Conspecific Brood Parasitism and Population Dynamics

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Abstract: Conspecific brood parasitism (CBP), defined as parasitic laying of eggs in a conspecific nest without providing parental care, occurs in insects, fishes, amphibians, and many birds. Numerous factors have been proposed to influence the evolution of CBP, including nest site limitation; effects of brood size, laying order, or parasitic status on offspring survival; randomness of parasitic egg distribution; adult life-history trade-offs; and variation in parental female quality or risk of nest predation. However, few theoretical studies consider multiple possible types of parasitism or the interplay between evolution of parasitism and population dynamics. We review existing theory of CBP and develop a synthetic modeling approach to ask how best-of-a-bad job parasitism, separate-strategies parasitism (in which females either nest or parasitize), and joint-strategies parasitism (in which females can both nest and parasitize) differ in their evolutionary conditions and impacts on population dynamics using an adaptive dynamics framework including multivariate traits. CBP can either stabilize or destabilize population dynamics in different scenarios, and the role of comparable parameters on evolutionarily stable strategy parasitism rate, equilibrium population size, and population stability can differ for the different modes of parasitism.

Keywords: intraspecific brood parasitism, conspecific brood parasitism, adaptive dynamics, evolutionary dynamics, evolutionarily stable strategy (ESS), bird population dynamics.

Conspecific brood parasitism (CBP) occurs in diverse taxa, including insects (Tallamy 2005), fishes (Wisenden 1999), amphibians (Summers and Amos 1997), and most prominently, birds (Yom-Tov 1980, 2001; Davies 2000). For example, more than 230 species of birds are known to lay eggs in the nests of conspecifics (Eadie et al. 1998; Yom-Tov 2001). Increasing interest in this phenomenon over the past two decades has led to a plethora of studies examining the fitness consequences to parasites and their hosts and the ecological factors influencing the frequency of CBP within and among populations (Petrie and Möller 1991; Eadie and Fryxell 1992; Nee and May 1993; Maruyama and Seno 1999a; Robert and Sorci 2001; Broom and Ruxton 2002, 2004; Ruxton and Broom 2002).

Less well appreciated are the possible roles of CBP in population dynamics and vice versa. In several species, parasitic egg laying appears to be strongly influenced by the availability of resources essential for breeding. For example, in many hole-nesting birds, parasitism is more frequent when population density is high, nest sites are limited, and many host nests are available (Haramis and Thompson 1985; Eadie 1991). Similar relationships with density occur for colonial-nesting species and for species concentrated on islands (Lank et al. 1990; Lokemoen 1991; Lyon and Everding 1996; Waldeck et al. 2004). High levels of CBP in turn may lead to increased levels of nest desertion and reduced hatching success of eggs or fledging success of young (Haramis and Thompson 1985; Semel and Sherman 1986, 2001; Semel et al. 1988; Eadie 1991; Eadie et al. 1998). Few models have considered CBP and population dynamics together, but those that did suggested that CBP could lead to fluctuating or unstable population dynamics (May et al. 1991; Eadie and Fryxell 1992; Nee and May 1993). Indeed, Semel et al. (1988) suggested that high levels of CBP, exacerbated by high densities of nest
boxes placed in close proximity, could result in population crashes in the cavity-nesting wood duck (Aix sponsa). Theoretical and empirical work in other systems highlights the fact that evolution shapes the traits affecting population dynamics, and population dynamics define the relative fitnesses on which evolution acts, so neither process can be fully understood without the other (Kokko and Lopez-Sepulcre 2007).

In this article, we show that the impact of CBP on population dynamics, in terms of population equilibrium and stability, depends on why and how parasitism occurs. In particular, scenarios with higher parasitism can give either more stable or less stable dynamics, depending on the model, and a factor such as value of a parasitic egg may affect dynamics differently in different models. Investigating the role of CBP on population dynamics leads to several modeling challenges. First, we want to build on existing theory about evolution of CBP, but that theory involves diverse models with different biological considerations and modes of parasitism. Therefore we begin by reviewing the theoretical literature with the aim of developing as a starting point a general model based on existing models of the three major types of parasitism that have been proposed, defined below as best-of-a-bad-job, separate-strategies, and joint-strategies parasitism.

We then incorporate population dynamics and density dependence into the general model and develop four specific cases. For each case, we examine the interactions between parasitism, equilibrium population size, and stability. For continuous strategy variables, we use the adaptive dynamics framework, which generalizes evolutionarily stable strategies to evolutionarily singular strategies that may be dynamical attractors (convergence stable) or branching points for simple evolutionary models (Eshel 1983; Christiansen 1991; Waxman and Gavrilets 2005). Most adaptive dynamics research considers only univariate traits, with exceptions such as work by Abrams et al. (1993), Dieckmann and Law (1996), Leimar (2005), and Brown et al. (2007). For model 4 below, we show that when total reproductive effort can evolve (constrained by adult costs of reproduction) in addition to parasitism strategy, the population dynamics consequences of CBP are qualitatively different than when only parasitism strategy evolves. Thus, while this article’s primary focus is on the role of CBP in population dynamics, it also extends theories of evolution of CBP. While our models do not cover all potentially important aspects of parasitism, they represent a synthesis and generalization of many ideas in the literature.

**Biology and Models of CBP**

At least 17 studies have developed models to examine the evolutionary dynamics of conspecific brood parasitism from an ESS perspective. Table 1 summarizes some of the major features included in these models, while key results of each model are described in table A1 in the online edition of the *American Naturalist*. Three major types of brood parasitism have been considered. In best-of-a-bad-job (BOBJ) parasitism, a parasitism strategy has lower fitness than nesting but is used by females who cannot breed otherwise, typically due to nest site limitation. In separate-strategy models, females either nest or parasitize but not both, and the strategies may have equal fitness under ESS conditions so that parasites are not just females who cannot obtain a nest site. An ESS of separate-strategy parasitism (separate ESS) can occur if, when parasitism frequency is low (or zero), an individual could obtain higher fitness by parasitizing than by nesting (Eadie and Fryxell 1992). Here the term “separate strategy” is the same as the “mixed strategy” of Eadie and Fryxell (1992; there distinguished from BOBJ parasitism) and the "professional" parasitism of Nee and May (1993). In joint-strategy models, the same individuals may nest and also parasitize other nests. In an ESS of joint-strategy parasitism (joint ESS), an individual must find it advantageous to trade some of its potential nest eggs for parasitic eggs it could lay in other nests, which may also increase the survival of its remaining nest eggs. Most of the studies summarized in table 1 consider only a single type of parasitism.

**Biology Included in Existing Models on Evolution of CBP**

The possibility of CBP increases not only the range of conceivable reproductive strategies but also the range of factors that may influence relative fitness between strategies, as reflected in various models (see table 1 for citations). Without CBP, evolution of reproductive effort involves trade-offs between quality and quantity of offspring as well as costs of reproduction. With CBP involved, there may also be trade-offs between laying one’s eggs parasitically or in one’s own nest and between nesting at all or reproducing completely parasitically. Each of these could potentially have different quantity versus quality trade-offs and costs of reproduction, although a full combination of possibilities would make a quite complicated model and has not been treated. Most models either assume fixed clutch sizes for each strategy or include one trade-off such as a cost of reproduction or a trade-off between own-nest and parasitic eggs.

For birds, offspring value typically depends on brood size, an effect included in most models. Parasitic eggs may be inherently less valuable (i.e., have lower fitness) than host eggs, a parameter that has been included in many models, but a dependence of laying order on offspring value has been included in only two models. The relative fitness of nesting versus parasitism may depend on the
### Table 1: Comparison of existing models of conspecific brood parasitism

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<td>Total brood size affects fledge success</td>
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<td>Parasite displaces/removes host eggs</td>
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<td>Inherent lower value of parasite eggs</td>
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Note: "Y" means an issue was included in the models of a paper; a blank cell means it was not; § indicates that an explanation is given in table A1 in the online edition of the *American Naturalist*. BOBJ = best of a bad job; ESS = evolutionarily stable strategy.
recently, Poysa and Pesonen (2007) considered variation hence inclusive fitness (see also Andersson 1984). Most
the influence of relatedness among hosts and parasites and nesting. These models are distinguished by their focus on
CPB as an alternative to cooperative breeding or solitary
dersson and Eriksson (1982) that CPB could exist as an
experimental approach. However, of all the models summarized
in specific rather than general terms. Here we ask the
question of how different types of CBP can affect population
dynamics. For simplicity, we incorporate density dependence such that its interaction with ESS parasitism levels is small.

Our Models
We examine the evolutionary stability of parasitism and its effect on population dynamics for several specific cases of a general model that includes many biological aspects of the separate models listed in table 1. First we introduce the general model and its assumptions, with parameters summarized in table 2. Then we give additional assumptions for the specific cases. The general model can lead to BOBJ, separate-ESS, and/or joint-ESS parasitism, although in the results presented here only one type of parasitism is considered in each specific case.

The general model allows two types of strategy, nesting and non-nesting. The nesting strategy allows eggs to be laid both in one’s own nest (nest eggs) and in other nests (parasitic eggs), while the non-nesting strategy allows only parasitic eggs. The nesting strategy involves total reproductive effort of $T$, split between $C_n$ nest eggs and $C_p/\tau$ non-nest eggs. Therefore each nest egg can be traded for $\tau$ parasitic eggs, and $C_p = \tau(T - C_n)$, with $0 \leq C_n \leq T$. The trade-off parameter $\tau$ may be greater or less than 1 depending, for example, on how much effort is required to find nests to parasitize and whether production of nest eggs is limited by ability to feed them versus physiological limits in producing them. The fraction of parasitic eggs that are not rejected (killed) by the host is $\eta$. The value of a parasitic egg relative to a nest egg, given that each survives the nest, is $\gamma$, and in the specific cases we assume $0 \leq \gamma \leq 1$.

The population fraction of non-nesters is $\pi$, each of which produces $C_n$ parasitic eggs. If non-nesters have equivalent physical state to nesters, then it is reasonable to assume $C_n = \tau T$, the maximum parasitic eggs that even
a nester could produce. Alternatively, \( C_n \) could be greater or less than \( \tau T \) depending on the costs and benefits of building and using a nest. Non-nesting may occur either as a separate strategy ESS or as a BOBJ strategy if there is nest limitation.

Parasitic eggs may be distributed either evenly or randomly among nests. It is assumed that parasitic eggs from nesters and non-nesters follow the same distribution and that the parasitic eggs of one parent are not aggregated in one or more nests. Survival rates of nest sites available (100 for model 1) for a resident strategy is via \( C_n \), while for a nester it is via \( C_n \). It would also be possible for adult survival for a nester to depend on the number of parasitic or total eggs it has raised.

For nesters, a strategy is defined by either \( C_n \) if there is no adult cost of reproduction and hence \( T \) can be assumed fixed at a physiological maximum, or by \( (C_n, T) \), if adult cost of reproduction creates a trade-off between total reproductive output and adult survival. To formulate fitness in an adaptive dynamics framework, define \( (C_n, T) \) as the resident strategy of an entire population and \( (C_n, T') \) as an invading strategy of a mutant individual.

The fitness of an invading nester strategy in a population playing a resident strategy is

\[
F_n(C_n, T'; C_n, T) = C_nE_{n \cdot Y}S_n(C_n, Y, W, N)] + \frac{\gamma YS_n(C_n, Y, W, N)}{E[Y]} + A_n(C_n, T', N).
\]

Finally, adult survival may either be constant or depend on reproductive strategy (costs of reproduction) and/or \( N \) (density dependence). For a non-nester, dependence on reproductive strategy is via \( C_n \), while for a nester it is via \( T \) and/or \( C_n \). It would also be possible for adult survival for a nester to depend on the number of parasitic or total eggs it has raised.

Table 2: Model parameters and notation

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Interpretation</th>
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<tbody>
<tr>
<td>( N )</td>
<td>Adult population size</td>
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<tr>
<td>( C_n )</td>
<td>Eggs laid by a nester in her own nest (equal to ( T ) for models 1, 2)</td>
</tr>
<tr>
<td>( C_p )</td>
<td>Eggs laid by a nester in other nests</td>
</tr>
<tr>
<td>( C_n )</td>
<td>Eggs laid by a non-nester (equal to ( \tau T ))</td>
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<tr>
<td>( T )</td>
<td>Reproductive effort (maximum number of own nest eggs, equal to ( 8 ) for models 1–3)</td>
</tr>
<tr>
<td>( \tau )</td>
<td>Number of parasitic eggs a female can produce instead of 1 nest egg</td>
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<tr>
<td>( X )</td>
<td>Strategy variable ( X ) with ( X = T ) or ( C_n ) for an invading strategy</td>
</tr>
<tr>
<td>( Y )</td>
<td>Number of parasitic eggs in a nest</td>
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<tr>
<td>( W )</td>
<td>Abstract vector of nest laying orders or other random quality variable</td>
</tr>
<tr>
<td>( S_n, S_p )</td>
<td>Offspring survival of host eggs and parasitic eggs, respectively</td>
</tr>
<tr>
<td>( m_n, m_p )</td>
<td>Negative exponential slope for offspring survival of host and parasitic eggs, respectively, as a function of total eggs in nest (equal to 1 in all models)</td>
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<tr>
<td>( B )</td>
<td>Negative slope of offspring survival as a function of ( N ) (.005 in models 2–4; 0 in model 1)</td>
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<tr>
<td>( D(N) )</td>
<td>Density-dependent factor in offspring survival, equal to ( 1 - bN ) or 0</td>
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<tr>
<td>( A_n, A_y )</td>
<td>Adult survival for nesters and non-nesters, respectively</td>
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<tr>
<td>( Q )</td>
<td>Maximum adult survival for model with adult cost of reproduction (.8 in model 4)</td>
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<tr>
<td>( K )</td>
<td>Negative slope of adult survival as a function of ( T ) for adult cost of reproduction (.05 in model 4)</td>
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<td>( H )</td>
<td>Number of nest sites available (100 for model 1)</td>
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<td>( \pi )</td>
<td>Fraction of adults using a parasitic strategy (derived for each model)</td>
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<tr>
<td>( \gamma )</td>
<td>Offspring value of a parasitic egg relative to a nester egg from same nest, ( 0 &lt; \gamma \leq 1 )</td>
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<td>( \eta )</td>
<td>Probability that a parasitic egg is not rejected by host (1 in all models)</td>
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<tr>
<td>( F_n )</td>
<td>Fitness of nesters</td>
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<tr>
<td>( F_p )</td>
<td>Fitness of non-nesters</td>
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<tr>
<td>( G(N) )</td>
<td>Population dynamics function: ( N(t + 1) = G(N(t)) )</td>
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eggs, and adult survival, respectively. The expected value in
the own-nest term is the average survival (per nest) of
the nest eggs across all random values of parasitic eggs per nest
and laying orders. The average survival of parasitic eggs (per
egg) that are not rejected is calculated as the average number
of parasitic eggs that survive per nest divided by the average
number of parasitic eggs per nest. (This is the average sur-
vival of a randomly chosen parasitic egg in the population
rather than the average survival of parasitic eggs in a ran-
domly chosen nest.) In all expectations, the distribution of
Y incorporates parasitic eggs from both non-nesters and
nesters (using the resident strategy) that are not rejected at
laying. The benefit to the invading strategy of parasitic eggs
is multiplied by their relative value ($\gamma$) and the proba-
bility that they are not rejected ($\eta$). Finally, adult survival of a
nester, $A_n$, may depend on reproductive effort and/or adult
population size.

For non-nesters, fitness is given by

$$F_n(C_n) = \gamma \eta C_n \frac{E[v(YS_n(C_n, Y, W, N))]}{E[v(Y)]} + A_n(C_n, N),$$

(2)

where $A_n$ is adult survival for non-nesters. The average
fitness in the population is

$$F = \pi F_n + (1 - \pi) F_c.$$  

(3)

The population dynamics are given by

$$N(t + 1) = N(t) F(N(t)) \equiv G(N(t)).$$

(4)

In equation (4), $F$ has been rewritten $F(N(t))$ to emphasize
that average fitness depends on population size via equa-
tions (1) and (2).

Several aspects of model formulation (1)-(2) deserve
comment. The model is closely related to the general model
of Broom and Ruxton (2004), which was formulated to
understand the evolution of CBP rather than its effects on
population dynamics. The model here includes rejection of
parasite eggs by hosts, density dependence, and non-nesters,
which are all omitted by Broom and Ruxton (2004). Their
model includes random numbers of nester eggs in their
own nest, which is omitted here simply to avoid extraneous
notation. Including that feature in our model would be
straightforward, accomplished by redefining $C_n$ as repro-
ductive effort for a nester’s own nest, which determines the
distribution of nest eggs laid, and by adjusting the expec-
tations accordingly. Both models are formulated with gen-
eral notation for laying-order effects that are not used in
specific cases. We included general notation ($W$) for laying
order effects to highlight its potential role in frequency de-
pendence (Broom and Ruxton 2002).

The model of Robert and Sorci (2001) is a subset of
our model, with $\tau = 1$, no density dependence, no adult
cost of reproduction or random laying order, and a non-
random distribution of parasite eggs. The model of Eadie
and Fryxell (1992) formulates the expected value of par-
asitic egg survival in a different but equivalent way than
(1)-(2). They formulate it as the expected per-nest survival
for all eggs in the population except one parasite’s eggs,
with that parasite’s eggs added for each term in the ex-
petation. This gives the same result as (1)-(2) but would
be slightly trickier to implement numerically if the dis-
tribution of eggs involves over- or underdispersion, such
as a negative binomial.

Perhaps the most important biological considerations
omitted from our model are ejection of host eggs by par-
asites as they deposit their eggs and trade-offs between egg
quality and quantity. It would be straightforward to in-
clude ejection of host eggs abstractly in (1)-(2), but that
could lead to a complicated stochastic process for a specific
case. Including trade-offs between egg quality and quantity
would also be straightforward to formulate, but that would
lead to additional strategy variables that are beyond the
scope of this article.

Analysis

Analysis of model (1)-(2) involves up to three types of
stability: evolutionary stability of the fraction of non-
esters, for which nester or non-nester are discrete strat-
egies; evolutionary stability of the continuous strategy vari-
bles $C_n$ and/or $T$ among nesters; and population
dynamics stability. These could be intertwined in general,
for example, with the evolutionary equilibria and stability
of nesting strategies affected by population dynamics pa-
rameters and vice versa. In the specific cases here, such
dependencies are minor, so analysis of each type of stability
is presented separately. Although $C_n$, $C_p$, and $C_n$ in reality
must be integers, we allow them to be real (continuous)
numbers for mathematical convenience.

Stability of Non-Nesting Fraction

An equilibrium of the fraction of non-nesters, $\pi^*$, is de-
ned as the value of $\pi$ such that $F_n = F_c$ (noting that $F_n$
and $F_c$ are both functions of $\pi$ and assuming $C_n$, $T$, and
$N$ fixed). It is a stable equilibrium if

$$\frac{\partial}{\partial \pi} (F_n - F_c) \bigg|_{\pi = \pi^*} > 0.$$  

This condition states that if an infinitesimally larger frac-
tion of the population than $\pi^*$ adopts the non-nesting
strategy, the fitness of nesters would be greater than that of non-nesters, so some of the non-nesters would have higher fitness if they nested, decreasing the non-nesting fraction back to $\pi^*$. 

**Stability of Joint Nesting–Parasitism Strategy Variables**

Next we introduce evolutionarily singular strategies and stability for the nester strategy variables, $C_*$ and/or $T$. Conditions are given here for $C_*$ when $T$ is fixed, and the multivariate conditions for $(C_*, T)$ are given in appendix B in the online edition of the *American Naturalist*. If there is no adult cost of reproduction, then $T$ will always be favored if there is no cost. Then $E_0(C_*, T; C_*, T^*) = E_0(C_*, C_*)$. An evolutionarily singular strategy $C^*$ is defined by

$$\frac{dE_0}{dC_*} |_{C_* = C_*^* = C^*} = 0.$$ 

This means that individual fitness is at an optimum at $C_* = C^*$ when the resident strategy is also at $C^*$. The optimum is a local maximum and therefore is stable to invasion of nearly similar strategies, if

$$\frac{d^2E_0}{(dC^*)^2} |_{C_* = C_*^* = C^*} < 0.$$ 

The final condition involves the direction of the selection gradient if the resident strategy deviates from $C^*$. The singular strategy has convergence stability if

$$\frac{d}{dC} \left[ \frac{dE_0}{dC_*} \right] |_{C_* = C_*^* = C} < 0$$

(Eshel 1983; Christiansen 1991). This states that if the resident strategy increased infinitesimally from $C^*$, then the slope of fitness with respect to an invading strategy, evaluated at the resident strategy, would be back toward $C^*$.

**Population Dynamics Stability**

Finally, a population dynamics equilibrium, $N^*$, is defined by $F(N^*) = 1$ or $G(N^*) = N^*$. The equilibrium is stable if

$$-1 < \frac{\partial}{\partial N} G(N) \bigg|_{N = N^*} < 1.$$ 

This condition states that if a deviation from equilibrium leads to a larger deviation at the next time step, either in the same direction or by overcompensation in the opposite direction, then the equilibrium is not stable. The $-1$ boundary is of interest here because values of $(\partial/\partial N) G(N) \big|_{N = N^*}$ less than $-1$ can give oscillatory dynamics. In interpreting results about population dynamics stability, it is important to interpret all values of the stability condition, $(\partial/\partial N) G(N) \big|_{N = N^*}$, rather than focusing solely on the boundary values ($-1$ and 1) and the bifurcation from stable equilibrium to cycles at $-1$. Values of $(\partial/\partial N) G(N) \big|_{N = N^*}$ that are closer to 0 will give quicker returns to equilibrium, that is, greater resiliency, than values farther from 0. In the specific cases below, parameters have been chosen to be biologically reasonable and to highlight changes in the stability condition by including a bifurcation (crossing $-1$). However, other parameters in each model give similar results for the stability condition even if it does not cross $-1$. In addition, effects of CBP on equilibrium population density are potentially as biologically important as effects on stability.

**Interactions among Stability Conditions**

In general, one could consider the evolutionary and population dynamics stability conditions all together. For example, if a model admits both separate strategies and joint strategies, then are the joint, variable singular strategies stable to perturbations in the fraction of non-nesters? Interactions with population dynamics could also require some assumptions about trait inheritance and plasticity. For example, in a joint-strategies model, if a stable ESS solution is a function of population density $N$, then one could consider different assumptions about how the strategies track population size. In the specific cases analyzed here, such complications are minimal. Only one type of strategy is considered for each model. For models 1–3, the strategy results are independent of $N$. For model 4, the strategy results depend on $N$, but the results about CBP and dynamics are unaffected by this dependence, so we assume the strategy variables are optimized for equilibrium population size.

**Assumptions Used for Specific Cases**

Next we give assumptions and specific functions used in the following cases.
1. A parasitic egg has the same effect on brood survival as a host egg. This is reasonable because once a parasitic egg has been adopted in a nest, its impact on factors such as food per nestling and attraction of predators could be similar to host eggs.

2. Laying order does not affect offspring survival.

3. In the BOBJ and separate-strategies model, given reproductive effort $T$, nesters lay $C_n = T$ eggs and parasites lay $C_p = \pi T$ eggs.

4. The effects of density dependence and brood size on offspring survival occur independently on a log scale. This means that each effect contributes a factor to the offspring survival function, and those factors are multiplied. For models 1–3 below (with no cost of reproduction), this assumption decouples strategy optimization from population size. In general, optimal clutch size could depend on population size, and our simpler assumption represents a step toward more complex modeling in the future.

5. Brood survival is a negative exponential function of brood size, which may differ for nest eggs and parasitic eggs:

$$S_b(C, \gamma, N) = S_0 e^{-m_b(C+\gamma)D(N)},$$

where $L$ is either $n$ or $\pi$; $S_0$ is a constant maximum survival, set to 1 in all cases; $m_b$ and $m_p$ are coefficients for the effect of brood size on survival for nest eggs and parasitic eggs, respectively, with $m_b = 0.125$ in all cases and $m_p = 0.125$ or 0.15; and $D(N)$ is the density-dependent effect of adults on offspring survival, with $0 \leq D(N) \leq 1$.

6. Nester clutch size in the absence of parasitism is at its optimal value, $1/m_b = 8$. An important consequence of assumption 5 is that this optimal clutch size does not depend on the number of parasitic eggs in the nest. If optimal own-nest clutch size depended on the number of parasitic eggs, then own-nest clutch size might evolve downward if parasitism is established in the population, and we do not consider such cases here.

7. $D(N)$ is either constant at 1 or a linear function of $N$ down to a minimum of 0:

$$D(N) = \max \{1 - bN, 0\}.$$ 

8. Adult survival is either constant (no cost of reproduction) or a linear function of total reproductive effort, $T$, down to a minimum of 0:

$$A_n(T) = \max \{Q - kT, 0\}.$$ 

9. Parasitic eggs are Poisson distributed among nests. The mean number of parasitic eggs per nest is

$$E_p[Y] = \frac{\eta [\pi C_p + (1 - \pi) C_n]}{1 - \pi}.$$ 

For a large number of nests, the Poisson distribution is essentially identical to the binomial distribution. This assumption makes parasitism less favorable because parasitic eggs are disproportionately in large broods, which have lower survival.

### Specific Cases and Simulations

Each model was implemented numerically, and the equations were solved for equilibrium population size, parasitism rate, and stability conditions. All evolutionary equilibria were stable, with one subtlety for model 4 described below, so they are evolutionarily plausible. Parameters for each model, including ranges of $\gamma$ and $\tau$ values, were chosen to make the models comparable while elucidating differences between models in the role of parasitism on population dynamics. The results are interpreted comparatively rather than as specific numerical predictions because the models do not incorporate all aspects of bird ecology.

### Model 1: Nest Limitation and BOBJ Parasitism

The BOBJ parasitism model by definition requires nest site limitation. This model makes sense only if parasitism is inferior to nesting for at least some individuals. For BOBJ parasitism, every non-nester favors some reproduction over none and so will parasitize if possible. We consider a BOBJ model with (in addition to the parameters specified above) no joint strategies allowed ($C_n = T$); constant adult survival that is lower for non-nesters than for nesters (such as if non-nesters are inferior competitors), $A_n = 0.4$, $A_p = 0.2$; no effect of adult density on offspring survival ($b = 0$); and equal brood survival for nest and parasitic eggs, $m_p = m_n$. In comparison to models 2–4, the assumption of no adult density effect amplifies the role of nest limitation in regulating density. The maximum number of nest sites is $H = 100$, and the fraction of non-nesters is

$$\pi = \max \left\{ \frac{N - H}{N}, 0 \right\}.$$ 

The range of $\gamma$ and $\tau$ values for model 1 was such that parasitism is never favored over nesting at equilibrium population density.
Model 2: Separate-Strategies Model

For separate-ESS parasitism to occur, non-nester fitness must be greater than nester fitness at low frequency and also must be frequency dependent such that at low frequencies non-nesting is favored and vice versa. For the separate strategies model, we assume that adult density affects brood survival ($b = 1/200$), there is no nest site limitation (no BOBJ parasitism), and we do not allow joint strategies ($C_e = T$). Then the frequency dependence must affect the difference between the expected survival of nest eggs in equation (1) and the expected survival of parasitic eggs in equation (2). This could occur if for any reason the difference between $S_n$ and $S_p$ depends on the fraction of non-nesters, $\pi$. For example, if later laying order decreases survival and parasitic eggs are disproportionately laid later, and if this effect is stronger when there are more parasites, frequency dependence would result. In the model of Eadie and Fryxell (1992), frequency dependence arose from the randomness of the parasitic egg distribution. Parasitic eggs are disproportionately in large broods to an extent that depends on $\pi$. This effect occurs in the model here, but here the frequency dependence it generates is weak; if we replace the exponential brood survival model with a linear model, then variance in parasitic eggs per nest generates stronger frequency dependence (results not presented).

For a generic model of frequency dependence, model 2 here assumes that parasitic eggs are slightly more sensitive to brood size than are nest eggs, $m_p = 0.15 > m_n$ (a very small difference), which could arise as a type of quality or laying order effect. Adult survival is the same for nesters and non-nesters, $A_n = A_p = 0.5$.

Model 3: Joint-Strategies Model with No Adult Cost of Reproduction

Like the separate ESS, a joint ESS requires frequency dependence in the fitness difference between laying nest eggs and parasitic eggs. However, in the joint-strategies model, the same individuals can lay nest and parasitic eggs, so frequency dependence arises automatically and does not require the mechanisms described for model 2. Model 3 is identical to model 2 except that joint strategies are allowed; brood survival is the same for all eggs, $m_n = m_p$; and adult survival is $A_n = A_p = 0.4$. For this model, smaller values of $\tau$ and $\gamma$ (than in model 2) allow evolution of parasitism. No parameters were considered for which a separate strategy would be favored (assuming it has the same adult survival and other parameters).

Model 4: Joint-Strategies Model with Evolution of Total Reproductive Effort

Model 4 includes an adult cost of total reproductive effort, with an intercept of $Q = 0.8$ and slope of $k = 0.05$ so that $C_e$ and $T$ must be jointly optimized. Preliminary results with other parameters that were the same as for model 3 gave a sharp transition from low parasitism to complete parasitism. When parasite egg value $\gamma$ and the trade-off between nest eggs and parasitic eggs $\tau$ are both low, no parasitism occurs, and $T$ is essentially the only strategy variable to maximize fitness. When $\gamma$ and $\tau$ are large enough, parasitism is favored, $T$ increases to its maximum possible value (such that adult survival is 0), and nearly all reproductive effort is parasitic. Based on these preliminary results, we added more frequency dependence to model 4 in the same manner as in model 2, $m_p = 0.15 > m_n$, to generate a larger range of stable parasitism levels.

Results

In the BOBJ model (model 1; fig. 1), as parasite fecundity $C_e = \pi T$ increases, the equilibrium population size decreases because the reproductive success of all eggs is decreased by the large brood sizes due to parasite eggs. Lower equilibrium population size implies lower parasitism rate, so higher $\tau$ leads to lower parasitism. Higher parasite offspring value $\gamma$ increases the fitness of parasites without affecting offspring survival, so it increases equilibrium population size and parasitism rate, but only slightly. Although higher $\tau$ leads to a lower equilibrium population size and parasitism rate, it destabilizes dynamics, as shown by the bifurcation diagram. Meanwhile, parasite offspring value $\gamma$ has negligible effect on stability. These results are explained by the population dynamics map of $N(t + 1)$ versus $N(t)$ (fig. 2). Parasitism does not affect the population dynamics when $N < H$, but for $N > H$, higher $\tau$ leads to a steeper negative slope in the population dynamics map around equilibrium, which is destabilizing.

For the separate-ESS model (model 2; fig. 3), parasitism increases as either $\tau$ or $\gamma$ increases because these represent greater parasitism fitness. This leads to lower ESS fitness for both nesters and parasites and hence lower equilibrium population size. The impact of parasite offspring value $\gamma$ on parasitism rate is much stronger than in the BOBJ model, and its impact on equilibrium population size and stability are opposite to the BOBJ model. Also, unlike the BOBJ model, parasitism in the separate-ESS model affects the entire population dynamics map (fig. 2), with higher parasitism causing lower $N(t + 1)$ for any given $N(t)$. This flattens the slope of the population dynamics map at equilibrium and hence stabilizes dynamics.
The joint-ESS model without costs of reproduction (model 3; fig. 4) has a stability picture that is more similar to the separate-ESS model than to the BOBJ model, but it allows parasitism for lower values of $\gamma$ and $\tau$ than does the separate-ESS model. In model 3, if the entire population uses a strategy that is entirely nesting ($C_n = D$), then a single individual that shifts some reproduction toward parasitism experiences three effects on its fitness. The offspring survival of all of its remaining nest eggs is increased by having a smaller total number of eggs in the nest, it gains the reproductive output from its parasitic eggs, and it loses the output of the eggs not included in its own nest. Since $T$ has been set at the optimal value for nesting alone, the loss of an egg from its own nest is worse than the gain of increased survival for the remaining eggs. However, the gain from parasitic eggs—even if each is worth less than nesting eggs—can make parasitism advantageous. As $\tau$ increases, making parasitic eggs easier to produce, the ESS rate of parasitism increases, net fitness decreases, and hence equilibrium population size decreases.

Like the separate-ESS model, the entire population dynamics map (fig. 2) is less steep, so the population dynamics are stabilized. Although the flattening of the population dynamics map is similar between models 2 and 3 with regard to $\tau$, the role of parasite offspring value $\gamma$ on population dynamics stability differs between these models. For both models, higher $\gamma$ favors higher parasitism, but for model 3, this actually increases average fitness and thus destabilizes the population dynamics.

The joint-ESS model with costs of reproduction (model 4; fig. 5) gives yet different results. Qualitatively, the results are more similar to model 2 than model 3, but with different parameters values and for different reasons. For
Brood Parasitism and Population Dynamics

Figure 2: Population dynamics surfaces. For each model, two relationships between $N(t+1)$ and $N(t)$ are shown for two evolutionarily stable strategy values of conspecific brood parasitism. For each model, the parameters are the same as in the bifurcation diagrams from figures 1 (best of a bad job), 3 (separate strategies), 4 (joint strategies without cost of reproduction), and 5 (joint strategies with cost of reproduction). The two values of parasitism are labeled and can be located on the abscissas from figures 1, 3–5. The dotted line shows the identity line ($N(t+1) = N(t)$), which crosses each population dynamics map at its equilibrium population size. When the slope of the population map crosses the identity line with slope steeper (less) than $-1$, the equilibrium is unstable.

A subtlety in stability of the evolutionary dynamics arises for model 4 (app. B). For parameters where the ESS solution involves intermediate levels of reproductive effort and parasitic effort, the convergence stability conditions are satisfied, but the invasion stability condition is neutral in the $T$ direction, suggesting that some distribution of strategies centered at the ESS may be supported. This result is not troubling for the overall analysis (one could assume slight curvature in $A_n$ to achieve complete stability), but it points to the potential for further interesting results if heritability of strategies is modeled explicitly.

Discussion

Our results show that one cannot easily or simply predict the effect of CBP on population dynamic stability without knowing more about how parasitism actually occurs. Nev-
Figure 3: Separate evolutionarily stable strategy model. Top left, equilibrium population size (contours) as a function of $r$ and $\gamma$. Top right, same for parasitism rate (contours). Bottom left, same for stability condition (contours). When the stability condition is below $-1$, the model is unstable. Bottom right, for fixed $\gamma$ and different values of $r$, the model was run for many time steps, and the last 50 population sizes were plotted for that $r$. When the model has a stable equilibrium, the last 50 population sizes fall on the same point and appear as one point. When the model has an unstable equilibrium, the last 50 population sizes oscillate between two values, which appear as two points.

Nevertheless, some general predictions do emerge from the models here. When CBP is caused by nest limitation, parasitism increases the strength of density dependence caused by nest limitation, decreasing equilibrium population size and destabilizing dynamics. When CBP is not caused by nest limitation, it may increase or decrease average fitness. If parasitism increases average fitness, it also increases population density and decreases stability. If parasitism decreases average fitness, it also decreases population density and increases stability.

While our model includes many biological considerations, the evolution and consequences of CBP are likely to be even more complex. For example, several models have included egg rejection behavior in relation to the degree of relatedness between hosts or parasites and to the ability to recognize kin (Zink 2000; Andersson 2001; Lopez-Sepulcre and Kokko 2002). Empirical studies of such inclusive fitness benefits are mixed in their support (Andersson and Ahlund 2000, 2001; Pöysä 2003a, 2004; Nielsen et al. 2006; Waldeck and Andersson 2006), but evidence is increasing that host-parasite interactions among conspecifics may be more complex than considered in many existing models of CBP. Recent work by Pöysä and colleagues demonstrates that, in at least some species, parasites are able to assess the relative safety of nests with respect to the risk of nest predation and differentially parasitize safe nest sites (Pöysä 1999, 2003b, 2006; Pöysä et al. 2001; Pöysä and Pesonen 2007). Pöysä and Pesonen (2007) included this factor and showed that selection for laying eggs in safe sites could have a strong influence on the occurrence and persistence of CBP. In addition to this spatial aspect of CBP, one could consider the temporal dynamics of reproductive seasons in more detail, including timing of nesting and egg laying.
We suggest several questions for future empirical work, which can be biologically important in their own right. First, estimates of parameters in the model and differences between nesters and non-nesters or nest eggs and parasitic eggs would be fundamental for improved understanding. For example, do nest eggs and parasitic eggs differ in brood survival or in fitness if they do fledge? Are there different adult costs to laying nest eggs or parasitic eggs? Under separate parasitism, do nesters and non-nesters differ in reproductive effort and/or survival? Do parasitic versus nonparasitic species adopt different strategies of egg quantity and/or quality?

Second, from a behavioral ecological perspective, when and where is each type of parasitism (BOBJ, separate ESS, or joint ESS) most prevalent? To date, most studies on birds suggest a mix of BOBJ or joint-strategy parasitism (Brown and Brown 1989, 1998; Eadie 1989, 1991; Pinxten et al. 1991; Lyon 1993a, 1993b, 2003; Sorenson 1993; McRae and Burke 1996; McRae 1998; Ahlund and Andersson 2001; Ahlund 2005). This is consistent with our model result that the separate ESS arises only if the joint strategy is assumed to be impossible in the specific cases considered.

Third, from a population ecological perspective, there is a remarkable paucity of studies examining the relationship between CBP and population density and dynamics. While a test of the full interplay between CBP evolution and population dynamics would be daunting (Kokko and Lopez-Sepulcre 2007), narrower aspects of their relationship can be tested. For example, a handful of studies on a small number of species (mostly hole-nesting ducks) have reported significant impacts of CBP on nesting suc-
Figure 5: Joint evolutionarily stable strategy model with adult cost of reproduction. Top left, equilibrium reproductive effort (contours) as a function of $t$ and $\gamma$. Top right, same for equilibrium fraction of reproductive effort invested in parasitism, $(T - C_\gamma)/T$. Bottom left, same for stability condition (contours). When the stability condition is below $-1$, the model is unstable. Bottom right, for fixed $\gamma$ and different values of $t$, the model was run for many time steps, and the last 50 population sizes were plotted for that $t$. When the model has a stable equilibrium, the last 50 population sizes fall on the same point and appear as one point. When the model has an unstable equilibrium, the last 50 population sizes oscillate between two values, which appear as two points.


Finally, we emphasize that the role of CBP on population dynamics may have practical, as well as theoretical, implications. If CBP does influence population stability, as our models suggest, and if the management of critical resources such as nest sites influences the frequency and intensity of CBP, as a number of empirical studies suggest (Semel and Sherman 1986, 1995, 2001; Semel et al. 1988; Eadie 1991), then a deeper understanding of the linkage between CBP and population dynamics will be essential to develop effective conservation and management strategies for the growing list of species in which this intriguing behavior occurs (Eadie et al. 1998).

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