

Patterns and coevolutionary consequences of repeated brood parasitism

Mark E. Hauber^{1,2*}, Pamela J. Yeh³ and John O. L. Roberts[†]

¹Department of Integrative Biology, Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720-3160, USA

²Behaviour, Ecology, and Conservation Research Group, School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand

³Section of Ecology, Behavior, and Evolution, University of California, San Diego, CA 92093, USA

* Author for correspondence (hauberm@socrates.berkeley.edu).

Recd 17.12.03; Acceptd 19.01.04; Published online 04.03.04

The absence of adaptive host responses to virulent parasites and pathogens is paradoxical. We explored the theoretical possibility that the evolution of anti-parasitic egg-ejection strategies was delayed by avian hosts' lifetime experiences with brood parasitism. An analytical model indicated that individual hosts' repeated exposure to parasitism decreased the relative benefits of learning-based rejecter strategies when parasitism was particularly costly. Because brood parasitic brown-headed cowbirds (*Molothrus ater*) and their hosts are typically philopatric across breeding attempts, spatially and temporally non-random patterns of parasitism may contribute to low levels of observed egg-ejection by vulnerable cowbird hosts. In support, we found that in three populations of two host species individual females experienced repeated cowbird parasitism during their lifetimes. We propose that repeated parasitism contributes to counterintuitive patterns of coevolutionary dynamics in spatially structured host-parasite populations.

Keywords: host–parasite coevolution; spatial modelling; philopatry

1. INTRODUCTION

Avian brood parasites inflict fitness costs on their hosts, and natural selection is expected to favour individuals that effectively counteract parasitism (Davies 2000; Servedio & Lande 2003). Brown-headed cowbirds (*Molothrus ater*) reduce the fledging success of parasitized broods in 29 common host species by an average of 58%, with a range of 0–100% (Hauber 2003). However, most cowbird hosts regularly do not eject parasitic eggs, especially in those species that are smaller, hatch more asynchronously and fledge fewer of their own young when parasitized (Rothstein 1975; Hauber 2003). This is surprising because egg-ejection is common in hosts of several other brood parasites (Davies 2000). Also, many cowbird hosts

engage in other antiparasitic behaviours, such as attacking adult cowbirds and deserting parasitized nests (Hosoi & Rothstein 2000). Why, then, is egg-ejection by vulnerable cowbird hosts not more prevalent?

Explanations for the absence of egg-ejection by cowbird host species are typically divided into two categories (Rothstein & Robinson 1998). First, when the benefits of parasite rejection and the costs of discrimination errors are comparable, then an evolutionary equilibrium will prevent the spread of rejecter mutations in exposed host populations. Alternatively, host and parasite may not have coexisted long enough for antiparasitic strategies to have evolved, implying an evolutionary lag. How these alternatives relate to cowbirds, other brood parasites and hosts with different life-history strategies is the subject of much current research (Langmore *et al.* 2003; Lawes & Marthews 2003; Servedio & Lande 2003).

Recent empirical evidence and theoretical models of both parasitic and mutualistic coevolutionary systems have emphasized the importance of spatial and temporal variation for the fitness outcome of host–parasite interactions (Røskaft *et al.* 2002; Thompson & Cunningham 2002). Structured spatial patterns of parasitism are predicted to occur in brown-headed cowbirds and their typical, small passerine hosts because both parasite and host are territorial within and between breeding seasons (Lowther 1993; Smith & Arcese 1994). Accordingly, the parasitism status of first clutches of eastern phoebe (*Sayornis phoebe*) nest sites was predictably associated with the same parasitism status of both second clutches in 1999 and first clutches in the subsequent year (2000) in Ithaca, NY, USA (Hauber 2001). Such non-random distribution of parasitism among host individuals is termed ‘repeated parasitism.’ We combine theoretical models and empirical surveys to test the hypothesis that spatial and temporal variation of individual hosts’ lifetime exposure to cowbird parasitism will influence the dynamics of host–parasite coevolution.

2. COEVOLUTIONARY CONSEQUENCES OF REPEATED PARASITISM

To examine the potential effects of repeated parasitism on host–parasite interactions, we can model the fitness of female hosts in the absence or presence of cowbird parasitism. Hosts are either egg-acceptors (A) or egg-rejecters (termed ‘clutch-learners’ (C)). While A females never reject parasitic eggs, each C female learns a template of her own eggs by examining her entire first clutch. Hence, when a C female’s first breeding attempt is not parasitized, she becomes a rejecter of parasitic eggs in subsequent breeding attempts. When a C female’s first clutch is parasitized, she incorporates the appearance of the parasitic egg into her recognition template and thus becomes a current and future acceptor (Rothstein 1975, 1978; Lotem 1993).

Our model includes the following variables: the probability of parasitism (p), the rate of repeated parasitism (n), and the fledging success of non-parasitized broods (F) and of parasitized broods of acceptors (L). The fledging success of parasitized broods of rejecters is set at $F - 1$ (Hauber 2003), representing the loss of one host egg to removal by the parasitic female (Lowther 1993). For mathematical simplicity, we assume that females with parasitized first broods have an n -times greater chance of subsequent parasitism, whereas females with non-parasitized first broods have a $1/n$ chance of subsequent parasitism.

[†]Deceased 20 October 1999.

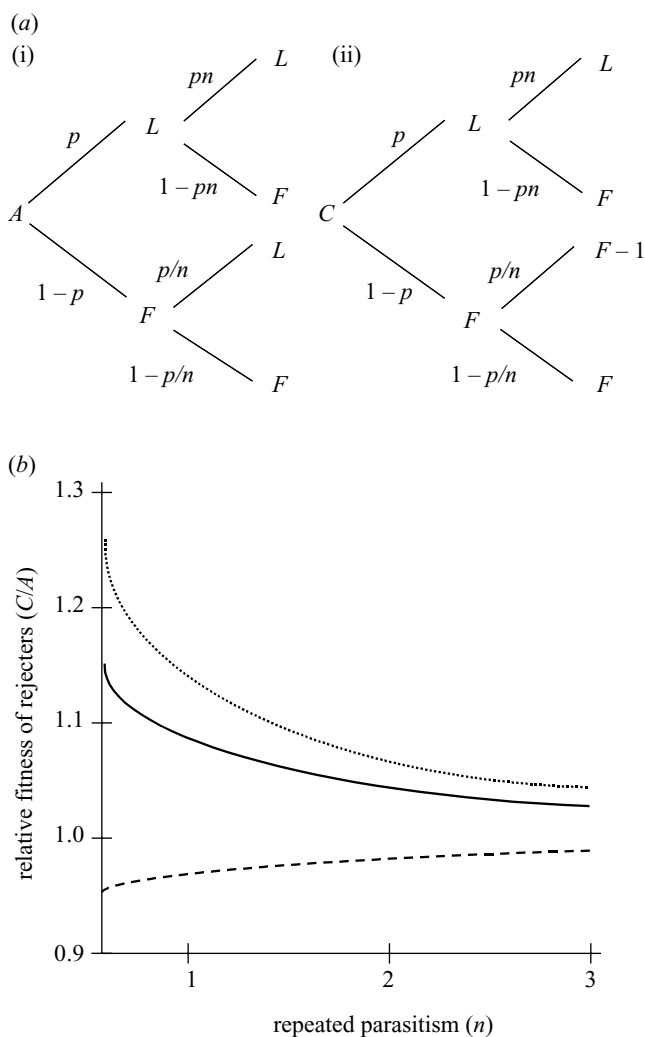


Figure 1. (a) Explicit models of the fitness pay-offs of (i) egg-acceptors and (ii) egg-ejectors. (b) Relationship of repeated parasitism and relative fitness of rejecters for biologically relevant parameters; values of $n > 1.0$ indicate repeated parasitism, $p = 0.3$, $F = 4.0$, and $L = 0.0$ (dotted line), $L = 1.0$ (solid line), or $L = 3.5$ (dashed line). $F = 4.0$, $L = 1.0$ and $p = 0.3$ are modal values in eastern phoebes parasitized by brown-headed cowbirds in Ithaca (Hauber 2001).

Relaxing this assumption does not change our qualitative conclusions. To calculate cumulative fitness, fledgling numbers are summed across two subsequent breeding attempts, representing single reproductive bouts either in the same year or in consecutive years (figure 1a).

The relative fitness benefits of egg-acceptance, A , versus the relative fitness benefit of clutch-learning-based egg-ejection, C , are calculated as:

$$A = p(L + F + pn(L - F)) + (1 - p)(2F + p(L - F)/n), \tag{2.1}$$

$$C = p(L + F + pn(L - F)) + (1 - p)(2F - p/n). \tag{2.2}$$

The function of the relative value of C and A is described as:

$$C/A = (U - 1/n)/(U - (F - L)/n), \tag{2.3}$$

where U in both the numerator and the denominator represents the same numerical value dependent on p , n ,

L and F for all $0 < p < 1$ and $0 < n \leq 1/p$, so that $np \leq 1$. When $F - L = 1$, there is fitness equivalence between acceptance and rejection as $C/A = 1$. Because the models do not include costs associated with hosts' rejection behaviours, including rejection errors, only the direction of change of C/A with respect to n is analysed here (Lawes & Marthews 2003). For instance, decreasing C/A with increasing n will result in a delay in the evolution of egg-ejection by hosts. The logic behind this approach is that when the relative benefit of rejection is smaller, the probability that the rejecter strategy can establish itself and invade a population of acceptors is also lower owing to stochastic effects of drift in limited population sizes (Rothstein 1975; May & Robinson 1985; Servodio & Lande 2003).

The relationship in equation (2.3) indicates that C/A consistently decreases with increasing n when $F - L > 1$ (figure 1b). Furthermore, the rate at which C/A decreases with n is greater for lower values of L . However, when $F - L < 1$, C/A decreases with increasing n . The condition of $F - L > 1$, under which increased n decreases C/A , applies to 16 out of 29 common cowbird host species (Hauber 2003). Counterintuitively, our result implies that hosts that pay larger costs of cowbird parasitism will benefit less from rejecting parasitic eggs in the context of greater repeated parasitism.

3. REPEATED PARASITISM OF INDIVIDUAL HOSTS

Confirming prior patterns of repeated cowbird parasitism of eastern phoebes (Hauber 2001), in our field observations we found that parasitized phoebe nests sites in year x were more likely to be parasitized by cowbirds in year $x + 1$ in two additional year-pairs in Ithaca, NY (2000/2001: $\chi^2 = 4.7$, $p < 0.030$; 2001/2002: $\chi^2 = 6.9$, $p < 0.01$; figure 2a). To examine further the generality of repeated parasitism across host populations, we extracted reproductive data from a 1966–1977 study by J. O. L. R. of eastern phoebes in Southern Ontario, Canada. As in Ithaca (Hauber 2001), cowbird parasitism pressure on phoebes in Ontario declined between first and second breeding attempts within the same year ($p < 0.0001$, paired sign-test of cowbird eggs per nest, $n = 138$ nest-years combined). We therefore analysed parasitism patterns across years using only the seasons' first clutches. There was a non-random pattern of parasitism across the same nest sites (combined for all nest years: $\chi^2 = 4.7$, $p < 0.030$; figure 2a).

We then surveyed a subset of the Ontario nest records in which the identities of breeding colour-banded female phoebes were recorded. We determined whether the parasitism status experienced in a female's first breeding attempt occurred at least once again in first clutches during her subsequent breeding years (average of 2.7 years, range of 2–6). As predicted, individual female phoebes experienced non-random patterns of parasitism across breeding seasons ($\chi^2 = 5.3$, $p < 0.021$; figure 2b).

We also compiled reproductive and parasitism histories of colour-banded female dark-eyed juncos (*Junco hyemalis*) from the University of California, San Diego campus in La Jolla, CA (1999–2002: Yeh 2004). Similarly to phoebes, we concentrated on known female juncos' breeding histories because, in species where females alone build nests and incubate, they are also the gender responsible

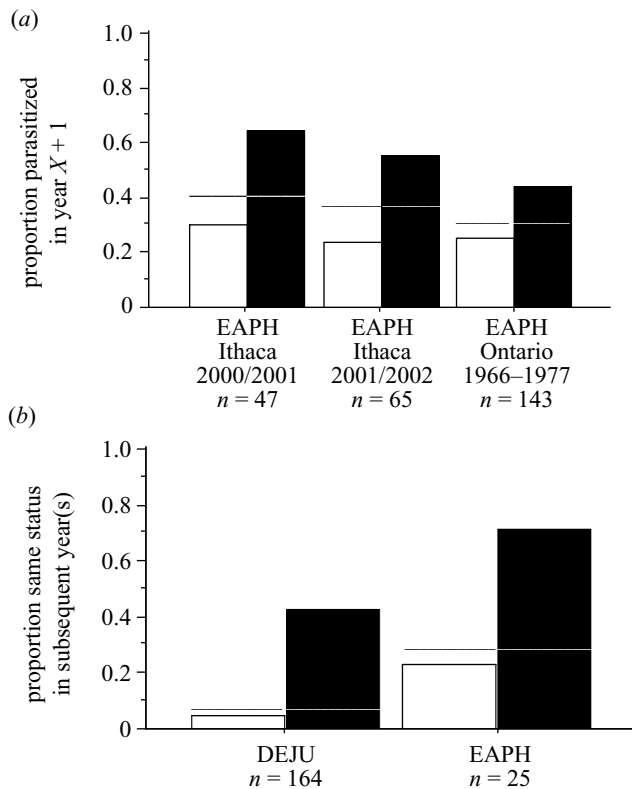


Figure 2. Repeated parasitism of brown-headed cowbird hosts by (a) nest site and (b) individual identity. Open bars, non-parasitized; filled bars, parasitized. Horizontal lines indicate population-wide parasitism rates in year x . EAPH, eastern phoebes; DEJU, dark-eyed juncos (*Junco hyemalis*).

for the ejection of parasitic eggs (Soler *et al.* 2002). Female juncos were included in the analysis when complete annual breeding records were available for two consecutive years. Individuals were categorized as parasitized if they had cowbird egg(s) in any nesting attempts throughout their first breeding year. We did not limit these comparisons to first clutches because juncos at La Jolla have prolonged breeding seasons that begin before and end after the cowbirds' local breeding season (Yeh 2004). Individual female juncos predictably experienced repeated parasitism across years ($\chi^2 = 17.3$, $p < 0.0001$; figure 2b).

Repeated parasitism can be calculated as the ratio of the current year's parasitism rate of previously parasitized nest sites or individuals to the population-wide parasitism rate in that previous year (figure 2). Consistently, in our data, $n > 1.0$; this indicates that repeated parasitism occurs at above chance levels: $n = 2.0$, 1.6 , and 1.5 in Ithaca (1999–2002), 1.5 at the Ontario phoebe nest sites, 2.0 for individual phoebes in Ontario and 7.8 for individual juncos in La Jolla (Hauber 2001).

4. DISCUSSION

There is much theoretical and empirical need to understand the risks and the consequences of brood parasitism at different spatial and temporal scales (May & Robinson 1985; Lindholm & Thomas 2000). However, only a handful of studies have examined the quantitative relationship between the cost of avian brood parasitism from single

breeding attempts to lifetime fitness (Smith & Arcese 1994; Payne & Payne 1998). Our model (figure 1) reveals that repeated parasitism delays the evolution of parasite resistance in more vulnerable hosts. Because the cost of brown-headed cowbird parasitism increases with decreasing host size and increasing hatching asynchrony between parasite and host chicks (Hauber 2003), the results may explain why most acceptor cowbird hosts are those that are smaller and have longer incubation periods than do rejecter hosts (Rothstein 1975; Davies 2000). Although the prevalence of repeated parasitism is unknown in hosts of most brood parasites, we found consistent patterns of repeated parasitism ($n > 1.0$) at the level of individual lifetime exposure in two host species of cowbirds (figure 2).

We do not know the causes and mechanisms of repeated parasitism, but we are investigating at least four alternatives: (i) habitat overlap between parasite and host individuals (Hauber 2001); (ii) nest site exposure due to physical attributes or behavioural aspects of host nest site choice and nest defence behaviours (Smith & Arcese 1994); (iii) parasite philopatry (Hauber 2002); and (iv) parasites' memory for hosts' nest sites (Reboreda *et al.* 1996). Nonetheless, our conclusions about coevolutionary dynamics will be valid irrespective of which mechanisms apply best to cowbirds. Specifically, the model predicts that both the selective consequences and the time-frame for the evolution of host resistance strategies depend on the costs of brood parasitism and the magnitude of repeated parasitism. This result therefore combines evolutionary equilibrium and evolutionary lag scenarios to explain the non-evolution of host resistance. We also suggest that the documented patterns and consequences of repeated parasitism will be relevant to other territorial avian brood parasites and hosts and, in general, to host–parasite, host–parasitoid and host–pathogen systems with finely structured spatial and temporal patterns (Thompson & Cunningham 2002).

Acknowledgements

We thank P. Fernandez for his collaboration and E. DuVal, S. Emlen, M. Hahn, A. Krakauer, E. Lacey, W. Monahan, R. Mueller, J. Parra, T. Price, S. Rovito, P. Sherman, J. Yeh and many others for comments. Funding was provided by fellowships from the Miller Institute for Basic Research in Science and the Howard Hughes Medical Institute to M.E.H. and the US Environmental Protection Agency to P.J.Y., and NSF grants to P. Sherman and T. Price. Access to Ontario breeding records was provided by Bird Studies Canada through S. Brenner, C. Frances and M. Bradstreet.

- Davies, N. B. 2000 *Cuckoos, cowbirds and other cheats*. London: T. & A. D. Poyser.
- Hauber, M. E. 2001 Site selection and repeatability in brown-headed cowbird (*Molothrus ater*) parasitism of eastern phoebe (*Sayornis phoebe*) nests. *Can. J. Zool.* **79**, 1518–1523.
- Hauber, M. E. 2002 First contact: conspecific social association and species recognition in brood parasites. *Ann. Zool. Fenn.* **39**, 291–305.
- Hauber, M. E. 2003 Hatching asynchrony, nestling competition, and the cost of interspecific brood parasitism. *Behav. Ecol.* **14**, 224–235.
- Hosoi, S. A. & Rothstein, S. I. 2000 Nest desertion and cowbird parasitism: evidence for evolved responses and evolutionary lag. *Anim. Behav.* **59**, 823–840.
- Langmore, N. E., Hunt, S. & Kilner, R. M. 2003 Escalation of a coevolutionary arms race through host rejection of brood parasitic young. *Nature* **422**, 157–160.

- Lawes, M. J. & Marthews, T. R. 2003 When will rejection of parasite nestlings by hosts on non-evicting avian brood parasites be favored? A misimprinting-equilibrium model. *Behav. Ecol.* **14**, 757–770.
- Lindholm, A. K. & Thomas, R. J. 2000 Differences between populations of reed warblers in defenses against brood parasitism. *Behaviour* **137**, 25–42.
- Lotem, A. 1993 Learning to recognize nestlings is maladaptive for cuckoo, *Cuculus canorus*, hosts. *Nature* **362**, 743–745.
- Lowther, P. E. 1993 Brown-headed cowbird (*Molothrus ater*). In *The birds of North America*, no. 47 (ed. A. Poole & F. Gill), pp. 1–24. Philadelphia, PA: The Academy of Natural Sciences.
- May, R. M. & Robinson, S. K. 1985 Population dynamics of avian brood parasitism. *Am. Nat.* **126**, 475–494.
- Payne, R. B. & Payne, L. L. 1998 Brood parasitism by brown-headed cowbirds: risks and costs on reproductive success and survival in indigo buntings. *Behav. Ecol.* **9**, 64–73.
- Reboreda, J. C., Clayton, N. S. & Kacelnik, A. 1996 Species and sex differences in hippocampus size in parasitic and non-parasitic cowbirds. *Neuroreport* **7**, 505–508.
- Rothstein, S. I. 1975 Evolutionary rates and host defenses against avian brood parasitism. *Am. Nat.* **109**, 161–176.
- Rothstein, S. I. 1978 Mechanisms of avian egg-recognition: additional evidence for learned components. *Anim. Behav.* **23**, 671–677.
- Rothstein, S. I. & Robinson, S. K. (eds) 1998 *Parasitic birds and their hosts: studies in coevolution*. New York: Oxford University Press.
- Røskaft, E., Moksnes, A., Stokke, B. G., Moskát, C. & Honza, M. 2002 The spatial habitat structure of host populations explains the pattern of rejection behavior in hosts and parasitic adaptations in cuckoos. *Behav. Ecol.* **13**, 163–168.
- Servedio, M. R. & Lande, R. 2003 Coevolution of an avian host and its parasitic cuckoo. *Evolution* **57**, 1164–1175.
- Smith, J. N. M. & Arcese, P. 1994 Cowbird parasitism, host fitness, and age of the host female in an island song sparrow population: a 16-year study. *Condor* **96**, 152–161.
- Soler, M., Martin-Vivaldi, M. & Perez-Contreras, T. 2002 Identification of the sex responsible for recognition and the method of ejection of parasitic eggs in some potential common cuckoo hosts. *Ethology* **108**, 1093–1101.
- Thompson, J. N. & Cunningham, B. M. 2002 Geographic structure and dynamics of coevolutionary selection. *Nature* **417**, 735–738.
- Yeh, P. J. 2004 Rapid evolution of a plumage pattern following population establishment in a novel habitat. *Evolution* **58**, 166–174.