

Evolution of conspecific brood parasitism under trade-offs between parasitism and nest guarding

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In organisms with expensive parental care, brood size is limited and cheaters can benefit by parasitizing someone else's brood. Conspecific brood parasitism (CBP) is a wide-spread phenomenon in birds [Rohwer and Freeman, 1989; Yom-Tov, 2001] and has been described in some insects [Villalobos & Shelly, 1996; Zink, 2003, Loeb, 2003]. Both costs and benefits of CBP are frequency-dependent, and conditions on the existence of the ESS of CBP have been previously obtained by means of game theoretic approaches [Zink, 2000; Robert & Sorci, 2001; Broom & Ruxton, 2002]. We introduce a new continuous multiplayer [Bulmer] model of CBP in birds, one which incorporates trade-offs between laying eggs in one's own nest and laying eggs parasitically and between the effort to parasitize nest of others and the effort to defend one's own nest against parasitism. We demonstrate that the evolutionary stable rate of parasitism increases with clutch size, with the time nests are left unattended, and with average relatedness within a population, while it decreases with the intensity of intra-brood competition in larger than average broods. There is a good agreement between the range of ESSs predicted by the model and the range of CBP observed in several species of swallows, starlings, ducks and coots.

Females of many birds [Rohwer & Freeman, 1989; Yom-Tov, 2001] and at least some insects lay eggs into the nests of other conspecific females. This phenomenon is known as conspecific brood parasitism and has long been considered to evolve through frequency-dependent mechanisms. Empirically, our knowledge of CBP in birds can be summarized as follows. Some parasites are females whose nest has been destroyed, and some are "floater" females [Calvo et al 2000, Lyon 1993] who do not make an attempt to nest (pure parasitism strategy). In this paper we will focus on facultative (mixed strategy) parasitism, which occurs when the parasite female also maintains its own nest. Typically, a parasitic female needs to find an unattended nest in which to lay an egg, although in swallows [Brown and Brown, 1989], moorhens [McRae 1996] and geese [Forslund 1995] parasitic eggs can be laid in the presence of and despite resistance from the host. Hosts and parasites are sometimes found to be relatives [Andersson & Ahlund, 2000], which may be the result of parasites preferring hosts who are their relatives, or hosts being more lenient towards a closely related parasite or, in case of male host, to a female who has had an extra-pair copulation with him. However, studies designed to detect such

leniency didn't find any evidence for it [Lyon et al, 2002];[Poeysae, 2004]. In most birds the parasite does not remove any of the host's eggs from the nest, although such behavior has been documented in starlings [Evans, 88; Lombardo et al 89] (but see [Yamaguchi, 2000]), swallows [Brown 1984] and coots [Lyon, 2003]. The host is typically unable to distinguish and remove a parasitic egg laid into its nest during its own egg-laying period, although in swallows[Brown and Brown, 1989] and starlings[Stouffer et al., 1989] removal of parasitic eggs sometimes occurs. Eggs laid parasitically outside of the host's egg-laying period are often detected and removed [Møller][Yamaguchi, 1997][Brown & Brown, 1989] or hatch asynchronously with the host's clutch and have, therefore, lower survival rate [Yamaguchi, 2000]. CBP is more frequently observed in colonial birds than in solitary birds, in precocial birds than in altricial birds [Rohwer & Freeman, 1989; Yom-Tov, 2001] and in birds with larger clutches [Arnold & Owens, 2002].

A rare parasite entering a population of non-parasites has the advantage of reducing its own intra-brood competition by forcing another individual to provide for an extra offspring. Clearly, costs and benefits of parasitism depend on the intensity of intra-brood competition. If the intra-brood competition is low, benefits of parasitism are low, but so are the costs of being parasitized. As pointed out by Lyon[1998], the costs and benefits of parasitism also depend on the order in which eggs are laid, since the eggs laid last usually have the lowest chances of survival and therefore the lowest fitness value. This effect, however, may not be as important in birds with delayed incubation, when all eggs hatch more or less simultaneously.

Previous frequency-dependent models of CBP evolution arrived at the following conclusions. CBP is favored when fitness gain from each offspring in female's own nest decreases with total clutch size, and when eggs are costly [Broom and Ruxton, 2002]. IBP also evolves when hosts have few opportunities to defend their nests against parasitism and when the parasite can achieve high overall fecundity [Zink, 2000], i.e., when total fecundity is not strictly limited. Hence, the occurrence of CBP in birds with determinate laying is surprising. Another conclusion of previous models is the higher prevalence of CBP in populations of close relatives [Andersson, 2001; Zink 2000]. Finally, theory predicts under certain conditions very high parasitism rate is favored so that there are no longer any conspecific nests to parasitize. This is interpreted as the evolution of either communal nesting [Zink, 2000] or obligate (i.e. interspecific) parasitism [Robert and Sorci, 2000].

In this paper we present a novel game theory model of the evolution of CBP by introducing two important trade-offs and relaxing some assumptions of previous models. We following the assumptions of the Broom and Ruxton [2002] model, with the following important changes. Firstly, we introduce is the trade-off between the number of eggs laid in an individual's own nest and the number of eggs laid parasitically. Previous model [B&R] did not constrain the total number of eggs laid by an individual bird. Two lines of evidence support the idea that this assumption is unrealistic: eggs are costly and the time interval of egg-laying is limited. Secondly, we introduce the trade-off between the effort of seeking a nest to parasitize and the effort to guard the individual's own nest against other potential parasites. The previous models [Zink, 2000; Robert & Sorci, 2001; Broom & Ruxton, 2002] did not reflect the fact that a parasite leaving its nest unattended to seek a nest to parasitize is increasing its own risk of being parasitized, thus loosing any benefits of parasitism. We model this trade-off in terms of time budget, which each

nesting bird has to split between foraging (and other necessary activities away from the nest), nest guarding and seeking unguarded nests to parasitize.

Thirdly, we relax the assumption [Robert & Sorci, 2001; Broom & Ruxton, 2002] that brood survival rate is a concave (exponential) function of clutch size. Instead, we describe brood survival by a logistic function, which allows a variety of more realistic survival curves, including those in which broods can accommodate an extra chick without experiencing a catastrophic mortality. This situation is realistic in many birds, in which clutch sizes are lower than those causing a severe survival decrease [Bulmer].

Finally, we relax Ruxton and Broom's assumption that all females start to lay eggs simultaneously. Our only assumption about nesting synchrony is that parasites do not discriminate in favor of nests, which contain fewer host's eggs at the time of parasitizing.

Assume that egg laying occurs over a period f days (each bird lays at average f eggs, some into her own nest, some parasitically). Each bird spends a portion of her time p seeking unattended conspecific nests to parasitize and a portion of her time t on foraging or other necessary activities away from the nest. (In species with both parents alternating each other at nest guarding t may be therefore 0). Thus, on a given day a parasite finds an unattended nest and lays an egg into it with the probability

$$kp(p+t), \quad 1$$

where k is a coefficient reflecting the probability of finding a conspecific nest (probably very close to 1 for most birds, particularly colonial breeders). All other eggs will be laid in the individual's own nest. Of the eggs laid parasitically a portion g will be accepted by the host and survive to hatching. If the parasite is related to the host with coefficient of relatedness r , parasitic eggs also contribute to the fitness of the host, discounted by this coefficient.

Consider a rare deviant from the population strategy p , who employs a strategy p^* . The total number of eggs in its own nest is

$$N_{io} = f(1 - p^*(p+t)k + gp^*(p+t)k), \quad 2a$$

while the fitness gain the individual obtains from caring for this brood, i.e., the number of its own eggs plus the number of parasitic eggs discounted by the coefficient of relatedness is

$$N_{io} = f(1 - p^*(p+t)k + rgp^*(p+t)k). \quad 2b$$

Likewise, the fitness gain from parasitizing a nest of a relative is

$$N_{ip} = f(gp^*(p+t)k + r) \quad 2c$$

and the total number of eggs in a host's nest parasitized by a given individual is

$$N_h = f(1 - gp(p+t)k(1-g)) + g. \quad 2d$$

Of course if all parasitic eggs are accepted ($g=1$), eq.2d simplifies to $f+1$.

The fitness value of an average egg decreases with the order of eggs laid in this nest, so the average value of an egg is [Lyon 98][B&R]

$$V(N) = \frac{\sum_{i=1}^N \beta^{(i-1)}}{N} S(N), \quad 3$$

where $S(N)$ is survival probability in a brood of size N described by a logistic function:

$$S(N) = K - \frac{K}{(1 - e^{-h(N-l)})} \quad 4$$

The fitness function is then defined as

$$F = N_{io} V(N_{io}) + N_{ip} V(N_h) \quad 5$$

and the ESS p^* is found by satisfying two conditions[Bulmer]:

$$\left. \frac{\partial F}{\partial p} \right|_{p=p^*} = 0 \quad \text{and} \quad \left. \frac{\partial^2 F}{\partial p^2} \right|_{p=p^*} \leq 0 \quad 6$$

Under a set of simplifying assumptions ($r=0$, $g=1$) an analytical solution of conditions 6 is possible. In other cases the root has been evaluated numerically. We did not attempt to prove that a single ESS exists, but in all cases only one root has been found within $0 < p^* < 1$. Maple worksheets with analytical and numerical solutions are available in Supplementary materials.

The model predicts a nearly linear increase of p^* and the corresponding frequency of eggs laid parasitically with clutch size (Fig.1) with the slope of the relationship increasing with the parameter t . Absence of parasitism is the ESS when $t=0$. Empirical data on prevalence of CBP [Suppl2] is well predicted by the model over the range of $0.1 < t < 0.2$. Predictions of the model for a select set of species, in which parameters of the model are available or can be assumed (Table 1) are shown on Fig.2. Given significant uncertainties in the estimates of the parameters and broad range of parasitism prevalence among different populations of the same species, the agreement between the predicted and observed values is remarkable.

In a broad agreement with previous results [B&R] ESS parasitism rate is higher when overall clutch value (survival rate is higher) and with intensity of intra-brood competition (data not presented). Interestingly, neither the strength of order effect β , nor the probability of rejecting the parasitic egg by the host as a drastic effect on the ESS p (Fig.3a,b).. On the one hand, egg rejection makes the gain from parasitism lower. The ability to reject a parasitic egg gives the host an alternative anti-parasite defense, so the host can take a risk of not guarding her own nest, making more space for the parasitism possible. As the result the effect of such ability on ESS parasitism rate is moderate and reverses its sign depending on the intensity of intra-brood competition. If an extra nestling over the average clutch size can be accommodated without a significant decrease of survival ($l = f+2$; thick lines on Fig. 3b), it is better to parasitize more as the rejection rate decreases (survival of parasitic eggs increases). If an extra nestling causes a quick drop in survival ($l = f$), it is better to parasitize less as the rejection rate decreases (survival of parasitic eggs increases).

In an agreement with previous models [Zink, 2000; Andersson, 2001], relatedness between individuals in a population has a drastic effect on the ESS (Fig.3c) and this result does not require the assumption about kin recognition by hosts and parasites [Andersson, 2001. When intra-brood competition is not intense ($l = f+2$) mean relatedness over 0.1-0.15 (i.e., in a population consisting of cousins) leads to an increase of ESS parasitism rate to 100%, i.e. to cooperative breeding. The effect of relatedness is less pronounced

when intra-brood competition is severe ($l = f$). In other words, communal breeding evolves if accommodating one or two closely related parasitic nestlings does not cause a catastrophic decrease of survival. Another factor promoting the evolution of communal nesting is the inability to protect the nest due to high time constrained to be spent away from nest ($t > 0.2$; see Fig.1).

Previous models of CBP correctly predicted several important patterns on its evolution but were not specific enough to be fitted to individual bird species. Here we show that the evolution of CBP can be understood more precisely by the incorporation into the model the trade-offs between investment into and protection of your own reproductive effort and parasitizing someone else's. We believe that this model applies to many more biological situations besides the CBP, such as the evolution of mate guarding and other forms of monogamy.

Table 1. Select species in which a species-specific prediction is possible and the values of parameters used. Time unattended is the sum of t (time constrained to be spent foraging) and time spent searching for nests to parasitize. Survival curve parameters h and l were estimated from published data on survival rate of clutches of different size by non-linear fitting of a logistic function (parameter K constrained to 1 except for the coots data in which it was left free and estimated as 0.5). Predicted and observed frequencies for these species are presented on Fig. 2; numbers correspond to point labels.

Species	Mean clutch size f	Antiparasite defense		Intra-brood competition		
		Time unattended, $t+p$ 0.4 [B. Lyon, pers. communication] 0.4 [Loos and Rohwer, 2004]	Survival of parasitic eggs, g	Survival curve inflection point location, $l-f$	steepness, h	β
1. American coot <i>Fulica Americana</i> [Lyon, 1993;]	8	0.4 [B. Lyon, pers. communication] 0.4 [Loos and Rohwer, 2004]	0.5-0.75	4 [Lyon et al., 2002]	2 [Lyon et al., 2002]	0.8-0.9
2. Ducks <i>Aythya spp.</i> [Dugger, Blums 2001]	8	0.4 [Loos and Rohwer, 2004]	1	0	0.1	1
3. Grey starlings <i>Sturnus unicolor</i> [Yamaguchi, 1997, 2000]	6	0.2	0.55-0.9 [Stouffer et al. 1987]	1.9	0.66	1
4., European Starlings <i>Sturnus vulgaris</i> [Evans, 1988]	5	0.2	0.55-0.9 [Stouffer et al. 1987]	0.19	0.88	1
5. Barn Swallow <i>Hirundo rustica</i> [Moller, 1987; A.P. Moller, pers. comm.]	5	0.3	1	2.2	0.69	1
6. Cliff swallow <i>Hirundo pyrrhonota</i> [Brown and Brown, 1989, 1997, Weaver and Brown, 2004]	3.6	0.11	0.85-1	0.23	2	1

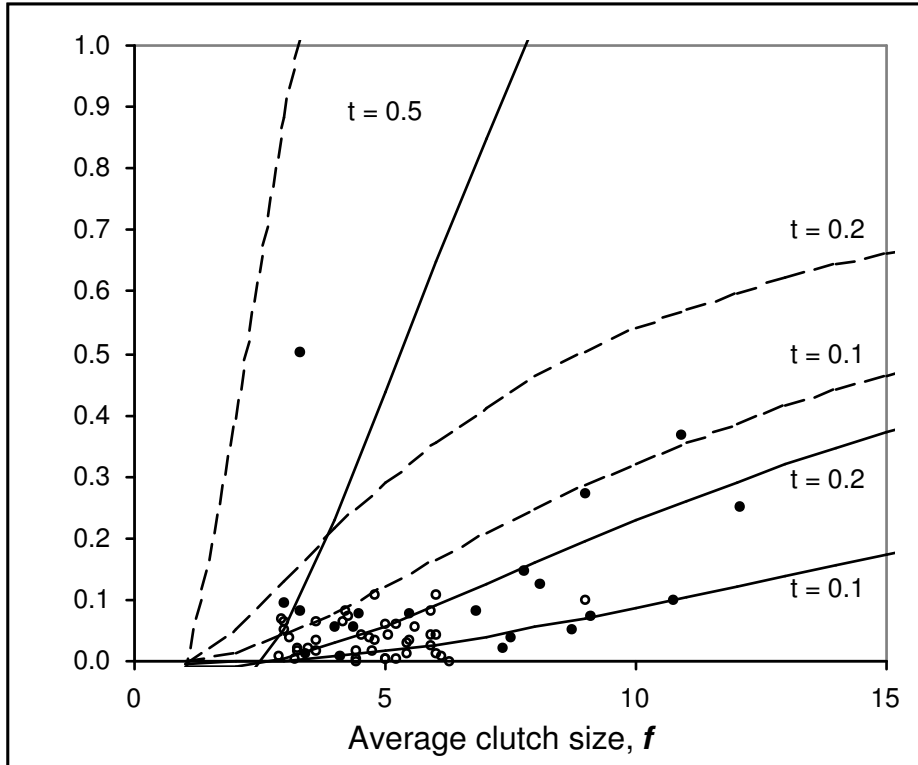


Figure 1. ESS of parasitism (portion of eggs laid parasitically) predicted by the model and observed rate of CBP in a number of bird species [Suppl.3]. Dashed lines: low intra-brood competition ($h = 0.5$), solid lines – intense intra-brood competition ($h = 2$). Open dots: altricial species; closed dots: precocial species. Other model parameters: $r = 0$, $g = 1$, $\beta = 0.99$.

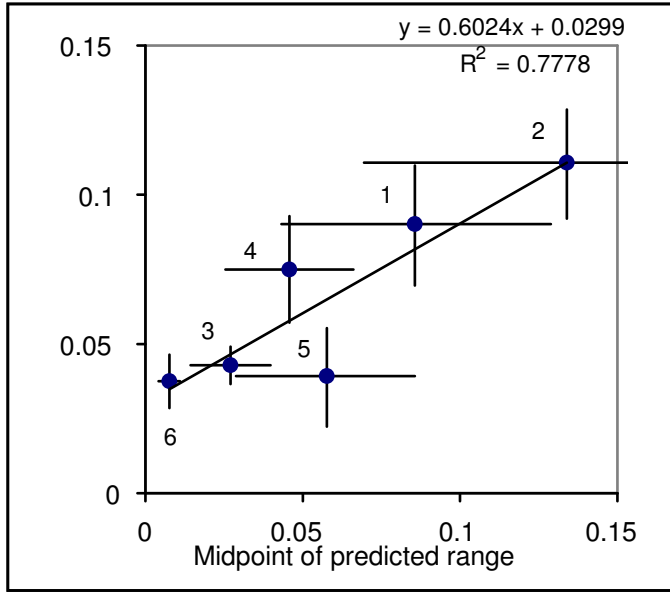


Figure 2. Species-specific predictions. Ranges of predicted values result from uncertainties in parameter estimates (Table 1). Ranges of observed values reflect variation among different populations of the same species. Significance level of the regression coefficient was estimated by resampling from a uniform distribution with each range (1000 replicates).

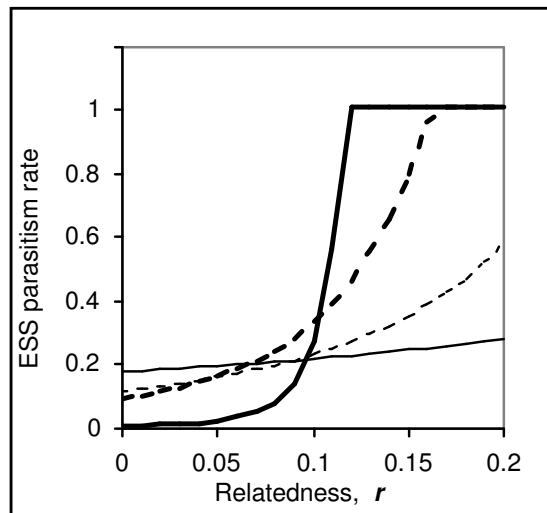
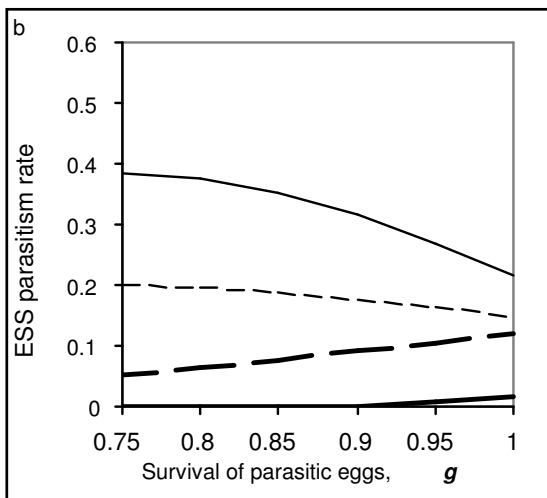
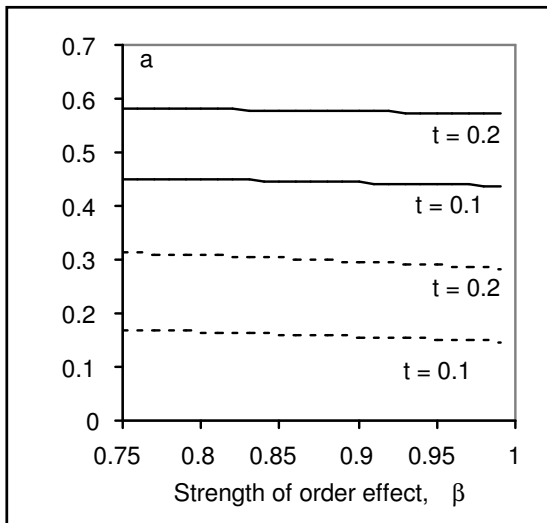


Figure 3. Effects of the strength of order effect (a), probability of survival of a parasitic egg (b) and relatedness (c) on the ESS rate of CBP. Clutch size $f = 5$. Logistic survival curve parameters as follows: Dashed lines: $h = 0.5$; solid lines: $h = 2$; thick lines $l = f+2 = 7$, thin lines $l = f = 5$. a: $r = 0$, $g = 1$; b: $r = 0$, $\beta = 0.99$; c: $g = 1$, $\beta = 0.99$.

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