Does the removal of avian brood parasite eggs increase host productivity? A case study with brown-headed cowbirds *Molothrus ater* and song sparrows *Melospiza melodia* near Ithaca, New York, USA

Mark E. Hauber
Concentration in Animal Behavior and Conservation, Department of Psychology, Hunter College of the City University of New York, 695 Park Avenue, New York, NY 10065, USA

Corresponding author e-mail: mhauber@hunter.cuny.edu

SUMMARY

Avian brood parasitism lowers host fitness through several mechanisms, including the reduction of productivity of parasitized breeding attempts. Even when both host and parasite are native species, anthropogenic factors (e.g. habitat alteration) may increase local parasitism burden on rare hosts so as to require conservation action. To reduce brood parasitism rates by brown-headed cowbirds *Molothrus ate*r (an increasingly abundant species within its North American range), most conservation action currently involves the removal of adult cowbirds in the hosts' breeding habitat. An alternative, but more labour intensive, management action is to remove cowbird eggs from host nests, but the benefits of such egg removal may be outweighed by the predatory behavior of cowbird females on host eggs if nests lack cowbird eggs. In this present study, parasitism of song sparrows *Melospiza melodia* near Ithaca, New York (USA) was used as a case study to evaluate the effect of removing cowbird eggs on productivity (i.e. young fledged per nest) of the host species. Although parasitized nests had naturally fewer host eggs than non-parasitized nests, there were no consistent differences in the numbers of host nestlings produced in non-parasitized, non-removal parasitized, and parasite-egg removal broods. Counter to the goal of removing parasite eggs, the proportion of host eggs producing nestlings was lower in egg-removal nests than in non-removal parasitized nests. It is therefore concluded that at this locality, conservation management to remove the eggs of brood parasitic brown-headed cowbirds is unlikely to increase song sparrow productivity.

BACKGROUND

Brood parasitic birds, whether interspecific parasites laying their eggs in other species' nests or intraspecific parasites laying eggs in conspecific nests, depress the reproductive output of hosts. From a conservation perspective, most brood parasitic birds are native to their current geographic distribution, with several species facing significant population losses and having become the subject of protection (Eaton *et al.* 2009). In contrast, other brood parasitic birds have benefitted from anthropogenic changes and have become more common, been introduced, or invaded areas where they had not occurred prior to human activity (Moreno 1997).

The brown-headed cowbird *Molothrus ater* (hereafter: cowbird) has been gradually extending its North American distribution, having successfully expanded into new open-country habitats created by extensive forest loss and fragmentation, and an increase in cattle farming (Morrison *et al.* 1999). As a result, cowbirds now often parasitize several previously rarely used hosts and also frequently impact evolutionarily novel host species, which have no coevolved defenses against cowbird parasitism

(Rothstein 1994). Although cowbirds are protected by national laws in North America (Lowther 1993), exceptions to destroy cowbirds for conservation reasons are frequently granted. Conservation action to protect rare host species by reducing the impact of cowbird parasitism has typically employed the trapping of adult cowbirds in affected habitats or involved the selective removal of adult females within their breeding range (Smith *et al.* 2000). Removing and destroying adult cowbirds has met with variable conservation success in different sites (e.g., Stutchbury 1997 vs. Smith *et al.* 2002).

More labour intensive approaches aiming to reduce the impact of cowbirds on host breeding success are to remove parasite eggs or to prevent cowbird eggs from hatching by non-egg removal methods (e.g. piercing or shaking the egg but leaving them in the host nest) (Oppel *et al.* 2004). Neither of these methods fully recovers the cost of cowbird parasitism imposed by adult females as these typically remove one or more host eggs to lay their own (Sealy 1994). Despite the management expense and effort, conservation programs have sometimes resorted to apply the egg removal method in an attempt to locally rescue breeding attempts and increase host productivity (particularly for rare species). This is because, all else being equal, removing cowbird eggs should still increase host reproductive output by eliminating the earlier hatching, larger, and more intensively begging cowbird chick(s), lowering the egg-to-fledging success of hosts (Hauber 2003a). However, adult cowbirds can be predators of host nests that contain no cowbird eggs (Arcese *et al*. 1996) and may also retaliate against the removal of the cowbird egg(s) through destroying host eggs and chicks (Hoover & Robinson 2007). Alternatively, non-parasitized nests may be associated with more frequent predation compared to parasitized nests (Ortega 1998), if, for example, cowbirds preferentially lay in safer or less predator-accessible nests or parasitize hosts which provide better nest defense (Hauber 2001).

As a consequence, the removal of cowbird eggs may not yield higher nest survival and chick productivity rates of host nests compared to non-parasitized broods overall and should be the subject of local assessment and evaluation prior to any conservation-intended action. Methodologically, host productivity following the removal of cowbird eggs should thus be specifically evaluated relative to host productivity in parasitized nests with the cowbird egg(s) left intact.

Here I capitalized on published host nest productivity data collected on song sparrows *Melospiza melodia* in Ithaca, New York, USA (Hauber 2000), in connection with concurrent but unpublished data on this hosts' breeding success that were collected following the removal of parasite eggs for a separate study that required raising cowbirds in captivity (Hauber 2002). Song sparrows, though also protected under federal law, are not a species of conservation concern at this site (Hauber 2000). Nonetheless, my aim is to present the outcome of my actions as data for a case study to evaluate the effects of removing parasite cowbird eggs from song sparrow host nests at this locality.

ACTION

Study species and study site: Song sparrows are host to brown-headed cowbirds throughout North America, and successfully fledge both cowbird and their own chicks from parasitized broods (Tonra *et al*. 2008). However, song sparrows pay an additional cost for cowbird parasitism relative to other host taxa (Lorenzana & Sealy 1999), by having both fewer of their own eggs and lower egg-to-fledging survival ratios in parasitized nests compared to non-parasitized nests (Hauber 2003b). I located song sparrow (*M.m.melodia*) nests, established clutch size, and detected brown-headed cowbird parasitism throughout the 1997-1999 breeding seasons in the grassy fields of a research station at Cornell University, Ithaca, New York, USA, a site where this species is the predominant host of the cowbird. The host-parasite interactions and nest data collection protocols are described in detail elsewhere (Hauber & Russo 2000).

Egg removal: I removed all cowbird eggs (n = 7 nests) from a haphazard subset of parasitized song sparrow nests each year and each month (May- July) of study. Because cowbirds are protected by federal law, all egg removal was conducted as planned for a separate hand-rearing experiment of captive-hatched cowbirds under government and institutional permits for that study (Hauber 2002). Therefore, even though cowbird egg removal was not random, the schedule and choice of egg removals were not *a priori* confounded by the directional prediction

tested here that removing parasite eggs would increase host productivity. *Post-hoc* analyses of variance showed no statistical confounds of year and month of clutch completion on nestling numbers compared to all nests monitored at this site (all $F < 1.7$, $P > 0.18$, see below). Furthermore, both egg-removal and non-removal parasitized nests had a median of 1 cowbird egg ($Z = 0.42$, $P = 0.97$).

Monitoring: All nests with egg removal were checked until the numbers of 5 day old (day 1 = day of hatching) song sparrow nestlings could be determined. Nests that were preyed upon or had eggs or chicks otherwise destroyed had 0 nestlings assigned. Nest checks were not conducted later so as to reduce premature fledging (i.e. accidentally inducing young approaching fledging age to leave the nest prematurely through nest disturbance) but in a previous study fledging success per parasitized nests correlated strongly and positively with the number of 5 day old cowbird host nestlings (Hauber 2003b). As comparisons, I used published data collected concurrently at the same study site (Hauber 2000) from two groups of unmanipulated nests with comparable monitoring effort and information available regarding complete clutch sizes and 5 day old nestling numbers; nests that were naturally not parasitized (n = 31) and nests that were naturally parasitized (n =11).

Evaluation: To evaluate host productivity in egg-removal nests relative to the two types of unmanipulated nests, I used a contingency analysis to compare the proportions of host nests producing any host chicks and conducted a two-tailed Kruskal-Wallis analysis of variance of the numbers song sparrow eggs at clutch completion and the numbers of song sparrow nestlings. The proportions of host eggs that produced nestlings per each nest was also calculated. A one-tailed Mann-Whitney test was used to evaluate the prediction that removing cowbird eggs increases the proportions of host eggs producing nestlings between egg-removal and non-removal parasitized nests. Statistical analyses were undertaken using Statview 5.0.1; non-parametric tests were applied because egg and nestling numbers were discontinuously distributed, while egg-to-nestling survival data were calculated as proportional values.

CONSEQUENCES

Of the total sample of 49 nests included in the experiment, 23 (47%) contained 5-day old song sparrow nestlings. Hatchling presence did not significantly covary with parasitism and egg removal status of the nests (non-parasitized: 48% (15 of 31) of nests contained sparrow nestlings; parasitized: 63% (7 of 11); and egg-removal: 29% (2 of 7), ($G^2 = 2.2$, $P = 0.34$).

Natural cases of brown-headed cowbird parasitism on song sparrows were associated with significantly fewer host eggs ($H = 17.2$, $P = 0.0002$), this being most likely attributable to one or two sparrow eggs being removed by female cowbirds (Sealy 1994). There was a median clutch size of five sparrow eggs in non-parasitized nests and three host eggs and one parasite egg each in both egg-removal and non-removal parasitized nests. In contrast, the numbers of song sparrow nestlings surviving to day 5 were statistically similar across all three nest types, irrespective of parasitism or egg-removal status. There was a median of no host nestlings produced in both non-parasitized and egg-removal nests and one host nestling in parasitized non-removal nests ($H = 1.97$, $P = 0.37$).

When limiting the analysis to those few nests only which produced any host chicks, non-parasitized nests had a median of four song sparrow nestlings, while parasitized and egg-removal nests each had a median of two host chicks ($H = 7.58$, $P = 0.026$) and non-removal parasitized nests had a median of 1 cowbird chick. Figure 1 shows the mean (+ SD) number of song sparrow eggs and 5-day old nestlings produced for each nest type across failed and surviving nests combined.

Amongst parasitized nests only, the proportion of host eggs producing nestlings was significantly lower for egg-removal than non-removal nests of ($Z = 1.76$, $P = 0.039$), with a median of 0% of host eggs producing nestlings in egg-removal nests and 75% of host eggs producing nestlings in non-removal nests.

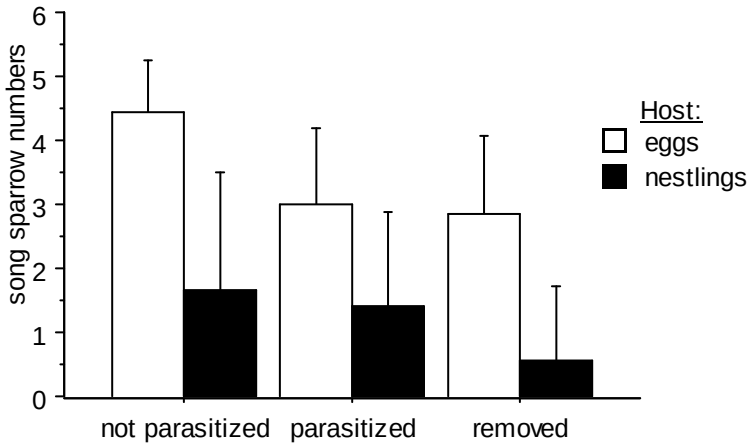

Figure 1. Variation in the mean (+SD) numbers of eggs and 5-day old host song sparrow nestlings according to brown-headed cowbird parasitism status and experimental parasite egg removal treatment in Ithaca, New York, USA.

Discussion: Contrary to the predicted outcome of increasing song sparrow productivity in parasitized nests by removing brown-headed cowbird eggs, no statistically significant differences were apparent in the numbers of host nestlings (to day 5) across nests with or without cowbird eggs and irrespective of egg-removal treatment. However, despite of the small sample sizes in the egg-removal treatment, of note was that the removal of parasite eggs was associated with a lower proportion of host eggs producing 5-day old nestlings than in broods with cowbird eggs left behind.

Although these patterns are consistent with the scenario that adult brown-headed cowbirds act as predators on song sparrow nests without parasite eggs at the Ithaca site (Hauber 2000), including nests with removal of the parasite eggs (this study), the limitations of my results include the small sample sizes involved in the egg-removal treatment and the lack of information on the causes of full and partial nest failures in each of the three host nest groups (Sealy 1994), including the number of different predators and parasites involved in putative nest predation events (Arcese *et al*. 1996). Also, the sex of the host chicks was not determined in this study, even though cowbirds are known to skew the sex ratio of surviving host chicks (Zanette *et al.* 2005) and sex-ratio biases in productivity may have critical impacts upon conservation management (Clout *et al*. 2002). From a potential conservation action perspective, it still remains to be determined if locally breeding cowbirds at the Ithaca locality might i) actively retaliate against experimental egg removal as seen by this parasite acting on other hosts in other localities (Hoover & Robinson 2007), ii) follow a general "farming" approach and destroy host nests without parasites so as to utilize hosts' re-nesting attempts for subsequent parasitism (Hoover *et al.* 2006), or iii) are not directly causing or indirectly facilitating the failure of non-parasitized host nests (McLaren & Sealy 2000).

Recommendation: Brood parasitism represents a complex set of behavioral and ecological contexts in which host nests cannot be considered as the unit of conservation action. Management plans are best formulated with an integrative approach by combining information about the habitat, the local host and the predator communities, and the behavioural tactics of the adult parasites and the affected hosts.

ACKNOWLEDGEMENTS

Financial support was provided by the Howard Hughes Medical Institute and the Human Frontier Science Program. For discussions and comments, I thank Zak Aidala, Beki Croston, Jim Dale, Steve Emlen, Jeff Hoover, Arnon Lotem, Paul Sherman, Dave Showler, David Winkler, and referees.

REFERENCES

Arcese P., Smith J.N.M. & Hatch J.I. (1996) Nest predation by cowbirds, and its consequences for passerine demography. *Proceeding of the National Academy of Sciences USA*, **93**, 4608-4611.

Clout M.N., Elliott G.P. & Robertson B.C. (2002) Effects of supplementary feeding on the offspring sex ratio of kakapo: a dilemma for the conservation of a polygynous parrot. *Biological Conservation*, **107**, 13-18.

Eaton M.A., Brown A.F., Noble D.G., Musgrove A., Hearn R.D., Aebischer N., Gibbons D.W., Evans A & Gregory R.D. (2009) Birds of Conservation Concern 3: the population status of birds in the United Kingdom, Channel Islands and Isle of Man. *British Birds*, **102**, 296-341.

Hauber M.E. (2000) Nest predation and cowbird parasitism in song sparrows. *Journal of Field Ornithology*, **71**, 389-398.

Hauber M.E. (2001) Site selection and repeatability in brown-headed cowbird (*Molothrus ater*) parasitism of Eastern phoebe (*Sayornis phoebe*) nests. *Canadian Journal of Zoology*, **79,** 1518-1523.

Hauber ME. (2002) First contact: conspecific social association and species recognition in brood parasites. *Annales Zoologici Fennici*, **39**, 291-305.

Hauber ME. (2003a) Egg-capping is a cost paid by hosts of interspecific brood parasites. *Auk*, **120**, 860-865.

Hauber M.E. (2003b) Hatching asynchrony, nestling competition, and the cost of interspecific brood parasitism. *Behavioral Ecology*, **14**, 224-235.

Hoover J.P. & Robinson S.K. (2007) Retaliatory mafia behavior by a parasitic cowbird favors host acceptance of parasitic eggs. *Proceedings of the National Academy of Sciences USA*, **104**, 4479-4483.

Hoover J.P., Yasukawa K. & Hauber M.E. (2006) Spatial and temporal structure of avian brood parasitism affects the fitness benefits of egg ejection and nest abandonment. *Animal Behaviour*, **72**, 881-890.

Kus B.E. & Whitfield M.J. (2005) Parasitism, productivity, and population growth: response of Least Bell's vireos (*Vireo bellii pusillus*) and Southwestern willow flycatchers (*Empidonax traillii extimus*) to cowbird (*Molothrus* spp.) control. *Ornithological Monographs*, **57**, 16-27.

Lorenzana J.C. & Sealy S.G. (1999) A meta-analysis of the impact of parasitism by the brown-headed cowbird on its hosts. *Studies in Avian Biology*, **18**, 241-253.

Lowther P.E. (1993) Brown-headed cowbird (*Molothrus ater*). In: *The birds of North America*. A. Poole & F. Gill (Eds.), No. 47. Academy of Natural Sciences, Philadelphia, USA.

McLaren C.M. & Sealy S.G. (2000) Are nest predation and brood parasitism correlated in yellow warblers? A test of the cowbird predation hypothesis. *Auk*, **117**, 1056-1060.

Moreno J.A. (1997) Review of the subspecific status and origin of introduced finches in Puerto Rico. *Caribbean Journal of Science*, **33**, 233-238.

Morrison L.S., Hall S.K. Robinson S.I., Rothstein D.C., Hahn, D.C. & Rich T.D. (eds.) (1999) Research and management of the brown-headed cowbird in Western landscapes. *Studies in Avian Biology*, **18**, 1-312.

Oppel S., Schaefer H.M., Schmidt V. & Schroder B. (2004) Cowbird parasitism of pale-headed brush-finch *Atlapetes pallidiceps*: implications for conservation and management. *Bird Conservation International*, **14**, 63-75.

Ortega CP. (1998) *Cowbirds and other brood parasites.* University of Arizona Press, Tucson, USA.

Rothstein S.I. (1994) The cowbird's invasion of the Far West: history, causes and consequences experienced by host species. *Studies in Avian Biology*, **15**, 301-315.

Sealy S.G. (1994) Observed acts of egg destruction, egg removal, and predation on nests of passerine birds at Delta Marsh, Manitoba. *Canadian Field Naturalist*, **108**, 41-51.

Smith J.N.M., Cook T.L., Rothstein S.I., Robinson S.K. & Sealy S.G. (eds.) (2000)

Ecology and management of cowbirds and their hosts. University of Texas Press, Austin, USA.

Smith J.N.M., Taitt M.J. & Zanette L. (2002) Removing brown-headed cowbirds increases seasonal fecundity and population growth in song sparrows. *Ecology*, **83**, 3037-3047.

Stutchbury B.J.M. (1997) Effects of female cowbird removal on reproductive success of hooded warblers. *Wilson Bulletin*, **109,** 74-81.

Tonra C.M., Hauber M.E., Heath S.K. & Johnson M.D. (2008) Ecological correlates and sex differences in early development of a generalist brood parasite. *Auk*, **125**, 205-213.

Zanette L., MacDougall-Shakleton E., Clinchy M. & Smith J.N.M. (2005) Brown-headed cowbirds skew host offspring sex ratios. *Ecology*, **86**, 815-820.