E-ARTICLE

The Evolution of Clutch Size in Hosts of Avian Brood Parasites

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ABSTRACT: Coevolution with avian brood parasites shapes a range of traits in their hosts, including morphology, behavior, and breeding systems. Here we explore whether brood parasitism is also associated with the evolution of host clutch size. Several studies have proposed that hosts of highly virulent parasites could decrease the costs of parasitism by evolving a smaller clutch size, because hosts with smaller clutches will lose fewer progeny when their clutch is parasitized. We describe a model of the evolution of clutch size, which challenges this logic and shows instead that an increase in clutch size (or no change) should evolve in hosts. We test this prediction using a broad-scale comparative analysis to ask whether there are differences in clutch size within hosts and between hosts and nonhosts. Consistent with our model, this analysis revealed that host species do not have smaller clutches and that hosts that incur larger costs from raising a parasite lay larger clutches. We suggest that brood parasitism might be an influential factor in clutch-size evolution and could potentially select for the evolution of larger clutches in host species.

Keywords: clutch size, brood parasitism, tolerance, defenses, costs.

Introduction

Interspecific brood parasites such as cuckoos (Cuculidae), cowbirds (Icteridae), and honeyguides (Indicatoridae) lay their eggs in the nests of other species, avoiding the costs of raising their own offspring (Davies 2000). The high costs of parasitism have led to the evolution of defense strategies in hosts, which in turn select for reciprocal strategies in parasites to evade host defenses (Davies 1999, 2000, 2011). Brood parasitism affects hundreds of host species worldwide and has shaped the evolution of numerous host traits, including egg phenotype (Stokke et al. 2002; Yang et al. 2010; Stoddard

and Stevens 2011), nestling morphology (Langmore et al. 2003; Payne 2005; Hauber and Kilner 2007), and breeding systems (Feeney et al. 2013).

Avian clutch size (the number of eggs laid per nest) is a central life-history variable, being a major determinant of avian reproductive effort and one of the best-recorded animal life-history traits (Jetz et al. 2008). For years, ecologists have tried to explain the huge variation in clutch size among birds, and it is now well known that variables such as latitude, nest type, and mortality risk are important predictors of clutch size (Jetz et al. 2008; Samas et al. 2013; Martin 2015). In this study, we test whether brood parasitism could also drive the evolution of clutch size in birds that serve as hosts.

It has been argued that when the survival of juveniles (but not adults) decreases, then optimal clutch size should decrease (Forbes and Lamey 1996; Hauber 2003; Servedio and Hauber 2006) and that this logic should apply specifically to increases in juvenile mortality due to brood parasitism (Brooker and Brooker 1996; Hauber 2003). The majority of cuckoos, honeyguides, and some cowbirds are highly virulent, and parasitism results in the death of host young, either through eviction of host eggs, attack on host nestlings by the parasite chick, or through starvation of host nestlings (Kilner 2005). The idea that brood parasitism selects for a smaller clutch size in hosts has been suggested explicitly for superb fairy-wrens *Malurus cyaneus* (Brooker and Brooker 1996), a main host of the Horsfield's bronze-cuckoo (*Chalcites basalis*). This argument is intuitively plausible: laying many small clutches rather than few large clutches means that if a clutch is parasitized (and there is no egg rejection) fewer eggs will be lost. This could conceivably lead to a higher lifetime reproductive success.

Despite its intuitive appeal, the argument that a bird can reduce the costs of parasitism by laying many small clutches, rather than few large clutches, involves flawed logic, which can be illustrated with a hypothetical example (fig. 1). Consider that the strategy of a host involves reducing the clutch size from five to four, which saves reproductive effort so that

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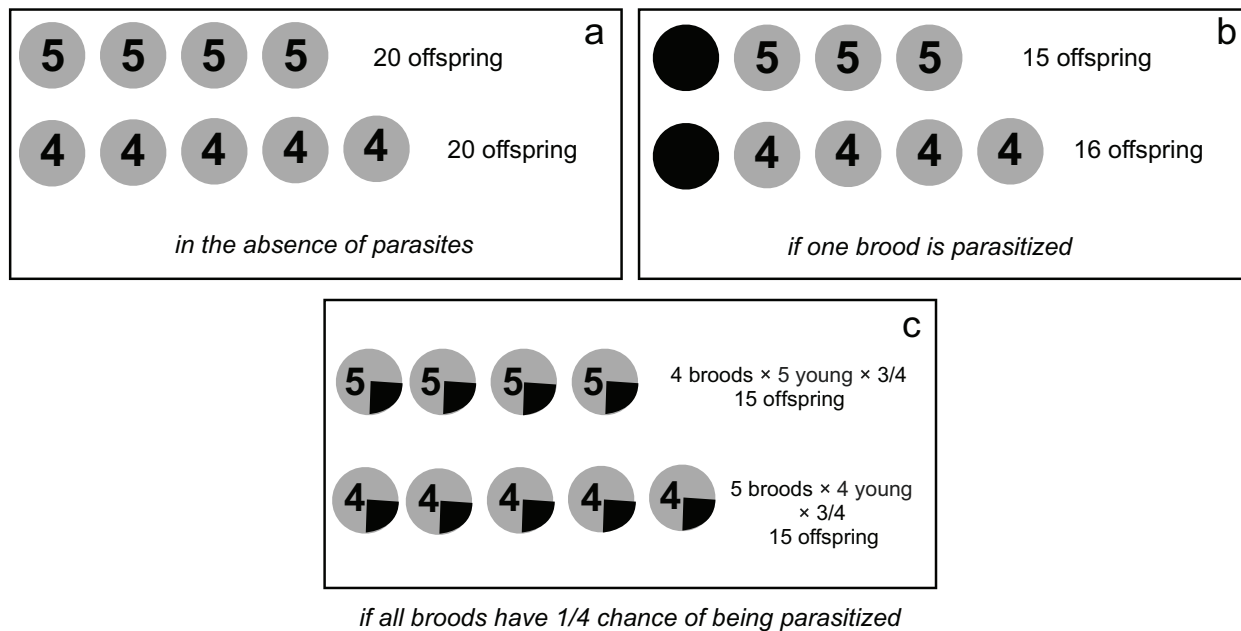
Figure 1: Representation of decreased clutch size as an adaptive mechanism in hosts and why the underlying rationale is flawed (see text for explanation). *a*, There is no parasitism. *b*, One brood is parasitized by a highly virulent parasite (e.g., a cuckoo). *c*, Each brood has the same probability (1/4) of being parasitized.

the parent now achieves, on average, one extra brood: in the example, it shifts from four to five broods in a lifetime, on average (fig. 1*a*). At first sight, this example seems to support the logic of an adaptive reduced clutch size. The presence of parasites shifts the four eggs per clutch (slow) life history from being no better than the faster strategy of five eggs per clutch—both achieving 20 offspring—to being apparently advantageous, with the small clutch strategy achieving 16 young and the large clutch strategy 15 (fig. 1*b*) since parasites destroy some broods.

However, this comparison assumes that there is only one parasitism attempt per lifetime. In reality, producing a larger number of broods (and smaller clutches) will also present brood parasites with more opportunities to parasitize. If we assume that phenotypes with small clutches are not also more resistant, we cannot assume that the additional brood in figure 1*b* will remain unparasitized. Correcting for this mistake requires taking into account that any brood may be parasitized, including any new ones that arise as a result of slowing down the reproductive rate.

Thus, if we correct the assumption such that the level of parasitism for the large clutch phenotype (one out of four, on average, lost) also applies to the small clutch one (fig. 1*c*), then the reproductive success of the phenotype with small clutches has to be revised to one-quarter of all the five broods lost, which means a total of 1.25 broods lost and 3.75 completed in a lifetime. The expected total number of offspring

it raises to independence is now $3.75 \times 4 = 15$, in other words, no improvement at all: having a reduced clutch size is still neutral now that parasitism probability has been included.

To our knowledge, there is currently no study in the literature that explores whether hosts of highly virulent brood parasites should change their clutch size in response to parasitism. The majority of avian brood parasites (∼70%) are evicting or highly virulent parasites (Davies 2000), destroying all the progeny of their hosts. However, we do not yet have a model that makes explicit verbal predictions that hosts of highly virulent parasites should evolve a reduced clutch size. Currently, models of clutch-size evolution and brood parasitism do so in a context of conspecific brood parasitism (Forbes and Lamey 1996; Lyon 1998) or the studies consider only hosts of nonevicting parasites such as cowbirds (Hauber 2003), for which costs of parasitism are much smaller. Our first aim is to provide this missing model, avoiding the pitfall of figure 1. The aim of our model is to examine under which conditions the organism's optimal response to parasitism would be associated with an increase or a reduction in clutch size. Given that species vary in their responses—eggs may be ejected or entire clutches may be abandoned—we also consider whether the clutch-size response depends on the type of defense displayed by the host.

Our second aim is to test in a comparative framework whether the costs of brood parasitism are correlated with

the clutch size of hosts and whether species that suffer higher costs of parasitism have evolved a smaller clutch size. Recently, it has been found that the relative size of the parasite can affect the outcomes of brood parasitism (e.g., increasing egg rejection rates) by imposing larger costs to the hosts (Medina and Langmore 2015). We perform a comparative analysis of clutch size across 828 species of hosts and nonhosts from Australia, Africa, and Europe. We predict that hosts that suffer higher costs of brood parasitism (e.g., parasitized by highly virulent and larger parasites) will show larger changes in clutch size.

Methods

The Model

As stated in the introduction, several studies have proposed clutch-size reduction as a host strategy to tolerate or diminish the costs of brood parasitism. Under this scenario, hosts would accept parasitism but reduce their clutch size to diminish their loss (fig. 1). The aim of our model is to examine the conditions in which the organism's optimal response to parasitism is associated with reduced or increased clutch size. This requires, first of all, specifying the alternative to acceptance. In some species, rejection behaviors take the form of ejecting suspicious eggs; in others, the entire nest is abandoned and there is the potential to renest (within limits dictated by potential seasonality and/or the number of times renesting can occur). We consider both options in the following model, by contrasting acceptance either with egg rejection (hereafter, egg rejection scenario) or with nest abandonment (nest abandonment scenario). Note that we do not consider the related question of what determines whether hosts evolve to reject eggs or entire nests (i.e., why they end up in either scenario), the focus of our study is on whether clutch-size adjustments can evolve under either kind of scenario.

Examining whether acceptance is associated with changes in clutch size requires studying two aspects of life history in a single model: host clutch-size evolution and whether the host accepts or rejects eggs that might be of parasitic origin. The phrase "might be" refers to the fact that recognition of foreign eggs, whatever its mechanism (e.g., detection of unusual sizes or colors of eggs, perhaps together with elevating the level of suspicion if a parasite has been detected near the nest) is not free of error. Regardless of the precise mechanism, we need to include terms in the model that indicate the probability of false positives and false negatives, respectively. In the egg rejection scenario, we make α denote the probability that a host rejects an egg that it has itself laid, while β denotes the probability that a parasitically laid egg is not rejected. In the egg rejection scenario, these effects apply independently to each egg in the nest. In the nest aban-

donment scenario, we make a whole-nest interpretation for α and β: α is the probability that a nest that contains no parasitically laid eggs is abandoned, and β is the probability that a parasitized nest is not abandoned.

The model derives fitness-maximizing clutch sizes for two kinds of hosts: those who always accept all eggs in their nest (the accepting strategy, denoted A) and those who exhibit rejection behaviors (denoted R and interpreted as either egg rejection or nest abandonment depending on the scenario considered; note that egg rejecters may reject more than one egg, if clutch size exceeds one). Parasitized hosts that fail to reject gain zero reproductive success from the current breeding attempt (i.e., the parasite is assumed to destroy all host young either at egg or chick stage). After the model has derived the optimal clutch size for rejecting and accepting hosts (step 1), we perform step 2: we compare whether R (when using its best clutch size) is better, in terms of lifetime reproductive success, than A (when using its best clutch). The better of these two strategies is assumed to be the best response to parasitism. In step 3, we compare this best response to the optimal clutch size for species for which the rate of parasitism is set to zero (i.e., nonhosts; these are assumed to never reject eggs or nests, as this could lead only to reductions in fitness of their own eggs).

Note that step 2 reveals the type of behavior that is expected to evolve in response to parasitism (i.e., rejection vs. acceptance), while step 3 asks whether this is associated with a change in clutch size, that is, whether optimally behaving hosts lay smaller or larger clutches than otherwise identical nonhost species. By "otherwise identical," we mean species that are identical for all ecological parameters that underlie the life history of the species in question. Because we intend not to constrain the life histories of potential host and nonhost species to a narrow subset of what is possible, we use a total of 10 parameters to describe the life history and/or the effects of parasitism (table 1). Parameters K and k specify how parental effort to raise a certain number of young translates into the subsequent survival of the parent (from one breeding season to the next; see appendix, available online, for the precise implementation of this and other parameters listed here). The survival of the parent thereafter impacts lifetime reproductive success, which equals the expected number of breeding attempts in a life span multiplied by the expected number of an individual's own young raised per breeding attempt. Small values for K and k both mean that effort cannot reach high values before substantial costs begin to be paid by the parent.

In addition to specifying how parental effort diminishes parental survival, we also need to specify how parental effort depends on laying the eggs versus the later stages of parenting and how the number of offspring fledged depends on clutch size. For these tasks, we use parameters a and b, with a describing the cost of incubating and feeding the young rel-

Table 1: List of parameters used in the model

Parameter	Interpretation	Range values
A	Host accepts eggs	…
R	Host rejects eggs or nests	…
P	Parasitism rate	[0, 1]
α	Probability of false positive judgment; host rejects when no parasite	Logarithmically distributed between 10^{-3} and 1
β	Probability of false negative judgment; host raises a parasite	[0, 1]
a	Costs of incubating and feeding relative to egg laying	[0, 10]
b	Feasibility of large clutches	[0, 10]
C	Costs of raising a parasite relative to raising own young	[1, 10]
K	Scaling of the parental effort level with respect to parental survival reductions	[1, 50]
k	Shape of the relationship between K and parental survival	[1, 10]
S	Annual survival after zero parental effort	[0, 1]
r	Probability that a host that has abandoned a nest can renest within the same breeding season	[0, 1]
W	Expected lifetime reproductive output	Evolves
F	Clutch size (best clutch sizes denoted F_A* and F_R*)	Evolves (to a value between 1 and b)
N	Number of own eggs that survive	Computed from F and other parameters

Note: The range of parameters refers to values used to collect 10,000 examples per scenario, with a uniform distribution within the range unless otherwise specified. Simulations were run in Matlab (MathWorks) such that one combination from the above distributions was used to compare nonhost fitness to hosts performing acceptance or rejection behaviors (as exemplified in fig. 2). The better host response—either accepting or rejecting—together with its associated clutch size was then compared to the nonhost clutch sizes to yield categories as described in the main text.

ative to laying the eggs and b describing the feasibility of large clutch sizes (small b means that most young die if they have many siblings; the model is built such that the optimal clutch size cannot exceed the value of b). These are not to be confused with the false positives and negatives α and β, respectively, which are also part of the set of 10 parameters.

We then also specify parameters that are relevant only for species that act as hosts. Parameter P specifies the probability that a nest is parasitized. Parameter C refers to the relative costs in nestling equivalents (i.e., a parasite costs the equivalent of C nestlings). For example, if one parasite requires as much effort to raise as five of a host's own nestlings, then $C = 5$. In the nest abandonment scenario, we also need to consider explicitly the timescale over which a parent who has abandoned a nest can attempt to breed again. We introduce a parameter r (for renesting) to quantify the possibility that the host can renest during the same breeding season, such that a fraction $1 - r$ of hosts (interpretable, e.g., as those who already started quite late) have to wait until the next breeding season before they can breed again—assuming they survived this time span. The possible values of r range between 0 (which implies that renesting is not possible before the next breeding season) and 1 (no host ever runs out of time to begin a new breeding attempt). Note that the high end $r = 1$ is probably somewhat unrealistic, but we consider the entire range of possibilities.

Finally, the maximum survival of the parent is set at S, which completes the list of parameters. We use the model

in two different ways. First, we show individual cases to expose the logic of why acceptance behavior typically does not lead to reduced clutch sizes. Then, we examine the generality of the argument by sampling randomly 10,000 parameter combinations and recording the outcomes according to category (acceptance or rejection evolves; clutch size is lower, the same, or higher than an ecologically equivalent nonhost species). We do this separately for the egg rejection scenario and for the nest abandonment scenario, to see if the answers differ depending on the type of defense that a rejecting host employs.

Phylogenetic Comparative Analysis

Species Used. To test whether hosts of brood parasites have evolved different clutch sizes depending on the costs of brood parasitism, we collected a data set that included nonhosts and hosts of both highly virulent parasites (such as cuckoos and honeyguides) and nonvirulent parasites (such as *Clamator* cuckoos and cowbirds). We chose 104 Australian passerine species based on Brooker and Brooker's (1989) classification of (i) species that are unsuitable as hosts and (ii) biological hosts of eight species of Australian cuckoos (see appendix). We excluded introduced species and species recorded as occasional hosts because we cannot infer the extent of coevolution with cuckoos in these species. For American species ($n = 89$), we used the published data by Soler (2014) and Friedmann and Kiff (1985) of hosts and

nonhosts of cowbirds, and we excluded the rare host category, or those species that had less than 10% of their nests parasitized, because it was not possible to infer the extent of selection on these hosts. For analyses of southern African species ($n = 635$), we used the host listing for all brood parasites in *Roberts Birds of Southern Africa* (Hockey et al. 2005). We included all species listed as hosts of honeyguides, cuckoos, and Vidua finches, as well as nonhost species, and excluded those listed as provisional hosts. This list includes nonpasserine hosts, which are parasitized by honeyguides (Indicatoridae), and some hosts that migrate to Europe or are also present in Europe (taken from Soler 2014).

Data Collection. Information on the average clutch size for each species was obtained from the supplementary material from Jetz et al. (2008). Clutch size varies with latitude, nest type, and body size (Jetz et al. 2008). To control for potentially confounding effects of latitude, we used the R package dismo to download 2,000 random records per species from the Global Biodiversity Information Facility (Hijmans et al. 2011) and calculated the median latitude of the records. This value represents where the species is more often recorded and possibly where the clutch-size information will be most likely to belong. To control for confounding effects of nest type and body size, we obtained information from the Handbook of the Birds of the World online (del Hoyo et al. 2014). Nest type was classified as 1 = open nest, 2 = domed nest, and 3 = cavity nester. The data set for this analysis and the R code have been archived in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.s20hm (Medina et al. 2017).[1]

Several studies in brood parasitism have considered parasitism as a binary trait (e.g., being either a host or nonhost), but the costs imposed by parasites may vary largely from host to host. First, we divided our analyses according to the virulence of the parasite (e.g., whether the parasite kills/evicts the progeny of the host). Furthermore, it has been shown that host species that raise larger parasites have very low cuckoo fledging success and higher egg rejection rates (Kleven et al. 2004; Medina and Langmore 2015). This suggests that relatively larger parasites impose greater costs on their hosts, making it harder to rear their progeny and thus selecting for better host defenses against parasitism. We included in the comparative analysis a measure of the cost of the brood parasite to each host species, which is comparable to the parameters *C*, *k*, and *K* in our mathematical model. We quantified the size discrepancy between the parasite and the host by dividing the size of the parasite by the size of the host, with larger parasites being more costly for smaller hosts, as applied in Medina and Langmore (2015). Information on the parasite's

body size was obtained from del Hoyo et al. (2014). We repeated the analyses using a subset of the data set, where all nonhost species belonged to genera where hosts are present. This type of comparison reduced the number of species studied ($n = 397$) but ensured that the differences aside from parasitism status between hosts and nonhosts were as small as possible.

Statistical Analyses. To correct for phylogenetic effects, we obtained 1,000 phylogenetic trees for each data set from www.birdtree.org (Jetz et al. 2012) and repeated the comparative analysis on each of these trees. These 1,000 trees are samples from a Bayesian estimate of the phylogeny of all birds and serve to represent our certainty and uncertainty about the relationships among the species in our analysis. By repeating our analyses across all 1,000 trees, we ensure that our biological inferences do not rely on the assumption that a single phylogeny is correct. Rather, our inferences account for the fact that certain parts of the phylogeny of birds are known with more certainty than other parts. This has been shown to be preferable to using a single phylogeny in a wide range of situations (Duchêne and Lanfear 2015; Hahn and Nakhleh 2015).

We used phylogenetic generalized least squares (PGLS) regression models to account for phylogenetic relationships between species. We report the 95% highest posterior density intervals for *P* value and β estimate for each predictor (not to be confused with the β parameter in the model). Models were run using the Caper package in R (Orme et al. 2012). We ran a model for each type of parasite virulence (e.g., one for highly virulent parasites and one for nonvirulent parasites). We did not combine the data sets because it is difficult to quantify how much more costly it is to raise a highly virulent parasite compared to a nonvirulent one. Each model included the relative size of the parasite to the host (parasitism cost), mean latitude, body weight, and nest type as explanatory variables and mean clutch size as the response variable. We ran models with and without including nonhosts. When nonhosts were included, we considered nonhost's costs to be zero, given that raising no parasite does not impose any additional cost on the species. Latitude was converted to absolute values and thus represents distance from the equator; weight was log transformed, given that it was nonnormally distributed. We also provide information on the phylogenetic signal of each model by reporting the value of the λ statistic. This value represents to which extent phylogeny is driving the association between traits. When $\lambda = 1$, it suggests that closely related species are evolving as expected by a Brownian motion model; hence, phylogeny is possibly driving the association we observe. Consequently, a value closer to zero would suggest that closely related species resemble each other less than expected by a Brownian motion model (Blomberg et al. 2003). Additionally, we used the dredge

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1. Code that appears in *The American Naturalist* is provided as a convenience to the readers. It has not necessarily been tested as part of the peer review.

function in the MuMIn R package (Barton 2012) to select the best model from the list of all possible models given the predictor variables, based on the corrected Akaike information criterion (AICc). We report which predictors were present most frequently in the best models when the analyses were repeated on each of the 1,000 phylogenetic trees.

## Results

Model Results

Parasitism Decreases Host Fitness and Potentially Changes Optimal Host Clutch Sizes. As the rate of parasitism increases, we expect fitness to decline for host species while the nonhost species are unaffected. In the example of figure 2, very low parasitism rates (the very left of the figure, where the blue curve lies above the red curve) predict that acceptance of the occasional parasitic egg leads to higher lifetime reproductive success than attempts to reject parasitic eggs (fig. 2*a*) or abandon parasitized nests (fig. 2*b*). Here, the risks of ejecting an own egg or abandoning an entire unparasitized nest outweigh the occasional fitness gain through

correctly dealing with a parasite. At higher parasitism rates, on the other hand, rejection behaviors lead to higher fitness than acceptance of all eggs.

While these results are intuitive, the central question is how the above is accompanied by evolutionary responses regarding clutch size. The colored numbers in figure 2 show the fitness-maximizing clutch size that produces the depicted lifetime reproductive success. Nonrejecting individuals (strategy A, blue curve in fig. 2) have, in a limited region of a moderate parasitism rate and in one of the two modeled scenarios (fig. 2*a*), a lower clutch size (two eggs) than what would be the best response if the species instead evolved rejection behaviors (three eggs). It is nevertheless difficult to use figure 2*a* to justify the evolution of a reduced clutch size, for two reasons: there is only a very narrow range of very low parasitism rates where acceptance of all eggs yields higher fitness than either type of rejection behavior; and more importantly, clutch sizes at no point (no value of *P*) evolve to be lower than that of nonhosts. Clutches are either predicted to be equally large or, at high parasitism rates, larger than those of nonhosts.
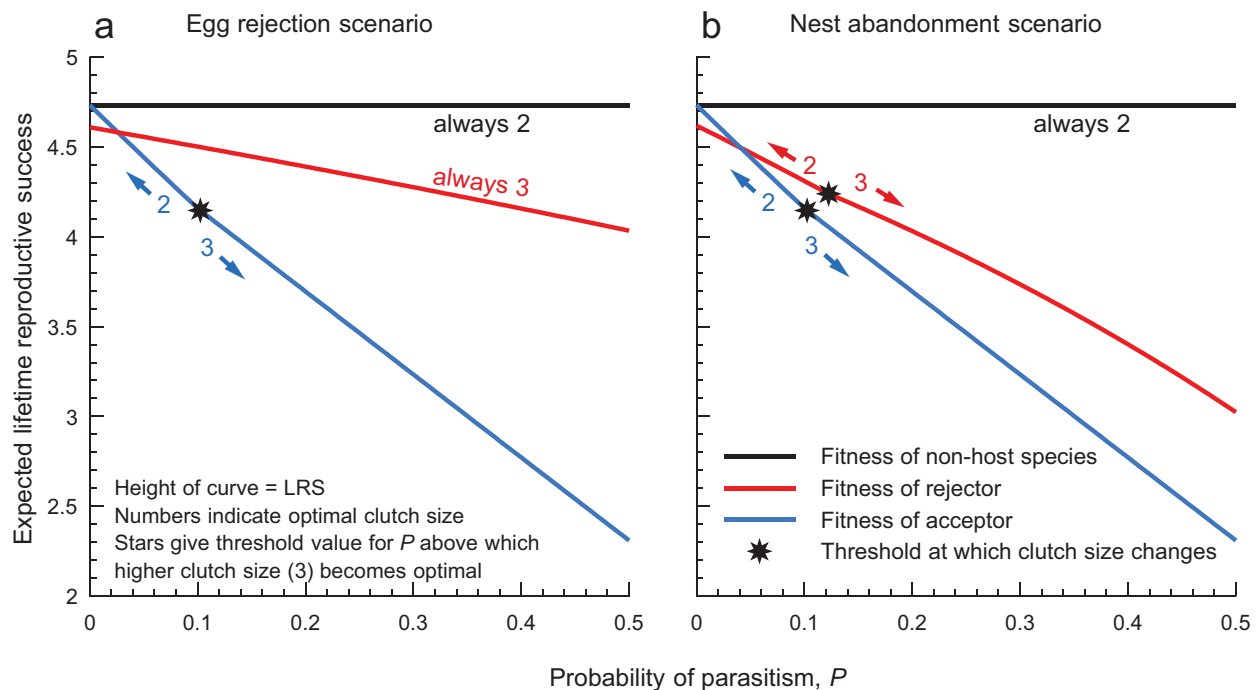
Figure 2: Comparison of fitness (lifetime reproductive success) of nonhosts (black line) and hosts (colorful lines) that either accept (blue) or reject—with error—attempts to parasitize their nests, plotted for the egg rejection scenario (*a*) and the nest abandonment scenario (*b*). Each strategy is allowed to evolve its fitness-maximizing clutch size, which is indicated as numbers along the curve: for nonhosts, this is always two; for egg rejectors in *a*, it is always three; and for the other two scenarios, the optimal clutch size changes from two to three when the rate of parasitism, *P*, increases (the respective threshold values are indicated with a star). The relative height of the curves indicates which behavior performs best among the parasitized cases, and the corresponding numbers—that is, optimal clutch sizes—indicate whether parasitism and the associated response also selects for changing the clutch size relative to the nonhost clutch size (which, in this example, is three eggs). Parameter values used in this example are $K = 25$, $k = 5$, $a = 5$, $b = 7$, $\alpha = 0.05$, $\beta = 0.2$, $C = 3$, $S = 0.7$, and $r = 0.5$.
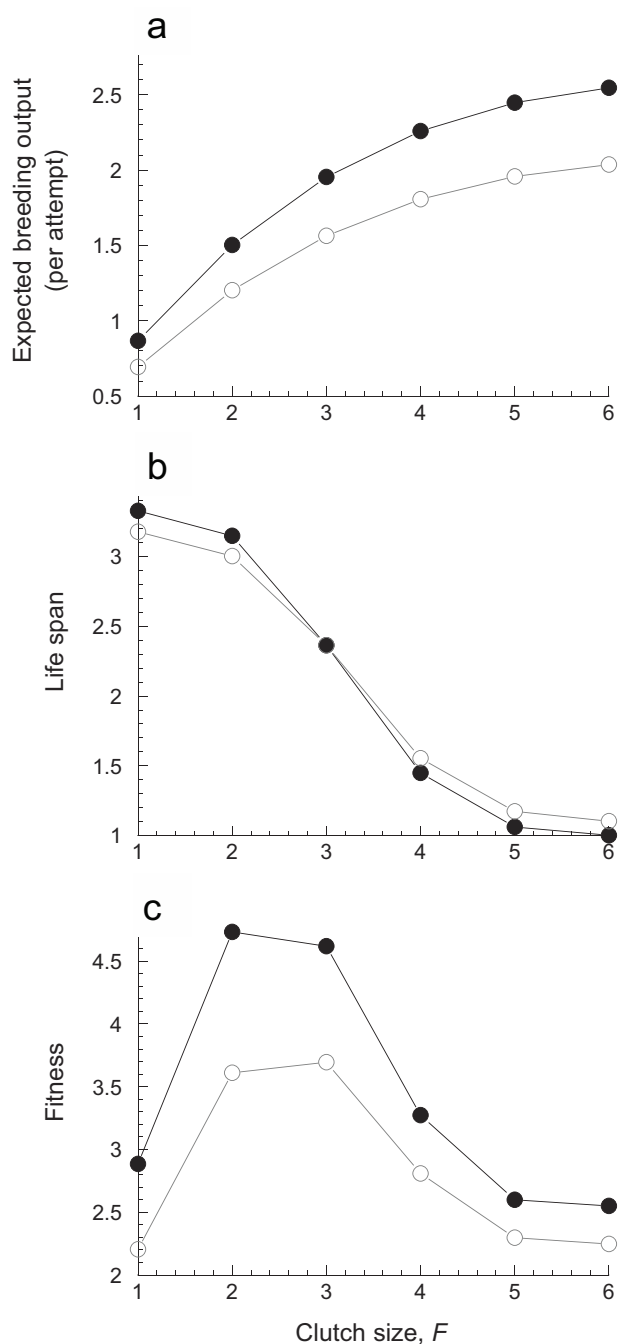
Figure 3: Fitness components expected breeding output per breeding attempt (*a*), expected life span (*b*), and lifetime fitness (*c*)—that is, the product of the two components above—for two cases of figure 2: nonhosts (in black) and hosts that are acceptors (in gray) plotted against potential clutch sizes, with only the relevant ones from 1 to 6 shown for clarity. Parasitism always decreases the expected success of a single breeding attempt (*a*), but the effect on host life span (*b*) is more subtle: it creates a less steep relationship between the host's initial clutch size and the parenting costs. In other words, the reduction in parental survival is less strongly dependent on clutch size in hosts than in nonhosts, because sometimes effort is spent on raising parasites (a

Parasitism Can Increase Clutch Sizes of Hosts by Weakening the Relationship between Host Clutch Size and Parenting Costs. The responsible factor for the increase in clutch size can be deduced by a detailed examination of a specific case, which we show, for clarity, for a particular frequency of parasitism ($P = .2$) and making only one of the possible contrasts in figure 2: we now compare the nonhost life history with that of hosts that are acceptors (black closed and gray open circles, respectively, in fig. 3). The parasite obviously creates a clear difference in breeding output, that is, the number of its own young fledged per breeding attempt, between hosts and nonhosts (fig. 3*a*). It also creates a more intriguing effect on life span of its hosts. Nonhosts obey a relatively steep relationship between their own clutch size and the life span of parents (fig. 3*b*, filled circles). This relationship becomes milder in hosts (fig. 3*b*, open circles). This is because hosts raise their own brood only some of the time; in the remaining cases, the total effort is largely determined by C, the cost of raising a parasite, and only partially by F, their own clutch-size decision (the cost of laying the eggs). This means that hosts' own clutch size becomes a weaker causal predictor of host life span. Put differently, it does not cost as much to try out large clutch sizes when the related costs are, in a large fraction of breeding attempts, never paid. The weaker relationship between cost and initial clutch size (fig. 3*b*) then has to be weighed against the nonlinearities that are also present in the fecundity curve (fig. 3*a*), and the net effect can be an increase in the best clutch size (fig. 3*c*, fitness peaks at two eggs for nonhosts and at three eggs for hosts).

Testing for Generality Reveals That Reduced Clutch Size in Response to Parasitism Is Possible but Remains Extremely Rare. Figures 2 and 3 are based on specific parameter values; they do not preclude the option that the nonlinearities of the clutch size–fecundity relationship permit other cases, such as a shift toward smaller clutch sizes in some cases. We therefore explored the generality of the above argument with respect to all the parameters listed in table 1. Because of the large number (10) of different parameters to be varied, we conducted an exhaustive search, collecting outcomes with randomly chosen parameter values in a realistic range (table 1). To decide what is realistic, we had to consider that most have not been measured, but logic dictates that, for example, rates of parasitism, P, cannot fall below 0 or above 1, and biological knowledge indicates that the probability of rejecting one's own offspring (α) is probably low. We chose to err on the side of caution in that we chose very wide parameter ranges (thus, any value of P between 0 and 1 was included) and deviated from a uniform distribution for only

fixed cost) rather than the whole of the host's own clutch (cost increasing with F). For this reason, the cost of a larger clutch can become acceptable in acceptor hosts when it would not be in nonhosts (*c*).

one parameter, as α is probably low. However, we also did not intend to leave large values out of the examination, choosing a uniform distribution for $\ln(\alpha)$ (thus the sampling most often considers low but positive values of α). This approach should give, through visual inspection, an indication of where in a broad parameter search different outcomes can be found.

As expected in a general life-history model, many parameter choices led to high reproductive effort and very low parental survival, that is, solutions that are close to semelparity. In an avian context, this can be simply interpreted as unrealistic (random choices of parameter settings that are unlikely to apply), as birds in reality are always iteroparous. Therefore, we considered all parameter settings unrealistic for birds if they made parents reduce their survival by more than 95% when caring for their young (e.g., if for the A strategy $e^{-(F+aF/K)^k} < 0.05$ at the fitness-maximizing F_A^*; see appendix for details) or if the evolved clutch size was outside the range $\{1, 20\}$ that we considered to cover the realistic range for a wide variety of birds. We collected parameter values using the ranges specified until we had 10,000 solutions that were not rejected as unrealistic as avian life histories. Solutions were thereafter classified into six (sub)categories, separately for scenarios where rejection was done through egg rejection or nest abandonment.

A—accepting strategy. The best option for a parasitized species is to accept parasitism rather than to evolve rejection behaviors, with three subcategories: being parasitized favors the evolution of higher clutch size than that of nonhosts (A+), being parasitized leads to no difference in clutch size relative to that of nonhosts (A0), and being parasitized favors the evolution of smaller clutch size than that of nonhosts, when all else is equal (i.e., an otherwise identical life history; A−).

R—rejection strategy. The best option for a parasitized species is to evolve rejection behaviors despite this being error prone (the frequency of errors being α and β, as explained above), again with three mutually exclusive subcategories, so that being parasitized leads to higher clutch sizes (R+), no change in clutch sizes (R0), and smaller clutch sizes (R−).

Each randomly chosen parameter combination was indicated as a cyan circle if clutch size did not change (A0, R0), as a red plus sign if clutch size increased (A+, R+), and as a green triangle if clutch size decreased (A−, R−) in response to parasitism. The symbols are plotted on the left panels in figure 4 if acceptance evolves (A) and on the right panels if rejection evolves (R). In each case, the plotting is repeated five times, to be able give information on all 10 parameters, with two axes per panel. We plot only the first 2,500 cases to avoid overloading the figure with overlapping symbols (we give a statistical summary of all 10,000 cases below).

Figure 4 gives a visual tool to assess, for the egg rejection scenario, the impact of each parameter (see fig. A1 for the corresponding nest abandonment scenario; figs. A1, A2 available online). Whether circles are mainly assigned to the left or right panel gives information about the relative prevalence of acceptance and rejection. For example, regardless of all other parameter values, egg rejection never evolves (no symbols of any color) if α and β are both very high (fig. 4f). The changing density of different-colored symbols within a panel gives information about how a particular parameter impacts clutch-size changes. In figure 4e, 4f, for example, let us deduce that changes in clutch size in response to parasitism are more likely to occur if mistakes of rejecting own eggs are common (α is high).

For the nest abandonment scenario, we can use similar visual inspection to deduce that while rejection as a response to parasitism is often associated with a clutch-size increase, acceptance does so only very rarely and is instead typically neutral with respect to clutch-size evolution (fig. A1).

The 10,000 test cases yielded outcomes in all categories, but two of the six categories occurred extremely rarely. In the egg rejection scenario, the strategy A− (i.e., acceptance with reduced clutch size) was observed to be the best in only 18 out of 10,000 cases (i.e., 0.18% of cases), while in the nest abandonment scenario, this figure rises slightly, but only to 0.60%. From figures 4 and A1, it is possible to state some apparent correlates of the occurrence of these rare strategies. For example, a low a and high survival S appear to be prerequisites for A− to occur in the nest abandonment scenario (fig. A1). However, the overall rarity of the A− case means that the above should not be interpreted to imply that reductions in clutch size are in any way an expected outcome as soon as a is low and/or S is high.

Furthermore, our model also predicts a significant relationship between clutch size and parasite size C; if we fit a model $y = \text{constant}_1 + \text{constant}_2 \times C$ to the data of 10,000 simulated cases, this relationship takes the form $0.054 + 4.83\ C$ for egg rejectors and $0.030 + 3.09\ C$ for nest-abandoning hosts.

Phylogenetic Comparative Analysis

There were no significant differences in average clutch size between hosts and nonhosts (mean nonhosts: 3.21 ± 1.57; mean hosts of highly virulent parasites: 2.97 ± 0.94; mean hosts of nonvirulent parasites: 3.47 ± 1.03). However, within hosts of highly virulent parasites, the analysis showed that the relative size of the parasite and latitude were significantly positive predictors of clutch size (table 2; fig. 5) as well as present in all the best models, regardless of the phylogeny used (ΔAICc against null model > 20; table A1; tables A1, A2 are available online). The same pattern was found if we included nonhosts (as having zero costs) in the analyses (PGLS,
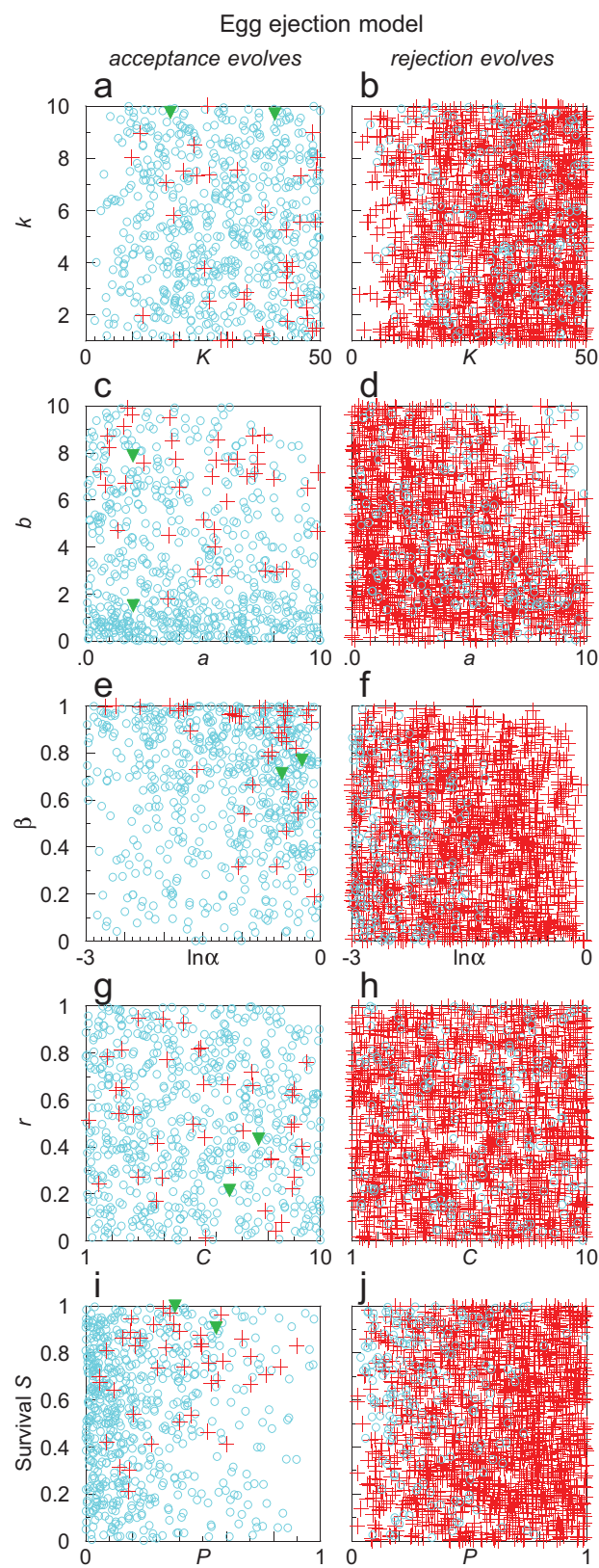
β for costs = 0.046–0.057, P for costs = 0.02–0.07). The β estimate presented here and in all the comparative analyses represents the slope of the regression. Hosts of costly parasites had significantly larger clutches than hosts that raise smaller, less costly parasites (fig. 5). The same pattern was detected when we did the analyses using only suitable hosts, and this was also evident when we compared clutch size within genera that contained both hosts and nonhosts (table A2; fig. A2). Within genera, species that are nonhosts have a smaller clutch size. When the analyses were performed using hosts of nonevicting parasites, only latitude was a good predictor of clutch size (β = 0.014–0.022, P = 0.002–0.038, AIC against null model > 4).

Discussion

The evolution of a smaller clutch size has been argued to provide a potential defense mechanism in hosts of avian brood parasites, who may decrease the costs of parasitism by losing smaller clutches to parasitism events (Brooker and Brooker 1996; Hauber 2003; Servedio and Hauber 2006). However, we show that the theoretical support for this rationale is poor. We modeled the evolution of clutch size in hosts of highly virulent brood parasites and explored the theoretical plausibility of evolving egg acceptance and a smaller clutch size. We found that, contrary to previous suggestions, this strategy is not likely to be a common outcome. In almost no sets of parameters do hosts achieve the highest fitness by reducing their clutch size. In fact, according to our model, the best strategies for acceptor hosts should be to either show no change in clutch size or to evolve a larger clutch size. This outcome is initially surprising but makes sense if we consider that the presence of brood parasites in a population implies that some breeding attempts will not lead to realized fecundity and the cost structure of those attempts differs from those of nonparasitized broods: the total parental effort is now not as strongly dependent on the host's own clutch-size decisions as when there are no parasites. This makes it worthwhile to lay a large clutch in the hope of not encountering a parasite.

The size of the clutch is, of course, also impacted by other variables, such as incubation efficiency and provisioning (Lerkelund et al. 1993). Our model captures these effects

Egg ejection model

acceptance evolves   *rejection evolves*

Figure 4: First 2,500 cases of the 10,000 collected outcomes for the egg rejection scenario, categorized such that cases where accepting behavior (A) outperforms rejection (R) are plotted in the left-hand panels (*a, c, e, g, i*), while cases where the opposite is true are depicted on the right (*b, d, f, h, j*). Each parameter set contains 10 parameters, thus we use five rows to show the location of outcomes with respect to all parameters. Cyan circles indicate that the outcome involves no change in clutch size, red crosses that clutch size of the host is larger than that of nonhost species, and green triangles that it is smaller.

Table 2: Results of phylogenetic regression predicting clutch size

Predictor	Estimate β	P	λ (signal)
Relative parasite size (cost)	.177 to .222	**.0001 to .0003**	.90 to 1
Latitude	.024 to .030	**Always < .0001**	.90 to 1
Weight	.215 to .406	.006 to .128	.90 to 1
Nest type 2 vs. type 1	.427 to .724	**.001 to .029**	.90 to 1
Nest type 3 vs. type 1	.694 to .947	.326 to .486	.90 to 1

Note: Statistics are for each parameter for each predictor of host clutch size for hosts of highly virulent parasites, such as most cuckoos and honeyguides. We report the 95% highest posterior density intervals across 1,000 phylogenetic trees for each parameter. Significant values are indicated in boldface. The r^2 for the whole model was between 0.23 and 0.35, depending on the tree used.

through a variety of associations, relating clutch size and the consequent brood size to costs paid by parents. We also show that the evolution of rejection increases in likelihood when it is possible for the parents to eject individual eggs rather than abandon entire nests. High chances of recognition errors or low parasitism rates, in turn, lower the probability that rejection behaviors will evolve (Davies et al. 1996).

Our model cannot incorporate all possible effects that can occur in nature; one possibility that the model ignores is that hosts improve their ability to identify foreign eggs as a result of learning. Incorporating such an effect would alter the trade-offs by reducing the false positives and false negatives for older hosts. Calculating lifetime fitness would then become a considerably more complex task, but it appears a priori unlikely that such an exercise would drastically change the conclusions, as no value of the relevant error parameters α and β lent support for clutch-size reductions in the present model.

In line with our model, our broad-scale comparative analysis does not support the hypothesis that increasing costs of parasitism lead to the evolution of smaller clutches in host species. In fact, it shows a positive association between clutch size and the costs of raising a parasite: host species that incur larger costs lay more eggs if they are hosts of highly virulent brood parasites. We did not find any pattern for hosts of nonvirulent parasites, further supporting the importance of the costs of parasitism in this coevolutionary interaction: only hosts of costly and highly virulent parasites have larger clutches. There are at least two possible explanations for the positive correlation that we observed. First, the costs of parasitism might select for an increase in host clutch size, as suggested by our model. In fact, in our 10,000 simulated cases, there is a significant relationship between clutch size and parasite size C, although this relationship does not consider the interactions with all the other parameters. Second, larger brood parasites might target hosts with larger clutches, be-
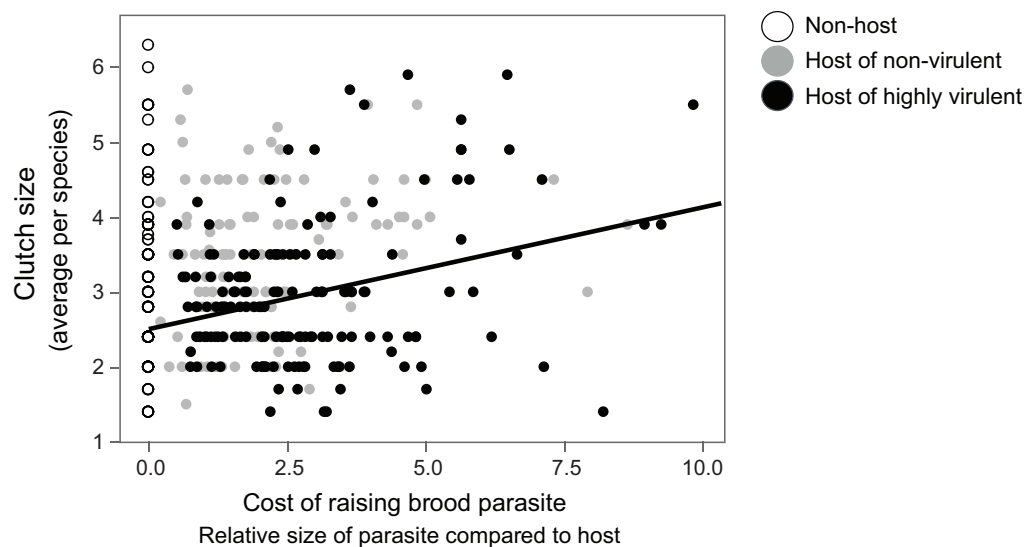
Figure 5: Association between clutch size and the costs of raising a parasite. For hosts of highly virulent parasites (such as most cuckoos and honeyguides), there is a positive association between the clutch size of the host and the costs of raising a parasite. For hosts of nonvirulent parasites (such as cowbirds and *Clamator* cuckoos), there is no association.

cause these hosts may be better providers for the parasitic chick. Determining whether the latter mechanism operates in the wild may be possible by experimentally manipulating clutch sizes; if parasites prefer larger clutches, one should observe an increase in rates of parasitism for experimentally increased clutch sizes. However, experimentally determining whether the first mechanism occurs would be much more difficult, as it relies on the long-term evolution of clutch sizes in response to the selection pressures induced by brood parasites. In this sense, the continued development of models such as the one we present here may represent our best opportunity for understanding this system.

Currently, there is some evidence in the literature supporting a link between parasitism and increased clutch size (Svensson and Råberg 2010). Eurasian magpies (*Pica pica*) have higher clutch sizes in populations where parasitism rates are higher (Soler et al. 2001). Although magpies are not parasitized by evicting cuckoos, their parasite, the great spotted cuckoo (*Clamator glandarius*), is a very costly parasite, reducing to zero the reproductive output of their hosts in 75% of the cases (Soler et al. 2001). Similarly, in *Acrocephalus scirpaceus*, a host of the common cuckoo (*Cuculus canorus*), populations with higher parasitism rates also had higher average clutch sizes (Stokke et al. 2008). It would be interesting to study whether an increase in clutch size is observed in other host-parasite systems that vary locally in rates of parasitism, especially in hosts where parasitism is very costly.

Our results can also be used to predict the evolution of clutch size in other brood parasitic systems, such as that of many insects. We would not expect a change in clutch size in most hosts of insect brood parasites for two main reasons. First, brood parasitism in insects is usually not completely virulent; meaning that at least some of the progeny of the host survives (Buschinger 1986). Second, the size of the parasite progeny is usually equal to or smaller than that of the host, which would impose lower costs and, hence, less selection for an increase in clutch size in the host (Buschinger 1986; Aron et al. 1999).

Finally, contrary to what has been previously proposed, we show that there are neither theoretical nor empirical grounds to suggest the reduction of clutch size as an adaptation in hosts of evicting brood parasites. In fact, we show that, theoretically, clutch size should increase or remain the same in response to brood parasitism pressures, and brood parasitism has the potential to affect the evolution of clutch size. An increase in clutch size in hosts is further supported by some empirical examples (Soler et al. 2001, 2011; Cunningham and Lewis 2006; Stokke et al. 2008) and our comparative analyses, where hosts that experience the highest costs of brood parasitism also lay larger clutches. Our results contrast with previous studies suggesting clutch-size reduction as a defense mechanism in hosts of brood parasites (Brooker and Brooker 1996; Hauber 2003). However,

these studies did not control for other variables known to be related to clutch size, such as latitude or body size; and one of them focused only on hosts of nonevicting brood parasites (Hauber 2003). Furthermore, our study supports the idea that the costs of parasitism vary among hosts, and this can have critical evolutionary consequences (Kilner 2005; Medina and Langmore 2015). Finally, we would also like to highlight the importance of testing verbal predictions with an integrative approach.

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