Animal Behaviour 144 (2018) 45–51

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Resistance is futile: prohibitive costs of egg ejection in an obligate avian brood parasite host

Brian D. Peer [a], [*], Robert A. McCleery [b], William E. Jensen [c]

[a] Department of Biological Sciences, Western Illinois University, Moline, IL, U.S.A.
[b] Department of Wildlife Ecology & Conservation, University of Florida, Gainesville, FL, U.S.A.
[c] Department of Biological Sciences, Emporia State University, Emporia, KS, U.S.A.

ARTICLE INFO

Article history:
Received 14 March 2018
Initial acceptance 14 May 2018
Final acceptance 25 June 2018

MS. number: A18-00194R

Keywords:
behavioural plasticity
brood parasitism
coevolution
cowbird
dickcissel
egg ejection
rejection costs

Most hosts of the parasitic brown-headed cowbird, *Molothrus ater*, demonstrate an astonishing lack of defences against parasitism, typically explained by evolutionary lag. We investigated antiparasite strategies of the dickcissel, *Spiza americana*, whose apparent acceptance of parasitism is unlikely to be explained by lag because its historic centre of abundance overlaps with that of the cowbird. Cowbirds parasitized almost half of dickcissel nests (343 of 767 nests), and dickcissels suffered significant costs when attempting to eject cowbird eggs. Our predicted responses indicated that acceptance of parasitism would lead to the loss of 0 hosts eggs, attempted ejections would lead to the loss of 1.2 host eggs and successful ejection of cowbird eggs would lead to the loss of 1.6 host eggs. There was no significant cost of raising a single cowbird nestling, but parasitized nests had 1.1 fewer host eggs due to removal by female cowbirds or when the thick-shelled cowbirds eggs struck the host eggs during laying. After accounting for damaged eggs that still hatched, acceptance of parasitism yielded a loss of 1.1 eggs/nestlings, those that attempted to eject the cowbird egg lost 1.8 eggs/nestlings and those that ejected the cowbird egg lost 2.0 eggs/nestlings. The prohibitive costs of egg ejection combined with the relatively low costs of raising a cowbird nestling may explain why most dickcissels (64%) accepted parasitism or stopped trying to eject cowbird eggs. However, some birds persisted in their ejection attempts, so there are likely additional carryover fitness effects on hosts of raising and sharing nests with cowbirds. Because of the difficulty in ejecting cowbird eggs, dickcissels would benefit from a strategy that emphasizes frontline defences to prevent parasitism from occurring in the first place.

Animals are expected to behave optimally to maximize their fitness as a result of natural selection (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005; Houston, McNamara, & Steer, 2007; McNamara & Houston, 2009). Obligate avian brood parasitism reduces host fitness (Davies, 2000), and hosts should evolve defences to lessen these costs, although there may be some instances where acceptance can be induced (Chakra, Hilbe, & Traulsen, 2016; Hoover & Robinson, 2007). Many common cuckoo, *Cuculus canorus*, hosts eject nonmimetic eggs and some also adjust their response to parasitism based on the costs of ejection (Antonov, Stokke, Moksnes, & Røskaft, 2009; Davies, Brooke, & Kacelnik, 1996). In contrast, hosts of the brown-headed cowbird, *Molothrus ater* (hereafter ‘cowbird’), show an astonishing lack of defensive behaviour towards parasitism and almost no evidence of flexibility in their response to it (Peer & Sealy, 2004a; Rothstein, 1975). Unlike cuckoos, cowbirds do not evict host nestlings and the host nestlings must compete with the cowbird nestlings, although in many instances only the cowbird survives (Peer, Rivers, Merrill, Robinson, & Rothstein, 2018; Peer, Rivers & Rothstein, 2013). Cowbirds and their hosts have also coevolved for less than half the time as cuckoos and their hosts (2.8–3.8 Ma and 6.3–8.4 Ma, respectively; Rothstein, Patten, & Fleischer, 2002). As a result, this apparent maladaptive behaviour by cowbird hosts has largely been assumed to be a consequence of evolutionary lag (Peer & Sealy, 2004a; Rothstein, 1975a), whereby hosts have not yet evolved defences, and once the appropriate mutation occurs, ejection of parasite eggs will spread rapidly throughout host populations (Rothstein, 1975b).

Evolutionary lag can account for acceptance of parasitism by hosts that nest in heavily forested habitats rarely penetrated by cowbirds (Hosoi & Rothstein, 2000; Peer & Sealy, 2004a). However, hosts that have nested within the historic centre of cowbird

---

[*] Correspondence: B.D. Peer, Department of Biological Sciences, Western Illinois University, Moline, IL, 61265, U.S.A.
E-mail address: BD-Peer@wiu.edu (B. D. Peer).

https://doi.org/10.1016/j.anbehav.2018.08.002
0003-3472/© 2018 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

abundance have been exposed to parasitism for a much longer time and should be the species most likely to express sophisticated responses to parasitism (Hosoi & Rothstein, 2000; Mayfield, 1965; Peer, Robinson, & Herkert, 2000). Therefore, lag is not likely the best explanation to account for their acceptance. Instead, it is possible that in some cases acceptance of parasitism may be the superior strategy depending on the costs of expressing defences relative to their benefits. Costs associated with egg ejection include recognition and rejection errors. Recognition errors occur when hosts eject their own eggs from a parasitized nest and are more common when the parasite lays an egg that resembles the host's eggs (Davies & Brooke, 1988; Davies et al., 1996). Rejection errors take place when a host damages its own eggs in the process of removing the parasitic egg and are more likely to occur in hosts with small bills that puncture-eject parasite eggs (Rohwer & Spaw, 1988; Rothstein, 1975a; Røskaft, Rohwer, & Spaw, 1993). Parasites have thick-shelled eggs (Antonov et al., 2013; Jaeckle et al., 2012; Picman, 1989), and bills of small-billed hosts bounce off the parasite egg and onto their own eggs, causing damage to them (Antonov et al., 2013; Antonov et al., 2009; but see Sealy, 1996). If the costs of raising a brood parasite are relatively small, but the costs associated with egg ejection are excessive, then a host may maximize its fitness by tolerating parasitism (Rohwer & Spaw, 1988). Here we demonstrate, for the first time, the prohibitive costs of egg ejection in a cowbird host, the dickcissel, *Spiza americana*, which combined with the relatively low costs of raising a cowbird nestling may favour acceptance of parasitism in some instances.

METHODS

Experimental Procedures

Dickcissel nests were monitored for cowbird parasitism and were experimentally parasitized in McDonough County, Illinois, U.S.A. (40°16′48″N, 90°43′48″W) during 2006–2008. Nests were parasitized with real cowbird eggs collected from other nests freshly laid, or with artificial eggs composed of plaster of Paris that were similar to real cowbird eggs (Peer, Kuehn, Rothstein, & Fleischer, 2011; Rothstein, 1975a). A subsample ($N = 10$) of our artificial cowbird eggs measured 21.3 × 16.4 mm and weighed 3.6 g. Real cowbird eggs measure 21.5 × 16.4 and weigh 3.0 g (Lowther, 1993). Dickcissels lay blue eggs, whereas cowbird eggs have a white background with brown and grey spots. No host eggs were removed in conjunction with experimental parasitism because this behaviour varies and there is little evidence it affects cowbird host response (Rothstein, 1975a). Eggs were added during laying (53%) and early incubation (47%) when cowbirds typically lay (Rothstein, 1975a). Nests were checked for host response and natural parasitism every 1–3 days, although most (>90%) were checked daily. Eggs in control nests were monitored for damage and treated in the same manner as experimental nests except no parasitic eggs were added to them. We did not control for the possibility that flushing hosts during experimental parasitism could influence ejection behaviour, which has been shown to occur in a single cuckoo host (Hanley et al., 2015). Eggs were considered ‘ejected’ if they were removed from the nest and they were considered ‘accepted’ if they remained in the nest for at least 5 days with parents still attending the nest and no host eggs disappeared or were damaged following parasitism (Rothstein, 1975a). Responses were considered ‘attempted ejections’ when cowbird eggs were not removed from the nest. In these cases, artificial cowbird eggs had peck marks or paint chipped off by the host's bill, or host eggs were damaged after the host's bill bounced off the real or artificial cowbird eggs onto their own eggs, causing them to break or dent (see below). The number of host eggs lost per ejection attempt included those that were broken, dented or found below the nest. We interpreted these as losses because eggs were never found below unmanipulated control nests, nor were damaged eggs found in control nests (see below). Any nebulous results were excluded from analysis.

Nestling Losses

Collecting nestling data at our primary study site was not logistically feasible, thus we examined nestling mortality (number of nestlings failing to fledge) in 466 dickcissel nests monitored in 2001 and 2002 across eight sites in eastern Kansas and northeastern Oklahoma (Jensen & Cully, 2005). No experimental manipulations of nests were conducted and nest contents were monitored every 3–4 days until nest completion. Nests used for analysis were active during the nestling stage and where incubation or hatch day were observed so that the number of host and cowbird offspring entering the nestling stage was known. If incomplete hatch was observed prior to finding the nest empty on the subsequent visit (i.e. depredation), these nests were omitted from analyses because the number of hatched host and cowbird young entering the nestling stage was uncertain. Nestling histories therefore accounted for losses of dickcissel young due to starvation and removal by parents as well as partial and complete depredation by predators.

Statistical Analyses

We predicted that the cost of parasitism (number of host eggs lost) would be driven by host response (accept, eject, attempted ejection). When a host accepts an egg outright, it does not suffer rejection costs. However, when it ejects or attempts to eject a cowbird egg, it could damage some of its own eggs. Before we could test this prediction, we had to determine whether the different treatments (natural parasitism, experimental parasitism using real cowbird eggs, experimental parasitism using artificial cowbird eggs) influenced costs. To determine the relationship between the number of host eggs lost (cost = dependent variable) and the different treatments applied (independent variable), we used a generalized linear mixed model (GLMM) fitted to a Poisson distribution with a log link. We used nest identity as a random effect in all models to avoid pseudoreplication because birds were not banded and some individuals may have been retested in multiple years. Finding no difference between treatments ($P > 0.4$) from our GLMM, we evaluated our prediction without treatment as a variable (no influence of treatment on cost) or separately based on the different treatments (treatment influenced cost).

To determine the factors influencing the cost of parasitism, we created a GLMM with different responses (accept, eject, attempted ejection) as well as potential alternative explanations for responses, including variation between years and clutch initiation date (measured by Julian date) as independent variables (cost ~ response + year + date). Responses could vary yearly depending on the likelihood of being parasitized (Davies et al., 1996) and also by clutch initiation date, with hosts being more likely to eject earlier (Lotem et al., 1992) or later in the nesting season (Lang, Bollinger, & Peer, 2014). We also evaluated whether the number of host eggs present at the time of parasitism and the timing of parasitism (i.e. during laying or incubation) influenced cost. Number of host eggs present could influence response because the more host eggs present, the more that could potentially be damaged during ejection attempts. Timing of parasitism could influence ejection because some hosts are less likely to eject when eggs are laid during incubation (Rothstein, 1976). Because of missing values for the two latter factors, we developed an additional GLMM model with a reduced number of observations that included number of eggs and timing as well as any relevant predictors from the model on the full