]) for cooperatively breeding groups with changes in relatedness between communal breeders (r_{ns}) and hosts, where $r_{nh} = r_{sh}$. The area above the surface represents region of group stability (cooperative breeding). Here $V_h = 6$, $V_n = E_h = 5$, $E_s = 3$, $k = 0.5$. Note that kinship with host has a greater influence on stability, relative to kinship between females N and S, and that the negative relationship between r_{ns} and stability increases with increasing kinship to host. H represents host female, N represents nesting female, and S represents secondary (nonnesting) female. See table 1 for definitions of the parameter values used in the model.
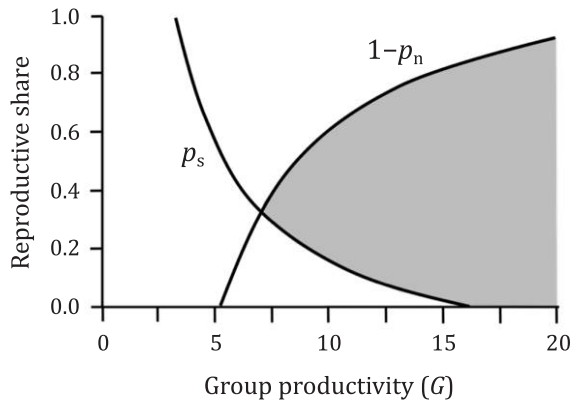
Figure 4: Potential share of the reproduction belonging to a non-nesting secondary female (S) versus group output (G). Other variables are fixed: $V_h = V_n = 5$, $E_h = E_s = 6$, $k = 0.8$, $r_{nh} = r_{sh} = r_{ns} = 0.2$. The descending line is S's minimum reproductive share (p_s) to stay in the group, and the ascending line is S's maximum reproductive share ($1-p_n$) below which the reproduction demanded by N to keep female S is satisfied. Between the two lines lies the (shaded) region of group stability. Note that, at $G = 16$, the helping threshold has been reached, and cooperation is stable even when $p_s = 0$. See table 1 for definitions of the parameter values used in the model.

to make nonbreeding (helping) a stable strategy by secondary females. This relationship between group fitness and helping behavior by female S, versus reproductive sharing, is depicted in figure 5. Note that helping is more likely with increasing values of r_{ns}.

A secondary female is more likely to join as a helper (i.e., eq. [21] is satisfied) when r_{ns}, r_{sh}, and k increase. This suggests that, as outside options for brood parasitism decrease, helping by the secondary female is more likely to evolve; conversely, as parasitism becomes more profitable, helping behavior is less likely to evolve. Similarly, equation (21) is more likely to be satisfied as the number of parasitic eggs (E_s) decreases and as host egg clutch size (E_h) increases. Again, this result suggests that, as outside options for brood parasitism decrease, helping by the secondary female is more likely to evolve. The relationship between group stability and V_h (host clutch size without a parasite) is much more complicated and is highly dependent on the relative values of E_h and E_s.

Discussion

The potential evolutionary links between cooperative breeding and conspecific brood parasitism have been noted previously (Vehrencamp 2000; Zink 2000; Andersson 2001; Vehrencamp and Quinn 2004). Our new model examines unexplored links between cooperative breeding and a second form of CBP, parasitism by females that do not have the option of nesting on their own in the same year they

lay parasitically. Ultimately, our model reveals how variation in the outside options available to secondary females affects their optimal solutions for reproductive sharing in cooperative nests. As the outside option of brood parasitism becomes less profitable (e.g., as hosts become rare, through decreased density, or the costs of parasitic eggs to hosts increases), female S is more likely to pursue cooperative breeding. As the outside option of solitary nesting becomes less profitable (in terms of offspring survival with only one female present), female N becomes more tolerant of female S as a cooperator. Finally, as these outside options decrease for S and N (when cooperation is stable), either of the two cooperative breeders is willing to accept a smaller fraction of the group reproduction.

Our model reveals that cooperatively breeding groups (females N and S nesting together) will always be less likely to form with any increases in r_{ns}. The decreased likelihood of these groups forming when nesting and secondary female kinship increases is a unique outcome of this model, especially given that the minimum required reproductive shares for each female have the potential to decrease with increasing kinship under a broad array of conditions. This result of kinship driving group stability is also unique because, in previous models of reproductive skew, kinship consistently drops out of the stability conditions altogether (Reeve and Ratnieks 1993; Johnstone 2000; Buston and Zink 2009). Buston and Zink (2009) emphasized that a positive or
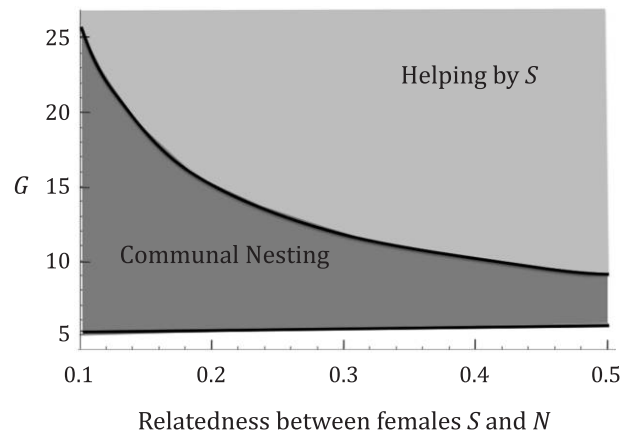

Figure 5: Relationship between group productivity and the threshold for helping behavior by a nonnesting secondary female (S; area above the upper line; light gray area. This threshold decreases with increasing relatedness between nesting females. The stability solution for communal nesting (area between the lower line and the upper line; dark gray area), which increases slightly with increasing relatedness. Note that the distance between the two curves (i.e., the conditions under which groups are stable but helping is not) can vary across different values of r_{ns}. Here $V_h = 6$, $V_n = E_h = 5$, $E_s = 3$, $k = 0.5$, and $r_{nh} = r_{sh} = 0.5$. See table 1 for definitions of the parameter values used in the model.

negative correlation between female kinship and reproductive shares often depends on a model's initial assumptions. Our model predicts that both females in a cooperative nest (N or S) will have the same directionality in their relationship between minimum required share and kinship (with each other), but the direction of this relationship can be either positive or negative. The inclusion of the third (host) female in our model also adds rich complexity to the social dynamics, because the stability of cooperative groups is potentially influenced by relatedness patterns involving all three possible dyads of females. For example, when a primary female rejects a secondary female and forces her to pursue brood parasitism, the primary female can suffer reduced inclusive fitness when the host is a relative (e.g., dashed line vs. shaded region in figs. 1 and 2).

A central feature of our model is the window of reproductive sharing, which represents the area of parameter space under which cooperation is the best strategy for both the primary and secondary female (fig. 4). The width of the window defines the parameter space in which cooperation is evolutionarily stable and should therefore indicate the likelihood that cooperation will evolve. Kokko (2003) has pointed out that solutions for traditional transactional models of reproductive skew are constrained to the maximum or minimum threshold boundaries of this window; as a result, any error in assessment or policing could result in maladaptive instability of the group. This issue disappears in our model; the wider the window of reproductive sharing, the more likely the evolution of cognitive mechanisms that can maintain a cooperative association and a larger margin of error for mistakes in reproductive partitioning (Nonacs 2006).

Although a larger window of reproductive sharing indicates a larger range of parameter space in which cooperative breeding is stable, it may also mean more scope for conflict or cheating within such groups (and less tranquil societies). This conflict arises because, although cooperation is generally mutually beneficial, the two females differ in their optimal share of reproduction. This conflict could lead to the evolution of cognitive, physiological, or behavioral mechanisms for each female to increase her reproductive shares across this range (Nonacs 2006). For cooperatively breeding birds, mechanisms that could influence skew within this window of reproductive sharing include egg tossing (Vehrencamp 1977; Koenig and Mumme et al. 1983), deserting a reproductive attempt (Vehrencamp et al. 1986), and contests to establish relative degree of social dominance (Reeve and Ratnieks 1993). For any of these mechanisms, our model predicts that the scope of conflict will be positively correlated with the width of the window of reproductive sharing.

When the window of reproductive sharing encompasses complete skew (where the secondary female does not reproduce), our model addresses the conditions under which

females remain at a primary nest and act as helpers. However, it is important to note that we are focusing on females, whereas most helping in birds involves male helpers (but see Cockburn 2004). Our results appear to indicate a very restricted set of situations where the incentives for outside options (brood parasitism) are so low that female helping is favored. This could potentially explain the paucity of female helpers in birds. Specifically, cooperation by secondary females requires shared reproduction to offset fitness gains from the alternative of brood parasitism, whereas brood parasitism is not an option for males, and thus cooperation without reproduction is more likely to be stable for males.

Although previous work has suggested that the costs and benefits of brood parasitism are likely to be frequency dependent (Eadie and Fryxell 1992; Lyon and Eadie 2008; Jaatinen et al. 2011*b*), we do not directly address the frequency-dependent aspect of alternative tactics in our model. This is primarily because we treat parasitism as a rare strategy and solve for conditions under which it will spread in a population relative to communal nesting. In addition, previous work has shown that factors such as population density, host limitation, and fecundity constraints will often limit a population from approaching a frequency-dependent equilibrium (Eadie and Fryxell 1992; Lyon 2003). Similarly, our model assumes that a solitary primary female nester will not receive parasitic eggs. This approach is appropriate, again, for invasion criteria of parasitism over cooperation. Finally, although we have treated the primary and host females as different females, some of the hosts targeted by parasites might also be females that could engage in cooperative breeding. On the other hand, cooperating females are likely to be much more successful in repelling potential brood parasites relative to host females, a pattern that has been noted for interspecific brood parasitism (Feeney et al. 2013). Therefore, future treatments of our model could consider equilibrium frequencies (rather than invasion criteria) by specifically addressing how the ratio of parasites to hosts will affect the payoffs for female N (given that she herself may be parasitized) or female H (given that host and nesting females may be experiencing differential costs of high parasite frequency).

As alternatives, we expect either brood parasitism or communal nesting to evolve as the favored strategy, and therefore, all else being equal, our model does not always predict the occurrence of both at the same time in a population. Nevertheless, we might expect to see both CBP and cooperative breeding within the same clades, allowing for direct comparisons between closely related species. A more general prediction of our model is that, if brood parasitism and cooperative breeding influence each other's evolution as evolutionary alternatives, they should co-occur more often than expected by chance in some clades. Brood

parasitism and cooperative breeding do seem to co-occur in several avian clades, such as ratites, waterfowl (order Anseriformes), rails (family Rallidae), starlings (family Sturnidae), weavers (family Plociidae), and woodpeckers (family Picidae) (Lyon and Eadie 2008). This suggests that a comparative analysis would be fruitful. Our model might provide a useful framework for comparing the life history traits of species with brood parasitism versus cooperative breeding in these clades.

There is one taxonomic group in particular, the waterfowl, for which our model may have particularly important implications. Conspecific brood parasitism is widespread in waterfowl (Eadie et al. 1988; Rowher and Freeman 1989) but standard cooperative breeding (joint nesting) is rare, occurring in just one species, the Magpie Goose (*Anseranas semipalmata*; Vehrencamp and Quinn 2004). However, most waterfowl have precocial offspring that feed themselves, so it is likely that a single attending parent is sufficient to provide care to a brood. Thus, breeding systems that appear to be parasitic (i.e., mixed maternity broods tended by just one female, with or without a male) might actually reflect cryptic forms of cooperation (Andersson 1984, 2001; Eadie et al. 1988). A primary female that allows a relative to lay eggs in her nest, when nesting sites are limited and the costs of additional eggs are low, gains inclusive fitness if such facilitation increases the number or the success of the eggs laid by the parasitic female (Andersson 2001). Our model of cooperative breeding could also be adapted to encompass brood amalgamation in waterfowl, where females incubate their own eggs, but broods amalgamate after hatching and are tended by a single female (Eadie et al. 1988; Eadie and Lyon 1998).

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Left, a few species, like the common moorhen (*Gallinula chloropus*), exhibit both cooperative breeding and brood parasitism, even in the same population. *Right*, more commonly, species either show parasitism or cooperative breeding, but not necessarily both. In American coots (*Fulica americana*), for example, brood parasitism is common, but cooperative breeding has not been observed. Photo credit: Bruce E. Lyon.