Chinese Birds 2013, 4(1):31–38
DOI 10.5122/cbirds.2013.0005

REVIEW

Does landscape structure contribute to the long-term maintenance of generalized parasitism in cowbirds?

Scott ROBINSON [1,✉], **Wendy SCHELSKY** [2], **Jeffrey HOOVER** [2]

[1] Florida Museum of Natural History, University of Florida, Museum Road at Newell Drive, Gainesville, Florida, United States
[2] Illinois Natural History Survey, Prairie Research Institute, University of Illinois, 1816 South Oak Street, Champaign, Illinois, United States

Abstract Unlike most brood parasites, several species of cowbird (*Molothrus*) are generalists that parasitize multiple host species across their range and within the same communities; likewise, there is little evidence that individuals within a population specialize on host species. This situation has variously been attributed to the recency of cowbird evolution (the "evolutionary lag" hypothesis) or to hidden costs of rejection by hosts (the "equilibrium" hypothesis). Both hypotheses have some support as cowbirds are indeed a relatively young clade compared with more specialized cuckoos and cowbirds are capable of sophisticated behaviors such as retaliation against rejection ("mafia" behaviors) that would select for acceptance of cowbird eggs. Nevertheless, many species in the Americas have evolved specialized defenses against cowbird parasitism, almost all of which live in more open habitats (e. g., grasslands, shrublands, riparian strips), which indicates that coevolutionary processes can operate in ways that select for host defenses in spite of cowbird counterdefenses. We propose that the structure of landscapes in North America may explain why forest-nesting birds lack defenses against parasitism and reinforce the long-term maintenance of generalized brood parasitism in cowbirds. Because cowbirds require open habitats in which to feed, they are rare or absent in large forest tracts, which dominate much of the forest cover of the Americas. These tracts act as "source habitats" that produce surplus young that recolonize populations in smaller, fragmented forest patches in which rates of both cowbird parasitism and nest predation are very high ("sink" habitats). Evolution of anti-parasite adaptations would be very slow in this situation because most hosts are produced in areas where there is little or no cowbird parasitism. In addition, the interplay of host breeding dispersal, source-sink metapopulation dynamics, and fragmented forest habitat could further deter the evolution of host defenses against parasitism. Therefore, as long as large forest tracts remain widespread in North America, most forest birds will likely continue to lack defenses against cowbird parasitism, guaranteeing a steady supply of naïve hosts in forest habitats, even in fragmented landscapes. This situation will, in turn, favor host generalist cowbirds that actively avoid more open habitats in favor of parasitizing forest bird communities. These forest communities may also act as source populations for cowbirds, which might pump surplus generalist cowbirds into more open habitats further slowing the coevolutionary process. As long as large forest tracts are a common part of the landscape, generalist parasitism may persist indefinitely.

Keywords brood parasitism, cowbird, forest fragmentation, geographic mosaic theory of coevolution, nest predation, source-sink metapopulation dynamics

Introduction

Most cowbirds in the genus *Molothrus* are host generalists (Rothstein and Robinson, 1998; Davies, 2000).

Received 25 December 2012; accepted 24 February 2013

✉ Author for correspondence (Scott Robinson)
E-mail: srobinson@flmnh.ufl.edu

Some species of cowbirds have more than 200 known hosts (*M. bonariensis* with over 250 and *M. ater* with more than 200) and individual cowbirds are known to parasitize multiple host species (Woolfenden et al., 2003; Strausberger and Ashley, 2005). The maintenance of this system has long puzzled students of brood parasitism because coevolutionary processes should lead to the kinds of specialization documented in most other brood parasites (Davies, 2000). Three nonexclusive hypotheses have been proposed to explain the evolution and maintenance of generalized brood parasitism, each of which has some empirical support.

The first of these hypotheses, the evolutionary lag hypothesis, proposes that cowbirds are a young lineage that has only recently come into contact with hosts, especially those in forest habitats (Rothstein and Robinson, 1998). Unlike most brood parasites, cowbirds do not feed in the same habitats where most of their hosts reside (reviewed in Robinson and Hoover, 2011). Instead, they feed largely in open habitats such as grasslands and in the company of grazing ungulates (hence the name cowbird) that create the short grass or bare ground where cowbirds feed. They then commute up to 15 km (Goguen and Matthews, 2001) to sites where their hosts breed in search of nests to parasitize. As a result, the deforestation and fragmentation of habitats in much of North America following settlement by Europeans (and, for that matter from the indigenous populations of Native Americans) created conditions that were very favorable for the cowbird by exposing them to many forest-nesting hosts that previously would have had only very limited contact with brood parasitism (Rothstein and Robinson, 1998). In this view, naïve forest hosts simply have not yet had the time to evolve defenses against parasitism because the contact has been so recent (Rothstein and Robinson, 1998).

The second hypothesis, the equilibrium hypothesis, proposes that defenses against cowbirds have costs that slow the rate of evolution of host defenses (reviewed in Davies, 2000). Unlike cuckoos and several other brood parasites in which the chicks kill all of their nestmates, cowbird nestlings do not kill their nestmates, which makes it possible for some host young to fledge from parasitized nests. Therefore, the costs of rejecting eggs (e. g., damage to host eggs, errors made while ejecting eggs) may outweigh the costs of raising cowbird chicks. Recent studies showing that cowbirds are capable of using "mafia" tactics and might even "farm" unparasitized nests would further add to the cost of ejecting cowbird eggs and slow or even stop coevolutionary processes in many species (Hoover and Robinson, 2007). Although smaller hosts that rarely raise any host young from parasitized nests might still be under intense selection to reject cowbird eggs, many larger hosts in communities might accept cowbird eggs further favoring more generalized parasitism by cowbirds.

The third hypothesis fits nicely within the geographic mosaic theory of coevolution (GMTC) (Thompson, 1999) and proposes that acceptance of costly brood parasitism persists for many species because of non-random gene flow between parasitized and non-parasitized lineages of hosts (Briskie et al., 1992; Grim, 2002; Røskaft et al., 2002) that is driven by source-sink metapopulation dynamics of both cowbirds and their forest hosts. According to the GMTC, coevolutionary dynamics are driven by three components of geographic structure: selection mosaics, coevolutionary hot spots, and trait remixing through gene flow. In theory, cowbird and forest-host population dynamics meet many of the criteria put forth by the GMTC such as selection mosaics driven by negative correlations between forest patch size or amount of forest in a landscape and cowbird parasitism (Donovan et al., 1995; Robinson et al., 1995a, 2000), the presence of coevolutionary hotspots where reciprocal selection between cowbirds and their hosts can occur (i.e. sinks; Robinson and Hoover, 2011), and moderate gene flow between host metapopulations (Veit et al., 2005; Colbeck et al., 2008). Source-sink metapopulation dynamics of cowbirds and their forest hosts can best be understood as a structured landscape of "hot" (i.e. sinks) and "cold" (i.e. sources) spots of reciprocal selection or coevolution. In general, even with a rare number of hot spots and moderate gene flow, there should eventually be a stable equilibrium of coevolved traits in the host population (Gomulkiewicz et al., 2000). The problem for forest birds in North America stems from the fact that most population-level selection on hosts occurs in population sources because the majority of host offspring are produced there. It is these offspring that later repopulate sinks (Pulliam, 1988; Robinson and Hoover, 2011) which can ultimately swamp out any selection towards coevolved traits in sink habitat. Indeed, several studies have shown that rejecter traits can arise in hot spots in sympatric host and parasite populations and be less common or absent in allopatric populations (Briskie et al., 1992; Martinez et al., 1999; Soler et al., 1999; Lindholm and Thomas, 2000; Røskaft et al., 2006). Of these examples, however, several were from European host-brood parasite systems (Martinez et al., 1999; Soler et al., 1999; Lindholm and Thomas, 2000; Røskaft et al., 2006), or from North American species which occur in more open habitats (Briskie et al., 1992), and all could point to gene flow from hot to cold spots as a primary explanation for the distribution of rejecter traits throughout the host population. The source-sink metapopulation dynamics of forest hosts could be dominated by restricted gene flow, primarily from sources to sinks, and could account for the current lack of defenses against brood parasites.

Clearly, the existence of host defenses in many cowbird hosts shows that coevolutionary processes can occur and that many species can circumvent cowbird adaptations, which indicates that the equilibrium hypothesis does not apply to all host species. Yet, the vast majority of the species that show host defenses nest in more open or second-growth habitats and the vast majority of species that nest only in forests show no evidence of effective defenses against cowbirds (Robinson et al., 1999). This might suggest that the evolutionary lag hypothesis is more plausible assuming that forest fragmentation is a recent phenomenon that has only exposed hosts to contact with heavy selective pressure from cowbird parasitism since human settlement of North America. Yet, if we take a deeper look at the history of forest cover in North America, there are reasons to suspect that forests might have been much more fragmented in the past. The diverse North American megafauna that disappeared coincident with the arrival of humans to North America (Ripple and Van Valkenburgh, 2010) likely would have greatly altered the forest cover of North America, especially considering the ecosystem-level effects of megaherbivores elsewhere in the world. Furthermore, the very limited distribution of forests during the peak of the ice ages in the past (Delcourt and Delcourt, 1987) further suggests that for extended periods, the forest cover of North America may have consisted of small patches in refugia where megaherbivores might have created sufficient internal disturbance to expose forest patches further to cowbird parasitism. Indeed, an entire genus of cowbirds became extinct at the same time that the North American megafauna became extinct (Steadman and Martin, 1984). Therefore, it is quite possible that even forest hosts have long been exposed to selection pressure related to cowbird parasitism.

In this paper, we propose that the spatial distribution of forest cover contributes to the maintenance of generalist brood parasitism in cowbirds. Furthermore, we predict that coevolutionary processes may essentially have halted in the current landscapes of the Americas. We develop our model mainly for eastern North America, but we suspect that the same arguments would apply to other landscapes where there are still large, unfragmented forest tracts. These arguments build upon the framework of Røskaft et al. (2002, 2006) and Robinson and Hoover (2011) and others who have hypothesized that the extent to which landscapes are structured as source and sink habitats profoundly affects the evolution of adaptive traits.

Our hypothesis is based on the following processes and assumptions:

(1) There is little or no selection for host defenses against cowbird parasitism in areas where most forest hosts breed. Although forest fragmentation is widespread in much of North America, much of the actual area of forest is tied up in large forest tracts where there is very little cowbird feeding habitat. Even in the famously fragmented forests of the American Midwest, there are still large forest tracts consisting of millions of hectares with only small openings where cowbirds feed (Robinson et al., 1995b). Even though cowbirds can commute long distances in search of hosts, parasitism levels in these forests are extremely low, apparently because cowbird populations are limited by feeding habitat (reviewed in Chace et al., 2005). Therefore, there is essentially no selection for host defenses against parasitism in large areas of forest. The small forest tracts in which cowbird parasitism levels are high may, in aggregate, represent only a small portion of the forest available in most areas. Unfortunately, we can find no data on the proportion of the forest cover of eastern North America tied up in forest tracts of different sizes, but even a cursory examination of the maps of forest cover of eastern North America show that much of the forest cover of North America is in areas where forests dominate entire landscapes (e.g., the Appalachians, New England, the Ozarks). Therefore, the selection mosaic for host defenses against cowbird parasitism within the majority of forested habitats would be absent or negligible at best.

(2) In areas where cowbird parasitism is high, nest predation rates also tend to be high. Nest predation and brood parasitism levels are strongly positively correlated with levels of fragmentation such that areas with high levels of brood parasitism also have high levels of nest predation. This situation has been very well documented in eastern North America (Robinson and Hoover, 2011), but may not apply to more western landscapes in which many forest-interior nest predators are actually rarer in fragmented landscapes (Tewksbury et al., 1998; Robinson and Hoover, 2011).

(3) Forest landscapes consist of sources and sinks as a result of the combined effects of cowbird parasitism and nest predation. The evidence for source-sink metapopulation dynamics (Pulliam, 1988) in forest birds has been reviewed recently (Robinson and Hoover, 2011). Data from models (Brawn and Robinson, 1996) and from empirical studies measuring output from marked populations (e.g., Trine, 1998) strongly suggest that fragmented landscapes consist of a mosaic of sources (reproductive output is above levels necessary to replace losses caused by mortality) and sinks (reproductive output is insufficient to compensate for mortality). Cowbird parasitism and elevated levels of nest predation both contribute to the likely sink status of many smaller forest tracts (Robinson et al., 1995b; Trine, 1998; Hoover and Brittingham, 1993; Hoover et al., 1995, 2006a; reviewed in Robinson and Hoover, 2011). Cowbirds may be especially problematic because they may not trigger host emigration from sites. Most species have adaptations for avoiding areas with high nest predation rates (decision rules, conspecific attraction) and finding and remaining in areas where nest predation rates are low (Hoover, 2003a; Ward and Schlossburg, 2004). There may not be any such adaptations, however, to avoid cowbird parasitism directly (Hoover, 2003b). Areas with high parasitism and low nest predation (e.g., Tewksbury et al., 1998) therefore may actually create ecological traps that can drain populations of hosts by continuing to attract naïve immigrants but serve as source areas for cowbirds.

(4) Small forest tracts have so little reproductive output that they qualify as "black hole" sinks (Holt, 1996; Holt and Gomulkiewicz, 1997). Although identifying source-sink thresholds is difficult because we know little about juvenile mortality (Robinson and Hoover 2011), reproductive output from small forest fragments is often (but not always: Friesen et al., 1999; Fauth, 2001) so low that they qualify as "black hole" sinks in which essentially no host young are produced. In metapopulations consisting of sources and black hole sinks, evolution of adaptive traits is greatly slowed (Holt and Gomulkiewicz, 1997), which would further slow the evolution of host defenses against brood parasitism.

(5) Cowbirds parasitizing nests in forest habitats are much more productive than those in more open habitats. Because most forest birds lack host defenses, cowbird productivity per parasitized nest in forest habitats is likely to be much higher than in more open habitats where many hosts have defenses against cowbird parasitism (Robinson et al., 1999). Given the extremely high nest predation levels that characterize many open habitats (Robinson et al., 1999), such second-growth or edge habitats may even act as population sinks for cowbirds (Winfree et al., 2006), although such calculations depend upon many variables such as cowbird fecundity that are not well known and on the proportion of forest hosts that nest close enough to cowbird feeding habitat to be accessible to cowbirds.

(6) Asymmetric gene flow from sources to sinks results in a lack of genetic structure among populations of forest hosts, but swamps out selection of host defenses in sinks. An important condition associated with the hypothesis that source-sink metapopulation dynamics can slow the evolution of host defenses against cowbird parasitism is that there is extensive asymmetric gene flow among populations. If defenses against cowbird parasitism were to arise, they would do so in habitat sinks where rates of parasitism are highest and reproductive success of hosts is the lowest. Maintenance of host populations in sinks is typically a function of naïve host progeny moving from sources, where selection for defenses against cowbird parasitism is largely absent, to sinks. Consistent gene flow of host progeny (i.e. juvenile dispersal) from sources to sinks will perpetually overwhelm any host defenses against parasitism that may arise. Indeed, sufficient gene flow to connect host species populations across their range has been confirmed in a variety of studies focused on genetic structure in migratory forest-dwelling species (Veit et al., 2005; Colbeck et al., 2008), but local movements of host progeny from sinks to sources may be lacking (Hoover and Reetz, 2006; Hoover and Hauber, 2007). Results of these studies indicate that populations within many host species interact genetically over vast (hundreds of kilometers) distances that would encompass much source and sink forest habitat, but the potential unidirectional movement of host progeny from source to sink populations may overwhelm any appearance of host defenses.

If the above assumptions and conditions are met, then generalist brood parasites may have a reproductive advantage over host specialists in any landscape in which large forest tracts remain. For host species, the reproductive advantage of nesting in larger tracts, where rates of nest predation and cowbird parasitism are low, would continue to slow the rate of evolution of anti-parasite defenses. Gene flow from larger tracts would likely swamp any selection for anti-parasite defenses in smaller tracts where nest predation and brood parasitism further diminish reproductive output.

If there is a strong learned component of rejection behaviors of hosts, this might also slow the rate of evolution of host defenses against cowbirds. Egg recognition in hosts, perhaps a learned behavior, is thought to be a critical step in the evolution of anti-parasite behaviors (Rothstein, 1974, 1978; Lotem et al., 1992, 1995; Moskát et al., 2010). Individual birds may use template-based recognition to learn which eggs to accept in their clutches (e.g. clutch-learning: Lawes and Marthews, 2003). Clutch-learning is the process whereby young birds imprint on the eggs present in the clutch of their first ever breeding attempt and accept that variability in egg appearance thereafter. If sinks are predominantly (re-) populated by first-time breeders produced in sources, and these young birds use some form of clutch-learning, then high rates of cowbird parasitism in sinks would result in those parasitized individuals accepting brood parasitism thereafter. This hypothesis, however, has not yet been tested.

Learning-based decision rules governing site fidelity and dispersal may further interact with learned egg-recognition to slow the evolution of host defenses. Forests that are sinks for hosts are usually categorized as such primarily because of high rates of nest predation. Many forest birds use experience-based decision rules in association with breeding dispersal to move between breeding seasons away from sinks following reproductive failure caused by nest predation (Hoover, 2003a) and may use the presence of conspecifics to subsequently settle in sources (Ward and Schlossberg, 2004). Hosts breeding in sources are likely to return to those sources following successful reproduction (Hoover, 2003a). The interplay of source-sink dynamics, clutch-learning, and breeding dispersal would lead many of the surplus host young produced in sources to 1) breed for the first time in sinks, 2) learn to accept cowbird eggs because many/most nests in sinks are parasitized, 3) experience reproductive failure because of nest predation, 4) disperse away from sinks and towards sources, and 5) end up as acceptors in source habitat thereby further diminishing the potential for the evolution of anti-parasite defenses.

Caveats/alternative scenarios favoring host-parasite coevolution

If any of the critical assumptions for our model are violated, then coevolutionary processes could proceed and lead to the evolution of host defenses and specialization by cowbirds. In western landscapes of North America, for example, nest predation rates are at least sometimes lower in fragmented forests because the most frequent nest predators are negatively affected by forest fragmentation (Cavitt and Martin, 2002; reviewed in Robinson and Hoover, 2011). In this scenario, the evolution of host defenses and specialization might actually be accelerated. Because many birds base their site fidelity and dispersal on the number of successful nesting attempts in a site, hosts may be continuously attracted to small forest tracts where nest predation rates are low enough to allow many host pairs to produce one or more successful nests per season. Even though the hosts may produce fewer host young per successful nest in small tracts as a result of cowbird parasitism, the successful hosts would be more likely to return to the site, which might further attract dispersing young to sites with large numbers of returning breeders. In this scenario, there would be extremely strong selection for defenses by hosts that showed any defenses against cowbird parasitism, the essential first step in the coevolutionary process. In such landscapes, cross-generational exposure to parasitism would continually enhance the coevolutionary process. If this pattern of reduced nest predation in smaller forest tracts is generally true in western North America, then we predict that forest hosts in western landscapes would be more likely to have host defenses than those in eastern landscapes of North America where high nest predation and brood parasitism rates go hand in hand.

Before we can fully assess the generality of our model, it is important to recognize that there is still a great deal that we do not know about the behavior of individual cowbirds in complex landscapes. Cowbirds as a species are host generalists, but we know little about whether individual female cowbirds are more specialized and focus on particular habitats (Teuschl et al., 1998), on one or many host species, or whether habitat or host use changes during the lifetime of a female. We also do not know whether young cowbirds imprint on habitat, specific hosts or the larger host community during their early development and what role this plays in their subsequent choices of habitat and hosts when parasitizing nests. Female cowbirds should parasitize hosts that provide the greatest lifetime reproductive success, but they may be constrained by which habitat and host they came from if there is an effect of that early experience on later breeding behavior. If many or most cowbirds are produced by the diverse species of naïve forest-dwelling hosts (i.e. migratory songbirds), then use of forests and forest hosts by cowbirds would continually be reinforced favoring cowbirds that specialize on forest habitat (Hahn and Hatfield, 1995) but continue to be generalists in terms of using hosts within the forest. Cowbirds nesting in more open habitats where many species have host defenses against cowbirds, however, might be more likely to evolve host specialization if the cowbirds actively select the host that raised them. As long as rates of nest predation remain generally high in small tracts of forest and near forest edges, and low in the interiors of large tracts of forest, selection may favor cowbirds venturing farther into source forest habitat as limited by the energetic costs of moving between foraging and egg laying areas. Were this to happen, it would increase the likelihood of the evolution of host defenses against cowbird parasitism in forest hosts.

Conclusions

Spatially structured and temporally consistent cowbird parasitism has the potential to affect the fitness benefits of rejection strategies in hosts (Hauber et al., 2004; Hoover et al., 2006b) and differences in virulence between different avian brood parasite species (Hoover and Hauber, 2007). Spatially structured and temporally consistent nest predation and cowbird parasitism within fragmented forests in combination with source-sink metapopulation dynamics of hosts may further affect the pace of the evolution of anti-parasite strategies in forest hosts and the propensity for cowbirds to remain a host generalist brood parasite. As long as rates of nest predation and cowbird parasitism remain highly correlated across landscapes comprising source and sink forest habitat for breeding birds, source-sink metapopulation dynamics will continue to play a part in slowing the evolution of anti-parasite behaviors in forest hosts. Given the apparent lack of genetic structure and ample gene flow in many species of forest-dwelling hosts, it likely would take the uncoupling of nest predation and cowbird parasitism over large portions of host geographic ranges to increase the chances of host defenses against parasitism evolving and withstanding the introgression of acceptor genes from distant populations.

References

Brawn JD, Robinson SK. 1996. Source-sink dynamics may complicate the interpretation of long-term census data. Ecology, 77:3–12.

Briskie JV, Sealy SG, Hobson KA. 1992. Behavioral defenses against avian brood parasitism in sympatric and allopatric host populations. Evolution, 46:334–340.

Cavitt JF, Martin TE. 2002. Effects of forest fragmentation on brood parasitism and nest predation in eastern and western landscapes. Stud Avian Biol, 25:73–80.

Chace JF, Farmer C, Winfree R, Curson DR, Jense WE, Goguen CB, Robinson SK. 2005. Cowbird ecology: a review of factors influencing distribution and abundance of cowbirds across spatial scales. Orn Monogr, 57:45–70.

Colbeck GJ, Gibbs HL, Marra PP, Hobson K, Webster MS. 2008. Phylogeography of a widespread North American migratory songbird (*Setophaga ruticilla*). J Hered, 99:453–463.

Davies NB. 2000. Cuckoos, Cowbirds and Other Cheats. T & AD Poyser, London.

Delcourt PA, Delcourt H. 1987. Long Term Forest Dynamics: A Case Study of Late-Quaternary Forests in Eastern North America. Ecological Studies 63. Springer-Verlag, New York.

Donovan TM, Lamberson RH, Kimber A, Thompson III FR, Faaborg J. 1995. Modeling the effects of habitat fragmentation on source and sink demography of neotropical migrant birds. Cons Biol, 9:1396–1407.

Fauth PT. 2001. Wood thrush populations are not all sinks in the agricultural Midwestern United States. Conserv Biol, 15:523–527.

Friesen L, Cadman MD, Mackay RJ. 1999. Nesting success of neotropical migrant songbirds in a highly fragmented landscape. Conserv Biol, 13:338–346.

Goguen CB, Mathews NE. 2001. Brown-headed cowbird behavior and movements in relation to livestock grazing. Ecol Appl, 11:1533–1544.

Gomulkiewicz R, Thompson JN, Holt RD, Nuismer SL, Hochberg, ME. 2000. Hot spots, cold spots, and the geographic mosaic theory of coevolution. Am Nat, 156:156–174.

Grim T. 2002. Why is mimicry in cuckoo eggs sometimes so poor? J Avian Biol, 33:302–305.

Hahn DC, Hatfield JS. 1995. Parasitism at the landscape scale: cowbirds prefer forests. Conserv Biol, 9:1415–1424.

Hauber ME, Yeh PJ, Roberts JOL. 2004. Patterns and coevolutionary consequences of repeated brood parasitism. Proc R Soc Lond B, 271:S317–S320.

Holt RD. 1996. Adaptive evolution in source-sink environments: direct and indirect effects of density-dependence on niche evolution. Oikos, 75:182–192.

Holt RD, Gomulkiewicz R. 1997. How does immigration influence local adaptation: A reexamination of a familiar paradigm. Am Nat, 149:563–572.

Hoover JP. 2003a. Decision rules for site fidelity in a migratory bird, the prothonotary warbler. Ecology, 84:416–430.

Hoover JP. 2003b. Experiments and observations of prothonotary warblers indicate a lack of adaptive responses to brood parasitism. Anim Behav, 65:935–944.

Hoover JP, Brittingham MC. 1993. Regional variation in cowbird parasitism of wood thrushes. Wilson Bull, 105:228–238.

Hoover JP, Hauber ME. 2007. Individual patterns of habitat and nest-site use by hosts promote transgenerational transmission of avian brood parasitism status. J Anim Ecol, 76:1208–1214.

Hoover JP, Reetz MJ. 2006. Brood parasitism increases provisioning rate, and reduces offspring recruitment and adult return rates, in a cowbird host. Oecologia, 149:165–173.

Hoover JP, Robinson SK. 2007. Retaliatory mafia behavior in a parasitic cowbird favors host acceptance of parasitic eggs. Proc Natl Acad Sci USA, 104:4479–4483.

Hoover JP, Brittingham MC, Goodrich LJ. 1995. Effects of forest patch size on nesting success of wood thrushes. Auk, 112:146–155.

Hoover JP, Tear TH, Baltz M. 2006a. Edge effects reduce the nesting success of Acadian Flycatchers in a moderately fragmented forest. J Field Ornith, 77:425–436.

Hoover JP, Yasukawa K, Hauber ME. 2006b. Spatially and temporally structured avian brood parasitism affects the fitness benefits of hosts' rejection strategies. Anim Behav, 72:881–890.

Lawes MJ, Marthews TR. 2003. When will rejection of parasite nestlings by hosts of nonevicting avian brood parasites be favored? A misimprinting-equilibrium model. Behav Ecol, 14:757–770.

Lindholm AK, Thomas RJ. 2000. Differences between populations of reed warblers in defences against brood parasitism. Behaviour, 137:25–42.

Lotem A, Nakamura H, Zahavi A. 1992. Rejection of cuckoo eggs in relation to host age: a possible evolutionary equilibrium. Behav Ecol, 3:128–132.

Lotem A, Nakamura H, Zahavi A. 1995. Constraints on egg discrimination and cuckoo-host co-evolution. Anim Behav, 49:1185–1209.

Martínez JG, Soler JJ, Soler M, Møller AP, Burke T. 1999. Comparative population structure and gene flow of a brood parasite, the Great Spotted Cuckoo (*Clamator glandarius*), and its primary host, the Magpie (*Pica pica*). Evolution, 53:269–278.

Moskát C, Bán M, Székely T, Komdeur J, Lucassen RWG, van Boheemen LA, Hauber ME. 2010. Discordancy or template-based recognition? Dissecting the cognitive basis of the rejection of foreign eggs in hosts of avian brood parasites. J Exp Biol, 213:1976–1983.

Pulliam HR. 1988. Sources, sinks, and population regulation. Am Nat, 132:652–661.

Ripple WJ, Van Valkenburgh B. 2010. Linking top-down forces to the Pleistocene megafaunal extinctions. Bioscience, 60:516–526.

Robinson SK, Hoover JP. 2011. Does forest fragmentation and loss generate sources, sinks, and ecological traps in migratory songbirds? In: Liu J,Hull V, Morzillo A, Wiens JA (eds) Sources, sinks and Sustainability across Landscapes. Cambridge University Press, Cambridge, pp 423–449.

Robinson SK, Thompson FR III, Donovan TM, Whitehead DR, Faaborg J. 1995a. Regional fragmentation and the nesting success of migratory birds. Science, 267:1987–1990.

Robinson SK, Rothstein SI, Brittingham MC, Petit LJ, Grzybowski JA. 1995b. Ecology and behavior of cowbirds and their impact on host populations. In: Martin TE, Finch DM (eds) Ecology and Management of Neotropical Migratory Birds. Oxford University Press, New York, pp 428–460.

Robinson SK, Brawn JD, Morse SF, Herkert JR. 1999. Use of different habitats by breeding brown-headed Cowbirds in fragmented midwestern landscapes. Stud Avian Biol, 18:52–61.

Robinson SK, Hoover JP, Herkert JR. 2000. Cowbird parasitism in a fragmented landscape: Effects of tract size, habitat, and abundance of cowbirds and hosts. In: Cook T, Robinson SK, Rothstein SI, Sealy SG, Smith JNM (eds) Ecology and Management of Cowbirds. University of Texas Press, Austin, Texas, pp 280–297.

Røskaft E, Moksnes A, Stokke BG, 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.

Røskaft E, Takasu F, Moksnes, Stokke B. 2006. Importance of spatial habitat structure on establishment of host defenses against avian brood parasitism. Behav Ecol, 17:700–708.

Rothstein SI. 1974. Mechanisms of avian egg recognition: possible learned and innate factors. Auk, 91:796–807.

Rothstein SI. 1978. Mechanisms of avian egg recognition: additional evidence for learned components. Anim Behav, 26:671–677.

Rothstein SI, Robinson SK. 1998. The evolution and ecology of avian brood parasitism: an overview. In: Rothstein SI, Robinson SK (eds) Parasitic Birds and Their Hosts: Studies in Coevolution. Oxford University Press, New York, pp 3–56.

Soler JJ, Martínez JG, Soler M, Møller AP. 1999. Genetic and geographic variation in rejection behavior of cuckoo eggs by European Magpie populations: an experimental test of rejecter-gene flow. Evolution, 53:947–956.

Strausberger BM, Ashley MV. 2005. Host use strategies of individual female Brown-headed Cowbirds (*Molothrus ater*) in a diverse avian community. J Avian Biol, 36:313–321.

Steadman DW, Martin PS. 1984. Extinction of birds in the late Pleistocene of North America. In: Martin PS, Klein RG (eds) Quaternary Extinctions. University of Arizona Press, Tucson, pp 466–477.

Teuschl Y, Taborsky B, Taborsky M. 1998. How do cuckoos find their hosts? The role of habitat imprinting. Anim Behav, 56:1425–1433.

Tewksbury JJ, Hejl SJ, Martin TE. 1998. Breeding productivity does not decline with area in a western landscape. Ecology, 79:2890–2903.

Thompson JN. 1999. Specific hypotheses on the geographic mosaic of coevolution. Am Nat, 153:S1–S14.

Trine CL. 1998. Wood Thrush population sinks and implications for the scale of regional conservation strategies. Conserv Biol, 12:576–585.

Veit ML, Robertson RJ, Hamel PB, Friesen VL. 2005. Population genetic structure and dispersal across a fragmented landscape in Cerulean Warbler (*Dendroica cerulean*). Conserv Gen, 6:159–174.

Ward MP, Schlossburg S. 2004. Conspecific attraction and the conservation of territorial songbirds. Conserv Biol, 18:519–524.

Winfree R, Dushoff J, Robinson SK, Bengali D. 2006. A Monte Carlo model for estimating the productivity of a generalist brood parasite across multiple host species. Evol Ecol Res, 8:213–236.

Woolfenden BE, Gibbs HL, Sealy SG, McMaster DG. 2003. Host use and fecundity of individual female Brown-headed Cowbirds. Anim Behav, 66:95–106.

景观格局对牛鹂泛性寄生的长期维持有影响么？

Scott ROBINSON [1], Wendy SCHELSKY [2], Jeffrey HOOVER [2]

（1 美国佛罗里达大学自然历史博物馆；2 美国伊利诺斯大学草原研究所）

摘要：与大多数巢寄生鸟类不同，一些牛鹂（*Molothrus* spp.）可以广泛寄生于其分布区内的以及同一群落内的多种宿主；也没有证据表明，同一种群内的寄生个体对宿主物种有专一性。对此，进化滞后假说认为，与其他专性寄生的杜鹃和牛鹂相比，泛性寄生牛鹂是新近才进化的一支；而进化平衡假说则认为，由于寄生牛鹂的“黑手党”效应，宿主识别和拒绝牛鹂寄生卵的代价太大。然而，北美的许多宿主鸟类已进化出特定的反寄生防御行为，这些鸟类几乎都栖息在开阔地带，如草地、灌丛和溪流边。我们认为，北美鸟类生境的景观格局，对长期维持牛鹂的泛性寄生非常重要，同时也很好地解释了为什么北美森林宿主鸟类没有进化出反寄生行为。寄生性的牛鹂需要开阔草地觅食，因而很少见于森林。森林作为“源栖息地”产生的许多宿主，仅由于一些个体的扩散才进入寄生率和捕食风险都较高的片段化森林斑块，即“汇栖息地”。如此，宿主的反寄生行为的进化将非常缓慢，因为大部分个体都来自牛鹂寄生率很低的生境。此外，生境片段化、宿主繁殖扩散和集合种群的动态变化也进一步阻止了宿主反寄生行为的进化。只要北美大片的森林景观依然存在，这种状况就能持续，森林鸟类宿主对牛鹂寄生的反寄生行为就无法快速进化，反过来，牛鹂的泛性寄生也就得以维持。

关键词：巢寄生，牛鹂，森林片段化，地质马赛克共进化理论，巢捕食，源-汇集合种群动态