

Interspecific brood parasitism and the evolution of host clutch sizes

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ABSTRACT

Life-history theory predicts that, over evolutionary time, increased juvenile mortality should decrease parental investment in the number of offspring produced at each breeding attempt. Because interspecific brood parasitism in birds typically reduces the survival of host eggs, nestlings and fledglings, but not that of adult hosts, a specific prediction of the theory is that co-evolution with interspecific brood parasites should lead to smaller avian clutch sizes. Furthermore, the severity of juvenile mortality caused by parasitism in the hosts, due to the parasites' activities and the hosts' rejection behaviours, should correlate negatively with clutch size. In a comparative analysis, both of these predictions were supported among hosts of obligate brood parasitic brown-headed cowbirds (*Molothrus ater*). Reduced clutch sizes appeared to be part of a trade-off strategy as parasitism was also associated with more annual breeding attempts. These findings suggest that, on an evolutionary time-scale, hosts' prolonged interactions with interspecific brood parasites lead to reduced clutch sizes at the taxon level and, qualitatively, these changes in life-history traits are similar to those associated with other types of parasitism and diseases whose main effects also lead to reduced juvenile survival.

Keywords: co-evolution, conspecific brood parasitism, cowbirds, optimal clutch sizes.

INTRODUCTION

Increased rates of parasitism, whether caused by micro- and macroscopic endo- and ectoparasites (Martin *et al.*, 2001) or intraspecific (conspecific) brood parasites (Power *et al.*, 1989; Lyon, 1998), have been suggested to be adaptively associated with decreased clutch sizes of avian hosts (Rothstein, 1990a; Ricklefs and Wikelski, 2002). The direction of these relationships provides support for a key prediction of life-history theory regarding ecological factors influencing juvenile survival and, consequently, adaptive levels of adult breeding effort (Lack, 1954; Skutch, 1975; Martin, 1987, 1995). According to qualitative (Lyon, 1998; Martin *et al.*, 2001) and quantitative (Forbes and Lamey, 1996) models, increased risk of juvenile mortality due to parasitism should lead to decreased reproductive output per reproductive attempt. Increased adult mortality due to parasitism or disease, in contrast, should result in increased reproductive output per breeding attempt. Life-history

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theory, therefore, predicts that avian species with increased losses of eggs and hatchlings, but with no difference in adult survival rates, should evolve lower clutch sizes (Ghalambor and Martin, 2001). Applying this argument to endoparasitic infestations of juveniles and intraspecific brood parasitism in bird nests leads to the prediction that parasitized populations and species should have smaller clutch sizes than non-parasitized populations and species (Power *et al.*, 1989; Lyon, 1998; Martin *et al.*, 2001).

More recently, however, claims of such intrinsic and causal relationships between increased parasite loads and reduced clutch sizes were challenged on grounds of a more extensive review of empirical data on avian immunity (Tella *et al.*, 2002) and a more formal mathematical approach concerning intraspecific brood parasitism in the presence of variable rejection rates (Ruxton and Broom, 2002). In light of these contrasting results, it remains unclear when and how parasitism should be related to the evolution of avian clutch sizes.

Obligate interspecific (heterospecific) brood parasites (e.g. *Cuculus* cuckoos, *Molothrus* cowbirds, *Vidua* finches, etc.) exploit the parental care of host species because, by definition, young parasites require care without increasing the inclusive fitness of foster parents from a different species (Ortega, 1998; Davies, 2000). Parasitism typically increases mortality rates of host nest-mates (Lorenzana and Sealy, 1999; Hosoi and Rothstein, 2000; Hauber, 2003) through both the parasite's own behaviour (e.g. host egg removal by parasitic mothers and more intensive begging and displacement of foster siblings by parasitic nestlings) and the hosts' own responses to parasitism (e.g. rejection and damage of host eggs while attempting to remove parasitic eggs, desertion of parasitized nests) (Ortega, 1998; Davies, 2000). The relationship, if it exists, of obligate brood parasitism to the survival and residual reproductive value of parasitized adults is less clearly understood (Hauber, 2002; Hauber and Montenegro, 2002). For example, in the handful of host species of the obligate brood parasitic brown-headed cowbirds (*Molothrus ater*) in which it had been examined, there was no overall detrimental effect of prior history of parasitism *per se* on aspects of residual reproductive output of foster parents (e.g. over-winter survival, re-nesting success, etc.: Smith, 1981; Payne and Payne, 1998; Sedgewick and Iko, 1999; Hauber, 2001, 2002). Therefore, according to life-history theory as viewed above, natural selection should favour the reduction of host clutch sizes because in these species interspecific brood parasitism consistently increases juvenile mortality, but not adult mortality.

An evolutionary dilemma associated with this prediction is how can reduced clutch sizes be favoured by selection and, consequently, evolve? On the one hand, although poorly understood in non-domesticated taxa, genetic traits are likely to influence avian clutch sizes (Both *et al.*, 1998). On the other hand, brood parasitism is a spatially and temporally variable trait (Ortega, 1998; Rothstein *et al.*, 2002), and a host's strategy to lay reduced clutches might frequently arise in individuals that are not affected by parasitism during their lifetimes (Roskaft *et al.*, 2002). Depending on the costs of rejection errors (Reeve, 1989; Roskaft *et al.*, 1990; Davies *et al.*, 1996), this would cause an evolutionary lag of adaptive responses to interspecific brood parasitism (Rothstein and Robinson, 1998; Hosoi and Rothstein, 2000) or the non-evolution of rejection strategies (Davies, 1999; Roskaft *et al.*, 2002). Even if the reduced clutch size arises in individuals with a high chance of brood parasitism, this trait could not spread unless it is outweighed by an increase in other aspect(s) of the lifetime reproductive output of these hosts with high chances of being parasitized. One possibility for such a trade-off is that hosts adjust their clutch sizes

according to the current probability of parasitism (e.g. by assessing parasite density: Brooke *et al.*, 1998). However, this is unlikely to be a stable strategy in some host–parasite systems, such as *Cuculus* cuckoos and *Molothrus* cowbirds and their respective hosts, because host species are typically short-lived songbirds that suffer high rates of overwinter mortality (Ortega, 1998; Davies, 2000) and would not be able to compensate for loss of fitness from a prior breeding attempt. In addition, there is no theoretical expectation of why years with high parasite densities should be consistently followed by years with low pressure of parasitism to ameliorate the fitness effects of laying smaller clutches in prior years.

Another possibility is that hosts engage in a trade-off strategy of decreasing clutch sizes for increasing numbers of seasonal breeding attempts: smaller first clutches may be followed by several additional breeding attempts within the same year. This is particularly likely for many passerine hosts of temperate-zone brood parasites because they often lay multiple clutches per breeding season and many studies have reported that second clutches are less likely to be parasitized by cuckoos and cowbirds (Lowther, 1993; Davies, 2000; Hauber, 2001). Therefore, an analysis of parasitism pressure and clutch sizes should also examine the difference in the number of repeated nesting attempts per season between parasitized and non-parasitized hosts.

In this study, I set out to examine the evolutionary history of current host species and several of their life-history traits that may be associated with interspecific brood parasitism by brown-headed cowbirds (hereafter, ‘cowbirds’). Due to much interest in this parasitic species and its interactions with neotropical migrant host species (Morrison *et al.*, 1999; Smith *et al.*, 2000), there is a considerable amount of information available on the costs of parasitism and the behavioural responses of host species (Lorenzana and Sealy, 1999; Hosoi and Rothstein, 2000; Hauber, 2003). To test the specific predictions outlined above, I used comparative analyses to ask the following questions:

1. Is host clutch size related to the evolutionary history of cowbird parasitism?
2. Is there evidence for a trade-off between reduced clutch sizes and increased numbers of repeated nesting attempts of cowbird hosts?
3. Is the clutch size of co-evolved cowbird hosts related to the cost of parasitism (i.e. increased juvenile mortality)?

METHODS

I examined the relationship between clutch sizes (eggs/nest) and interspecific brood parasitism in potential hosts of the North American brown-headed cowbird. A recent extensive comparative analysis (Hosoi and Rothstein, 2000) showed that nest desertion behaviour is an evolved response of those host species that have shared geographic ranges and breeding habitats (e.g. forest edges) with cowbirds during their evolutionary past (i.e. ‘old’ hosts). Presently, many other species (e.g. inner-forest birds) also act as hosts but primarily because recent human-caused alterations of landscape ecologies brought their habitats into contact with that of cowbirds (i.e. ‘new’ hosts) (Smith *et al.*, 2000; Rothstein *et al.*, 2002).

Based on the outlined theoretical considerations, I predicted that old hosts should have smaller clutch sizes than new hosts. To control for potential confounding factors, I also included several other life-history traits in a multiple analysis of variance (Table 1). Because I was interested in species-level effects, I collected life-history information, including clutch size (eggs/nest), for host species from an independent source that was not

compiled to examine evolutionary hypotheses regarding cowbirds and their hosts (Baicich and Harrison, 1997). I also collected data from this source to examine the prediction that old hosts have more yearly breeding attempts (nests/year) than new hosts (Table 1). These data on eggs/nest and nest/year represent taxon-level measurements of successfully breeding non-parasitized hosts and, therefore, do not incorporate the proximate effects of either host-egg removal by female cowbirds in parasitized nests or re-nesting following desertion of parasitized clutches. Finally, to control for taxonomic non-independence, I calculated independent contrast scores for each trait using a recently compiled phylogenetic hypothesis for cowbird host taxa (Fig. 1).

Table 1. A compilation of the life-history variables for hosts that were used for the analyses

English name	Host type	Desertion rate (%)	Host mass (g)	Nests/year	Eggs/nest	Incubation period (days)	Nest height (ft)
Acadian Flycatcher	New	12.0	12.9	1.0	3.0	13.5	16.5
Brewer's Sparrow	Old	69.0	9.9	1.5	3.5	12.0	2.0
Chipping Sparrow	Old	38.5	12.3	2.0	4.0	12.5	11.5
Clay-coloured Sparrow	Old	36.5	12.0	1.5	3.5	11.0	2.5
Common Yellowthroat	Old	22.5	9.9	2.0	4.0	12.0	0.5
Dark-eyed Junco	New	16.0	18.8	2.5	4.0	12.5	0.0
Dickcissel	Old	21.0	19.0	1.5	4.0	12.0	3.0
Eastern Meadowlark	Old	46.0	76.0	2.0	4.0	14.0	0.0
Eastern Phoebe	New	21.0	19.8	2.0	5.0	15.0	3.0
Field Sparrow	Old	59.5	12.5	3.0	4.0	10.5	0.5
Golden-cheeked Warbler	Old	75.0	9.4	1.0	4.0	12.0	12.0
Grasshopper Sparrow	Old	22.0	17.0	2.5	4.5	11.5	0.0
Indigo Bunting	Old	58.5	14.1	2.0	3.5	12.5	10.0
Kirtland's Warbler	New	9.0	13.8	1.5	4.5	14.0	1.5
Lark Bunting	Old	38.0	37.6	1.5	4.5	12.0	0.0
Louisiana Waterthrush	New	0.0	20.8	1.0	5.0	13.0	0.0
Magnolia Warbler	New	33.0	8.5	1.0	4.0	12.0	8.0
Mourning Warbler	New	25.0	12.0	1.0	4.0	12.5	1.5
Northern Cardinal	Old	30.5	43.9	3.5	3.5	12.0	5.0
Ovenbird	New	20.0	19.4	1.0	4.5	12.5	0.0
Prairie Warbler	Old	48.0	7.3	1.0	4.0	13.0	5.5
Red-eyed Vireo	New	32.5	16.7	1.5	4.0	12.5	7.5
Red-winged Blackbird	Old	4.3	52.6	2.0	4.0	11.0	5.0
Solitary Vireo	New	3.0	16.6	2.0	4.0	15.0	10.5
Song Sparrow	Old	10.7	20.5	3.0	4.0	13.0	2.0
Veery	New	50.0	31.2	1.0	4.0	12.0	3.0
Willow Flycatcher	Old	46.4	13.7	1.0	3.5	12.5	12.5
Wood Thrush	New	0.0	47.4	1.5	3.5	13.0	10.0
Yellow Warbler	Old	61.1	9.2	1.5	4.5	11.0	7.0

Note: Because this was a literature-based study, I collected taxon-level data just as they had originally been published and, accordingly, utilized species' names that had been current at the time of the publications of these sources. Old versus new host classifications were from Hosoi and Rothstein (2000) except for Eastern Phoebes, which I classified as a new host based on Rothstein *et al.* (2002). Data are from Baicich and Harrison (1997), Hosoi and Rothstein (2000), Lorenzana and Sealy (1999) and Roskaft *et al.* (1990).

In addition, I examined whether, among old hosts only, the extent of juvenile mortality specifically attributable to cowbird parasitism was negatively correlated with clutch size. Mortality of juvenile hosts induced by parasitism can be due to at least two separate factors: the parasites' own behaviour and the hosts' responses to parasitism (see Introduction). However, these two factors are not necessarily independent and the previous analyses by Hosoi and Rothstein (2000) showed that the severity of the cost of cowbird parasitism (i.e. the extent of juvenile mortality due to parasitism) was positively related with the frequency of desertion behaviour of hosts following parasitism (i.e. more vulnerable species are more likely to desert parasitized clutches). In turn, nest desertion by hosts directly increases juvenile mortality because eggs in abandoned clutches do not hatch. Therefore, I used host desertion rates following cowbird parasitism to estimate juvenile mortality due to parasitism in multiple regression analyses of clutch sizes. This approach is analogous to Martin and co-workers' (2001) method of treating quantitative differences between juvenile immune responses as approximate measures of the costs of endoparasitic infestations and microbial infections (but see Tella *et al.*, 2002). To determine whether nest desertion rates following cowbird parasitism are related to other aspects of the overall costs of cowbird parasitism (i.e. the difference in fledging success of host offspring from parasitized and non-parasitized clutches), I used a regression analysis between desertion rates and host size (i.e. adult female mass) for old hosts only and predicted a negative relationship. I did so because previous comparative analyses showed that greater host mass is related to lower

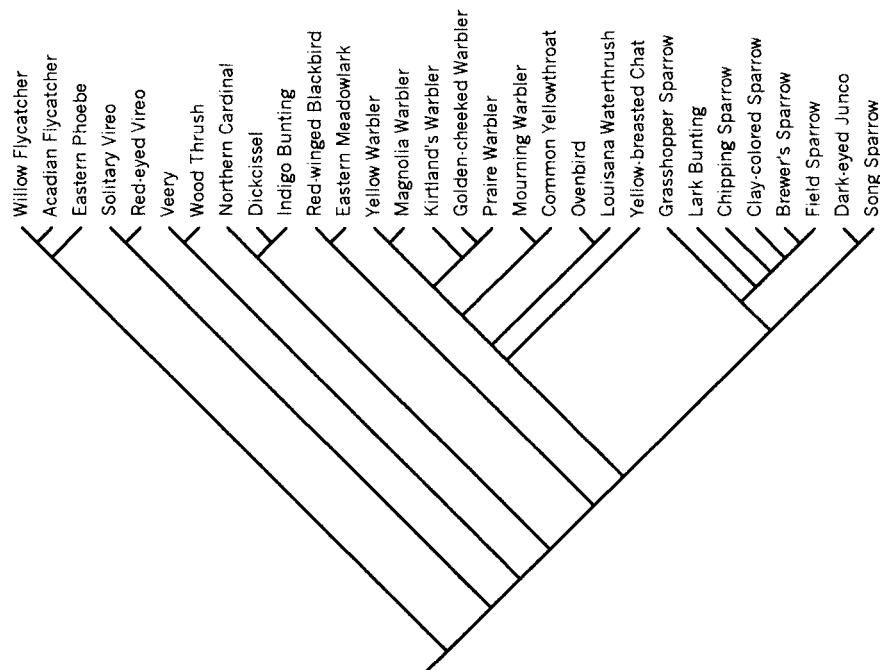


Fig. 1. Hypothesized phylogenetic relationships for the calculation of independent contrasts among cowbird host species were based on Lovette and Bermingham (1999) and Klicka *et al.* (2000), without weighting by branch lengths.

fledgling mortality in the presence of parasitic cowbird nest-mates (Lorenzana and Sealy, 1999; Hauber, 2003).

To control for phylogenetic relationships, I again calculated independent contrast scores to be used in multiple regressions. When ranges instead of mean or modal values were given for specific traits in any of the published sources (see Table 1), I used the mean values. Proportional variables were $\log [1+]$ transformed and all statistical tests were two-tailed.

RESULTS

I found statistical support for the predictions derived from life-history theory: new hosts had larger clutch sizes than old hosts (Fig. 2) when controlled for nest height ($F_{\text{old/new}} = 6.7$, $P = 0.015$; $F_{\text{nest height}} = 15$, $P = 0.0008$; $F_{\text{interaction}} = 4.2$, $P = 0.051$). In turn, the number of breeding attempts per year was greater for old than new hosts ($F_{\text{new/old}} = 4.4$, $P = 0.046$; Fig. 2). These relationships held up when controlling for phylogenetic history using independent contrast scores ($n = 29$): clutch size was lower for older host types ($P = 0.0099$, dummy variable of 2 for old and 1 for new hosts) when controlled for nest height ($P = 0.0006$); clutch size score = $3.8 - 0.36 \times \text{host type score} - 0.052 \times \text{nest height score}$ ($R^2 = 0.42$, $P = 0.0008$). In addition, the number of annual breeding bouts was greater for older host types: nests/year score = $2.7 + 0.68 \times \text{host type score}$ ($R^2 = 0.23$, $P = 0.0079$).

Among old hosts only, taxon-level trait measures of life-history variables (Table 1) were not significantly related with clutch size (all $P > 0.05$, regression analyses). However, in agreement with the predictions, the independent contrast scores ($n = 17$) of nest desertion rates ($P = 0.039$; Fig. 3) and seasonal breeding attempts (nests/year, $P = 0.030$) were both negatively correlated with clutch sizes: clutch size score = $5.1 - 3.3 \times \log \text{desertion score} - 0.34 \times \text{nests/year}$ ($R^2 = 0.23$, $P = 0.062$).

That desertion rate was relevant to the overall costs of cowbird parasitism in hosts was indicated by a negative relationship between mass scores of old cowbird hosts and their

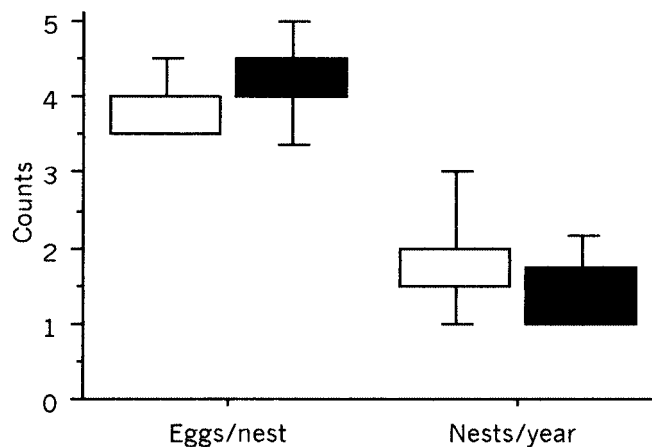


Fig. 2. Clutch size (eggs/nest) and seasonal number of breeding attempts (nests/year) of old (□, $n = 18$) and new (■, $n = 12$) hosts of obligate parasitic brown-headed cowbirds (whisker and box plots represent the 90th, 75th, 25th and 10th percentiles of each measure).

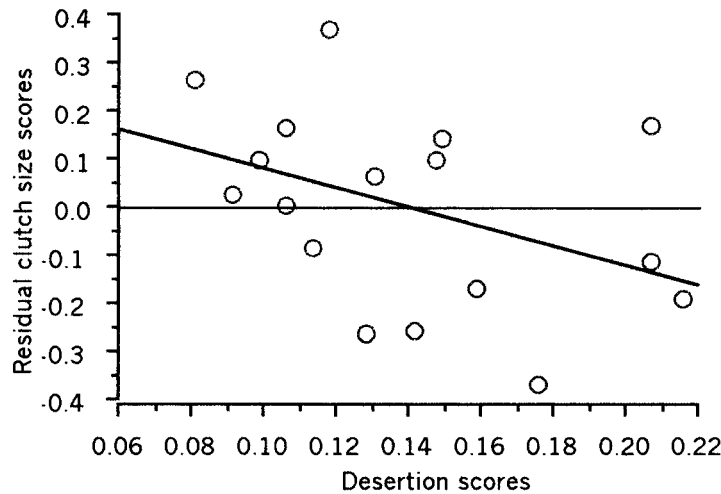


Fig. 3. The relationship between clutch size and desertion rate following parasitism, based on analyses of independent contrast scores of old host species ($n = 18$) of parasitic brown-headed cowbirds. To illustrate the results of a multiple regression analysis, residual values of clutch size scores are plotted from a statistically significant linear regression of clutch size scores with seasonal breeding attempt (nests/year) scores.

respective desertion rate scores: desertion rate score = $53 - 0.59 \times \text{host mass score}$ ($R^2 = 0.41$, $P = 0.0034$).

DISCUSSION

Brood parasitic brown-headed cowbirds, like many other obligate brood parasites, appear to have affected their host species through evolutionary time because many of these taxa evolved anti-parasitic behaviours that currently serve adaptive functions mostly in the context of interspecific brood parasitism (Rothstein and Robinson, 1998; Davies, 2000). These behaviours include ejection of cowbird eggs, increased nest attendance when exposed to high risks of parasitism, and recognizing and attacking adult cowbirds when near host nests (Hosoi and Rothstein, 2000; Tewksbury *et al.*, 2002). The results of the analyses presented here support the hypothesis that evolution also affected several life-history traits that had not previously been recognized to be related to interspecific parasitism. Specifically, the extent of old hosts' breeding effort per breeding attempt (i.e. clutch size: eggs/nest) is consistently smaller, while the number of seasonal reproductive bouts (nests/year) is consistently higher, in historically parasitized, old taxa versus historically non-parasitized, new host taxa (Fig. 2). These patterns are in agreement with predictions of life-history theory (Lack, 1954) regarding evolutionary effects of interspecific brood parasitism on host clutch sizes.

The comparisons of clutch sizes and yearly breeding attempts by old versus new host species do not constitute critical tests because other life-history variables (e.g. nest predation rates) may vary between old and new hosts (Lorenzana and Sealy, 1999; Smith *et al.*, 2000).

There is evidence that parasitized broods of cowbird hosts typically (but not always) also suffer greater nest losses due to predation than non-parasitized broods (Arcese *et al.*, 1996; Dearborn, 2000; Hauber, 2000). Higher predation rates on nests of old versus new hosts would affect the evolution of hosts' reproductive efforts (i.e. clutch sizes) in the same direction as predicted by interspecific brood parasitism (Martin, 1995). Nonetheless, for a subset of the taxa used in my analyses where data were available, there is no such bias regarding differential predation rates between old and new host species ($t_9 = 0.20$, $P = 0.84$). Similarly, Hosoi and Rothstein (2000) found no statistical relationship between their evolutionary response to cowbird parasitism (nest desertion) and predation rates. Furthermore, the results of a more critical test (i.e. one that was based on within-old host comparisons only) also show that increased costs of brood parasitism are related to decreased clutch sizes and increased numbers of yearly breeding attempts (Fig. 3). Nonetheless, whether cowbird parasitism influenced the evolution of reduced host clutches directly (e.g. via nest-mate competition) or indirectly (e.g. via attracting more predators) through the parasites' detrimental effects on host fledging success, remains to be explored further.

My observations suggest that brood parasitic cowbirds affected the evolution of life-history traits in many of their host species whose clutch sizes are smaller than expected in the absence of parasitism. Evidence for effects through evolutionary differences in life-history traits are essential prerequisites to demonstrate and establish a history of co-evolutionary dynamics between hosts and parasites (Roskaft *et al.*, 1990; Rothstein, 1990a; Rothstein and Robinson, 1998; Davies, 1999). Unfortunately, the evidence from the analyses presented does not allow me to address this possibility (Hosoi and Rothstein, 2000), or the absence thereof (Stokke *et al.*, 2002), in cowbird hosts because I did not examine another prerequisite of demonstrating co-evolution, namely that parasitic life-history strategies also respond to parasite-induced changes in host traits (Rothstein, 1990b).

The effect sizes of parasitism on the life-history traits reported here for old versus new hosts (difference of 0.1–0.2 eggs; Fig. 2) are an order of magnitude smaller than those observed for endo- and ectoparasites (Martin *et al.*, 2001) or intraspecific parasitism (Lyon, 1998) (difference of 1–2 eggs). In addition, several of the predicted cross-species correlations only achieved statistical significance when controlling for phylogenetic relationships. Nonetheless, these relationships may be robust because life-history traits for each species were taken from an unbiased source (Baicich and Harrison, 1997) that was compiled without regard to the hypotheses tested in this study. Taken together with other recent work (Lyon, 1998; Martin *et al.*, 2001), these results also imply that evolutionary outcomes of interspecific brood parasitism are similar to those caused by other types of parasitism (e.g. intraspecific brood parasitism and endoparasitic infestations) and diseases (e.g. microbial infections) that affect juvenile survival detrimentally.

It is conceivable to imagine an additional comparative study that is based on comparisons of clutch sizes among species that are known to serve as cowbird hosts versus species that are never parasitized by cowbirds. For example, brown-headed cowbirds do not typically parasitize cavity-nesting species, such as some wrens and swallows (Ortega, 1998). In turn, cavity nesters tend to have larger clutch sizes than open-cup-nesting species (the latter are the typical cowbird hosts in North America) (Lack, 1954; Martin *et al.*, 2001). However, cavity-nesters typically also have lower predation rates than cup-nesters because they raise their broods in enclosed nests. Future comparisons could examine clutch sizes between the several cavity-nesting hosts of the obligate parasitic shiny cowbirds (*M. bonariensis*) and other cavity-nester species that are not hosts of this South and Caribbean American

parasite with an expanding range into North America (Wiley *et al.*, 1991; Kattan, 1996; Ortega, 1998).

A recent analysis of host clutch sizes in European populations of black-billed magpies (*Pica pica*), which are parasitized by the great spotted cuckoo (*Clamator glandarius*) to varying extents, found that higher rates of parasitism are related to increased clutch sizes (Soler and Soler, 2000; Soler *et al.*, 2001). This finding appears to contradict the fundamental predictions tested in my study. Yet, this contradiction is not fatal to life-history theory! Instead, it can be used to highlight an implicit assumption of the previously outlined models. Namely, the prediction that increased juvenile mortality leads to reduced clutch sizes assumes that the proportional contribution to fitness represented by each additional egg laid by a female host is reduced by interspecific parasitism in proportions that are independent of the total clutch size (Lyon, 1998) (Fig. 4). On the one hand, this assumption is supported for host eggs in clutches enlarged by intraspecific brood parasitism (Lyon, 1998; but see Ruxton and Broom, 2002) and it is likely to hold true for clutches parasitized by endo- and ectoparasites because larger clutches per nest probably are more difficult to keep hygienically clean and have higher rates of infections (Martin *et al.*, 2001; but see Tella *et al.*, 2002).

On the other hand, this assumption is violated for the magpie-cuckoo system because the probability of fledging any host nestlings at all per magpie brood is positively related to the total number of host eggs laid in that clutch (Soler and Soler, 2000). In magpies, increased clutch sizes are beneficial because they increase the reproductive output of both parasitized and, of course, non-parasitized hosts (Fig. 4). In this respect, the magpie-cuckoo system falls in the analogous region of the graphical output of Ruxton and Broom's (2002)

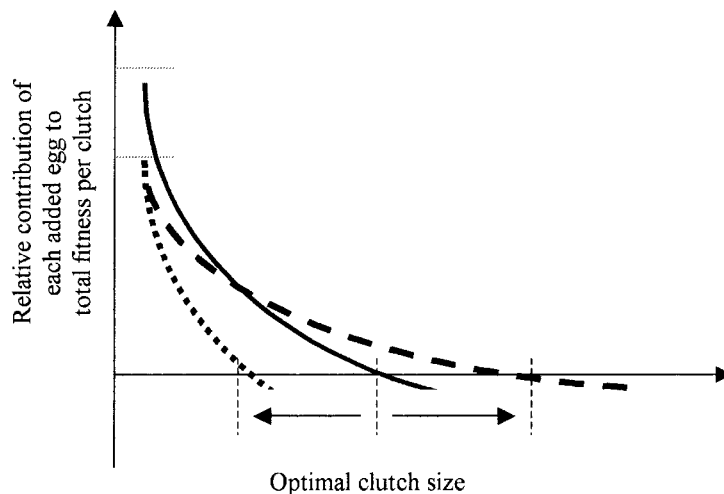


Fig. 4. Optimal clutch sizes in the absence (solid line) and presence (staggered lines) of interspecific brood parasitism with a constant amount of egg-forming resources (after Lyon, 1998). Optimal clutch sizes are indicated by the intersection of the fitness lines with the x-axis. Selection will favour the decrease in original (non-parasitized) clutch size if the fledging success per egg is reduced uniformly for parasitized clutches irrespective of the laying order of each additional egg (dotted line). Selection will favour an increase in the original clutch size if the fledging success per each added egg is higher than that of the previously laid egg (dashed line).

theoretical model where brood parasitism causes increased rather than decreased host clutch sizes (their Figure 1). Nonetheless, the magpie–cuckoo example appears to be fundamentally different from other host–parasite systems, such as the European cuckoo (*Cuculus canorus*) and the brown-headed cowbird and their respective hosts (Ortega, 1998). Increased clutch sizes in the latter hosts are selected against because of the reduced hatching success of larger clutches (Lerkelund *et al.*, 1993; McMaster and Sealy, 1997; Davies, 2000). In addition, *Cuculus* cuckoo chicks throw out all host eggs and nestlings (Davies, 2000) and cowbird chicks typically hatch earlier and grow faster than host nestlings (Lorenzana and Sealy, 1999; Kilpatrick, 2002; Hauber, 2003). Therefore, the hosts' reproductive success (i.e. the number of fledged young/parasitized clutch) when parasitized is not affected by the original clutch size (e.g. in cowbirds: Hauber, 2003). Finally, magpies, unlike most hosts of cuckoos and cowbirds, do not lay multiple clutches per breeding season (Soler and Soler, 2000), thereby eliminating the evolutionary route of trading off reduced clutch sizes of first nesting attempts for increasing the number of subsequent nesting attempts within the same breeding season.

Overall, these comparative analyses show that lower clutch sizes of historically parasitized versus recent cowbird hosts (Fig. 2) are in accordance with predictions of life-history theory because otherwise one would not expect to find a statistical relationship between the cost of brood parasitism regarding juvenile mortality (Hosoi and Rothstein, 2000) and the reproductive effort of hosts per breeding attempt (Fig. 3). It will be informative to expand the scope of future comparisons to examine whether similar relationships hold true in other co-evolving host–parasite systems at different geographic areas, scales and latitudes. Specifically, there is a greater diversity of obligate brood parasites in more southern latitudes (Davies, 2000) and perhaps differences in parasitism rates contribute to the variation of clutch sizes between species with more northern or southern breeding ranges (Skutch, 1975).

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