The Auk 117(4):943–951, 2000

USE OF LICE TO IDENTIFY COWBIRD HOSTS

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ABSTRACT.—Brood-parasitic nestlings have a unique opportunity to encounter host-specific lice (Phthiraptera). Lice are permanent ectoparasites found strictly on the body of the host, and they are transferred almost exclusively by bodily contact during copulation and care of young. We investigated whether Brown-headed Cowbird (*Molothrus ater*) nestlings become infested with lice from their host parents and carry these after fledging, in effect bearing ectoparasite indicators of the species that raised them. Examining lice on cowbirds to identify foster parents would be less costly than determining parasitism patterns in the conventional way by finding many host nests. The 244 cowbird fledglings that we examined carried 11 species and 6 genera of lice, almost the entire spectrum of louse genera known from passerines. We also examined 320 songbirds from 30 species of hosts. As a group, the diversity of louse species on hosts was comparable to that on fledgling cowbirds: 13 species and 7 genera. In contrast, most individual host species yielded only one or two louse species, significantly fewer than on cowbird fledglings. Of 44 fledgling cowbirds with lice, 11 were linked with probable avian foster parents, and 18 other fledglings were linked with one of two possible foster parents. We conclude that cowbird fledglings carry away host lice and that our technique provides a partial assessment of parasitism patterns. The incomplete state of louse taxonomy requires that users of the technique obtain a reference collection of lice from host species in addition to the sample collection from cowbird fledglings. Lice from cowbird fledglings can be identified by a taxonomist and linked to particular host species, and the principal difficulty is the scarcity of skilled louse taxonomists. We also found an unusually rich louse fauna on 219 adult cowbirds, which supports the interpretation that lack of opportunity due to physical isolation has been the fundamental factor in the host specificity of lice in certain avian orders. *Received 17 March 1999, accepted 27 April 2000.*

AVIAN LICE (Phthiraptera) share a very close relationship with their hosts and have long been used to illuminate phylogenetic relationships within the class Aves (e.g. Kellogg 1913, Hopkins 1942, Clay 1951, Ash 1960, Marshall 1981). Many genera of lice are restricted to certain orders of birds, and the species within these genera may be restricted to a single host species or even subspecies (Clayton 1990, Clayton et al. 1992, Tompkins and Clayton 1999). We hypothesized that host specificity of avian lice could be used to investigate patterns of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*). As nestlings, brood parasites have a unique opportunity to encounter lice that typically are host specific. Lice are permanent hemimetabolic ectoparasites, a group found strictly on the body of the host, and they are transferred almost exclusively by bodily contact between hosts during copulation and care of young (Marshall 1981).

We hypothesized that cowbird nestlings become infested with lice from their host parents and carry the lice after fledging, in effect bearing ectoparasite indicators of the species that raised them. If these lice survived even a few weeks on young cowbirds, investigators could collect them from recently fledged cowbirds and deduce the identity of the cowbird's foster parents. This approach would be much less costly than hiring a team to determine parasitism patterns in the conventional way by finding hundreds of songbird nests (Hahn and Hatfield 1995).

Cowbird abundance and parasitism patterns have been monitored in many regions because brood parasitism has been implicated in the decline of several endangered species and identified as a potential problem for many Neotropical migrants (Robbins et al. 1989, Rothstein and Robinson 1994). Brown-headed Cowbirds are host generalists that parasitize multiple host species in a single community, so the task of measuring parasitism levels is enormous. The level of financial support and skilled personnel required to find all host nests at a local-

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ity is available at only a few sites where major studies have been conducted (e.g. Hahn et al. 1999, Robinson et al. 2000, Sealy et al. 2000, Thompson and Dijak 2000). Consequently, we developed and tested an inexpensive technique using species-specific avian lice as bioindicators.

STUDY AREA AND METHODS

Study site.—Our study was conducted at the Patuxent Wildlife Research Center, Laurel, Maryland, a 5,000-ha wildlife refuge administered by the U.S. Fish and Wildlife Service. The refuge encompassed the watershed of the Patuxent River near Washington, D.C., and included a range of habitats such as abandoned and maintained old fields; upland oak (*Quercus* spp.) forest (including recently cut-over areas resulting in dense second growth); American beech (*Fagus grandifolia*)-white oak (*Quercus alba*) forest on river terraces and steep upland slopes adjacent to the flood plain; hedgerows and wood margins; and seepage swamps that consisted of red maple (*Acer rubrum*), sweetgum (*Liquidamber styraciflua*), pitch pine (*Pinus rigida*), and tulip tree (*Liriodendron tulipifera*). Impoundments and ponds totaled 230 ha, and 11 km of paved and unpaved roads wound through the grounds.

Capture of cowbirds and hosts.—Between 21 July and 12 August 1994, we collected lice from 244 Brown-headed Cowbirds trapped from a large flock composed entirely of hatching-year birds. We also collected lice from 219 adult cowbirds, 31 of which were caught between 2 June to 20 July 1994 and 188 between 17 March to 9 May 1995. Cowbirds were captured in walk-in traps baited with white millet. We removed cowbirds singly from traps and banded them with U.S. Fish and Wildlife Service aluminum leg bands. Each bird was subjected to a procedure to collect lice (see below) and subsequently released.

We also collected lice from individuals representing most of the local host species to have a reference set of louse species associated with these avian species. Passerine louse taxonomy is relatively incomplete (e.g. Price 1977, Wheeler and Threlfall 1986, Clayton et al. 1992), and no published records exist for the louse species associated with many species of songbirds. Some potential hosts (Northern Cardinal [*Cardinalis cardinalis*], Red-winged Blackbird [*Agelaius phoeniceus*], Common Grackle [*Quiscalus quiscula*], House Finch [*Carpodacus mexicanus*]) were trapped in walk-in ground traps, and the rest were mist netted from 15 August to 7 October 1994. We examined 320 individuals of 30 species of passerines for lice; each species is a known host for Brown-headed Cowbirds (Friedmann et al. 1977).

Collection of lice.—To collect lice, we exposed each cowbird's body to ethyl acetate vapors using an apparatus modified from that of Fowler and Cohen (1983). A quart glass jar held a few drops of the chemical on filter paper, and vapors were kept inside the bottle via a rubber collar with a hole cut for the bird's head. Following Malcomson (1960), we substituted ethyl acetate for chloroform as the vaporizing liquid that was squirted onto filter paper. The cowbird's head was secured above the rubber collar with a wire coat hanger bent to form a clamp, similar to the plastic clamp used by Fowler and Cohen (1983). We added a perch for the birds by putting eraser caps on both ends of a pencil and jamming the pencil into place in the neck of the jar. The white filter paper on the floor of the jar provided a background to see lice that dropped from the bird and to facilitate removal of lice from the jar. Each bird remained in the apparatus for 30 min, which was deemed by Fowler and Cohen (1983) to be the optimal duration of exposure.

When we collected lice from host species, we used both pint and quart jars depending on the size of the bird. A range of rubber collars was prepared with center holes of 15 to 24 mm for a bird's head so that a collar could be used that best fit each host species. Other than these changes, methods were similar to those used for the cowbirds.

When each bird was removed, we ruffled its breast, back, and wing feathers over the jar to dislodge any dead lice that remained. We removed the filter paper with forceps and placed it in a petri dish for examination under a dissection microscope. The jar was examined under strong light for any lice that might have landed on the sides of the jar. Lice were transferred using a camel's hair brush dipped in ethanol to individually labeled vials that contained 80% ethanol.

We removed the collected lice from vials and mounted them in Canada Balsam on microslides. Lice were then identified to genus and, when possible, to species. Voucher specimens were deposited in the collection of the Department of Entomology at the University of Minnesota.

Analyses.—After lice were identified, we matched the cowbird fledglings that carried each louse species with the passerine host that carried the same louse species. We analyzed differences among cowbird fledglings, cowbird adults, and hosts in terms of the number of louse species carried, the prevalence of lice, and the distribution of louse species within the group. To evaluate the effect of different sample sizes of cowbirds and hosts on the relative number of louse species collected, we ran a series of simulations based on the distribution of lice on fledgling cowbirds to estimate bootstrapped distributions (Magurran 1988:158, Dixon 1993) for hosts. These estimates yield the probability of collecting a specific number of louse species for the various sample sizes of hosts. Each simulation procedure was run 10,000 times and consisted of repeated, randomly sampled subsets of the data set from cowbird fledglings.

TABLE 1. Louse species obtained from 244 fledgling and 219 adult Brown-headed Cowbirds. Lice were found on 44 fledglings and 45 adults.

Louse species	Fledglings		Adults	
	No. with lice	No. of lice collected	No. with lice	No. of lice collected
Suborder Amblycera				
Menacanthus eurysternus	6	52	—	—
Menacanthus quiscali	—	—	4	4
Menacanthus chrysophaeus	1	4	—	—
Menacanthus sp. (immature)	2	26	—	—
Myrsidea fuscomarginata	2	18	6	9
Myrsidea sp. #2	5	25	—	—
Myrsidea sp. #4	1	2	—	—
Machaerilaemus sp. #1	—	—	2	12
Ricinus sp. #1	1	2	—	—
Suborder Ischnocera				
Brueelia ornatissima	5	169	34	163
Brueelia sp. #4	3	6	—	—
Brueelia sp. #5	2	2	—	—
Brueelia sp. #6	—	—	1	1
Philopterus agelaii	15	30	4	6
Sturnidoecus sp. #1	7	18	—	—
Total		354		195

We ran 15 simulations, one for each sample size of the potential hosts plus one for the sample size of adult cowbirds. From each simulation we calculated the expected mean number of louse species if the host birds had carried the same diversity of lice as did cowbird fledglings (see Appendix). We then used a paired Wilcoxon test to compare the observed number of louse species collected from each host bird with the expected number yielded by the simulations. We also calculated the *P*-value for the hypothesis that adult cowbirds carried fewer louse species than cowbird fledglings by summing the probabilities associated with 0, 1, 2, etc. up to 6 louse species, the latter being the number found on adult cowbirds.

RESULTS

The cowbird fledglings that we examined carried a rich fauna of lice that represented 11 species and 6 genera (Table 1). Of the 244 cowbird fledglings examined, 44 (18%) had a total of 354 lice (Table 1). The most abundant louse collected was *Brueelia ornatissima,* with 169 individuals obtained from 5 (11%) of the infested fledglings. We found *Philopterus agelaii* on 15 (34%) of the infested cowbird fledglings, which was more than twice as many fledglings as carried any other louse species (Table 1). *Philopterus agelaii* ranked third in overall numbers of lice collected from fledgling cowbirds. The second-most abundant louse was *Menacanthus eurysternus,* with 52 individuals collected from 6 (13.6%) cowbird fledglings. Five of the species of lice that we found on these birds had been recorded previously, and the other six were identified as distinct species but have not been described and named.

Most (90.9%) of the infested cowbird fledglings had only one louse species. Two young cowbirds each had two louse species, *Sturnidoecus* sp. #1 and *P. agelaii* in one case and *Sturnidoecus* sp. #1 and *M. chrysophaeus* in the other case. Two other young cowbirds each had three louse species, the first with *Myrsidea fuscomarginata, P. agelaii,* and *Menacanthus* sp. (immature) and the second with *Myrsidea* sp. #3, *Brueelia* sp. #2, and *Brueelia* sp. #3. Of the seven louse species that occurred in multiple infestations, five also were found as the only louse species on other cowbirds.

The adult cowbirds that we examined also carried a rich array of louse taxa (six species and five genera; Table 1). The prevalence of lice on cowbird adults (20.5%) and fledglings (18%) was similar ($\chi^2 = 0.47$, df = 1, $P = 0.493$). The mean abundance of lice on adult cowbirds (0.9 per bird) was a little more than half that on fledglings (1.5 per bird), but the difference was not significant ($F = 1.06$, df = 1 and 461, $P =$

TABLE 2. Potential host species of Brown-headed Cowbirds that were inspected for lice.

Species	No. of birds with lice	No. birds sampled	No. of lice collected	Louse species
Eastern Wood-Pewee (*Contopus virens*)		5		
Eastern Phoebe (*Sayornis phoebe*)	1	3	1	*Picicola foedus*
Least Flycatcher (*Empidonax minimus*)		4		
Acadian Flycatcher (*Empidonax virescens*)		3		
White-eyed Vireo (*Vireo griseus*)		7		
Red-eyed Vireo (*Vireo olivaceus*)	12	62	13	*Menacanthus curuccae*
			19	*Philopterus agelaii*
Carolina Wren (*Thryothorus ludovicianus*)		5		
Wood Thrush (*Hylocichla mustelina*)	3	7	17	*Myrsidea* sp. #2
			8	*Sturnidoecus* sp. #1
Veery (*Catharus fuscescens*)	2	6	2	*Brueelia* sp. #3
Blue-winged Warbler (*Vermivora pinus*)		4		
Northern Parula (*Parula americana*)		4		
Chestnut-sided Warbler (*Dendroica pensylvanica*)		4		
Prairie Warbler (*Dendroica discolor*)		5		
Yellow Warbler (*Dendroica petechia*)		2		
Black-and-white Warbler (*Mniotilta varia*)		23		
American Redstart (*Setophaga ruticilla*)	1	14	1	*Myrsidea* sp. #3
Worm-eating Warbler (*Helmitheros vermivorus*)		2		
Ovenbird (*Seiurus aurocapillus*)	4	33	20	*Menacanthus aurocapillus*
Common Yellowthroat (*Geothlypis trichas*)	3	38	10	*Menacanthus geothlypis*
			3	*Myrsidea* sp. #2
			1	*Brueelia* sp. #3
Hooded Warbler (*Wilsonia citrina*)		9		
Yellow-breasted Chat (*Icteria virens*)		2		
Scarlet Tanager (*Piranga olivacea*)		8		
Eastern Towhee (*Pipilo erythrophthalmus*)	1	8	3	*Menacanthus* sp.
Field Sparrow (*Spizella pusilla*)		2		
Chipping Sparrow (*Spizella passerina*)		2		
Northern Cardinal (*Cardinalis cardialis*)		10		
Indigo Bunting (*Passerina cyanea*)	1	4	5	*Machaerilaemus* sp. #1
Red-winged Blackbird (*Agelaius phoeniceus*)	14	33	48	*Brueelia ornatissima*
			44	*Myrsidea fuscomarginata*
			26	*Philopterus agelaii*
			1	*Menacanthus* sp.
Common Grackle (*Quiscalus quiscula*)	3	9	3	*Myrsidea fuscomarginata*
			5	*Brueelia* sp. #2
House Finch (*Carpodacus mexicanus*)		2		

0.304). We found four louse genera (*Menacanthus, Myrsidea, Brueelia, Philopterus*) on both adult and young cowbirds. In addition, we found *Machaerilaemus* only on adults and *Ricinus* and *Sturnidoecus* only on fledglings. Similar to the distribution pattern of lice in cowbird fledglings, most infested adult cowbirds (87.8%) had only one species of louse; each of the remaining six infested adults carried two species. Although adult cowbirds had a rich array of louse species, this richness was significantly lower ($P < 0.0001$) than that on cowbird fledglings, which carried 11 louse species (Table 1).

We examined 320 individuals of 30 species of host songbirds and found 230 lice on 45 individuals of 11 species (Table 2). Prevalence of lice on host birds (14.1%) did not differ from that on fledgling (18.0%) or adult (20.5%) cowbirds ($\chi^2 = 4.09$, df = 2, $P = 0.130$; Table 3). The distribution of louse species among hosts was similar to that in cowbirds: most (86.7%) carried only one species of louse, 11% carried two species, and 2.2% carried three species (Table 3).

However, the number of louse species on individual host species differed notably from that on cowbird fledglings (Table 2). In contrast to the large number (11) of louse species on fledgling cowbirds, most (81.9%) passerine host species had only one or two louse species. The number of louse species observed on each

TABLE 3. Summary of the incidence of louse infestation[a] on Brown-headed Cowbirds (244 fledglings and 219 adults) and their potential avian hosts (320 individuals of 30 species).

Descriptor	Brown-headed Cowbird		Potential cowbird hosts	
	Fledglings (%)	Adults (%)	Species (%)	Individuals (%)
Prevalence				
No. of infected hosts/no. of hosts examined	44/244 (18.0)	45/219 (20.5)	11/30 (36.7)	45/320 (14.1)
Mean intensity				
No. of individual parasites/no. of infected hosts	354/44	195/45	230/11	230/45
No. of parasite species/no. of infected hosts	11/44 (25)	6/45 (13)	13/11	13/45 (29)
Mean abundance				
No. of individual parasites/no. of hosts examined	354/244	195/219	230/30	230/320
Richness				
No. of parasite species	11	6	13	13
No. of parasite genera	6	5	7	7
Distribution of parasite species				
No. with 0 louse species	200	174	19	275
No. with 1 louse species	40 (90.9)	39 (86.7)	6 (54.5)	39 (86.7)
No. with 2 louse species	2 (4.5)	6 (13.3)	3 (27.3)	5 (11.1)
No. with 3 louse species	2 (4.5)	0	1 (9.1)	1 (2.2)
No. with 4 louse species	0	0	1 (9.1)	0

[a] Terms from Bush et al. (1997).

of these 30 cowbird host species was significantly lower than the number that would be expected if the songbirds carried louse distributions as rich in diversity as those observed on cowbird fledglings (paired Wilcoxon test, $z = 4.18$, $P < 0.001$; Appendix).

It is notable that most host species we examined carried only one louse species from a particular genus (Table 2), a pattern that is typical among passerine species (R. D. Price unpubl. data). In contrast, the group of cowbird fledglings carried multiple species of lice from the same genera: *Menacanthus* (2 species), *Myrsidea* (3 species), and *Brueelia* (3 species). Adult cowbirds carried one additional *Menacanthus* species and one additional *Brueelia* species (Table 1). This pattern of multiple louse species from the same genus on cowbird fledglings is the array that would be present if cowbirds had been raised by a diverse assemblage of passerine species.

Although individual host species carried significantly fewer louse species than did fledgling cowbirds, as a group (or assemblage), host birds and cowbird fledglings were infested with a similar diversity of louse species. Host species carried 13 species of lice from 7 genera, whereas cowbird fledglings carried 11 species of lice from 6 genera (Table 3). Most infested host individuals carried only one louse species, although several carried two (11.1%) or three (2.2%) species. This pattern of relatively few birds being infested with more than one louse species was similar to that observed in adult and fledgling cowbirds ($\chi^2 = 5.02$, df = 4, $P = 0.285$; Table 3).

We next used the louse species found on cowbird fledglings to infer the host species that had raised them. An overview of louse associations with cowbirds and their potential hosts showed certain linkages. Eleven cowbird fledglings could be assigned to their probable avian foster parents. Five fledglings that carried *Brueelia ornatissima* were linked with the Red-winged Blackbird, the only host that carried this louse; five fledglings that carried *Sturnidoecus* sp. #1 were linked with the Wood Thrush (*Hylocichla mustelina*), the only host that carried this louse; and one fledgling that carried more than one species of louse was linked with the Red-winged Blackbird because the combination of the three louse species the fledgling carried (*Myrsidea fuscomarginata, Philopterus age-*

laii, and *Menacanthus* sp.) was found only on that host species.

In addition, 18 cowbird fledglings were linked to one of two possible host parents, including 14 that carried lice that were found on Red-winged Blackbirds and one other host species, so no definite assignment could be made. One fledgling carried *Menacanthus fuscomarginata*, a louse we collected from Red-winged Blackbirds and Common Grackles. Thirteen fledglings carried *Philopterus agelaii*, which we collected from Red-winged Blackbirds and Red-eyed Vireos (*Vireo olivaceus*). In evaluating the likely foster parents of these fledglings, we noted that vireos were more abundant on our site than were Red-winged Blackbirds and that the latter are cowbird hosts more often than are Common Grackles (Friedmann et al. 1977). *Menacanthus fuscomarginata* is also carried by Bronzed Cowbirds (*Molothrus aeneus*), Greater Antillean Grackles (*Quiscalus niger*), and Carib Grackles (*Q. lugubris*; Price 1977), species that do not breed anywhere near our study area. The remaining four fledglings linked to two potential hosts carried *Myrsidea* sp. #2, which we collected from Wood Thrushes and Common Yellowthroats (*Geothlypis trichas*), both of which are frequent cowbird hosts and common in our study area.

Fifteen cowbird fledglings could not be assigned to a probable host parent. Five carried lice that were not collected on any host, and three were infested with a combination of two or three species that did not match those carried by any potential host. Six of these unassigned birds had the widely distributed *Menacanthus eurysternus*, which is associated with many passerines. One unassigned fledgling carried immature *Menacanthus* that could not be identified to species.

Perhaps one of the most significant observations about cowbird lice was that the total number of louse species collected on fledgling and adult cowbirds represented 14 species in 7 genera (Table 1). This remarkable breadth of taxa most likely results from transference of lice to nestling cowbirds from a variety of host species. Because the primary opportunity for a young bird to get lice is from its parent (Clayton and Tompkins 1995, Lee and Clayton 1995, Tompkins and Clayton 1999), lice on adult cowbirds may be interpreted as originating from a fledgling infestation. Additional collections of lice from cowbirds very likely will expand this list of louse taxa. It is also apparent that some louse taxa that pass from host to cowbird nestling can establish themselves on the cowbird, which may indicate a lower degree of host specificity than some workers have attributed to these lice.

Four conditions noted above make assignment of foster parents to cowbirds impossible. The first is when a particular louse is carried by more than one avian host. Second is the presence of a widely distributed louse (i.e. *Menacanthus eurysternus*) that occurs on more than 150 species of passerines and that is so widely distributed geographically that it probably will never be an indicator of cowbird foster parents. The third condition occurs when cowbird fledglings carry louse species that are not collected from any local host species, although the lice eventually may prove to be host specific and thus useful as indicators of a known local avian host. The fourth is when a species of louse is collected from an avian host but is not found on cowbird fledglings. The latter case could occur owing to sampling error because not all cowbird fledglings are captured. It also could be explained by the fact that cowbird parasitism of individual host species typically varies from year to year (e.g. Wiens 1963, Hahn and Hatfield 1995, Hahn et al. 1999). Thus, it is possible that none of the host species that carry the louse in question was parasitized in the year samples were taken from cowbirds, or that none of the hosts fledged cowbirds in that year.

DISCUSSION

It seems clear that cowbird fledglings carry lice that they obtain from their foster parents. Indeed, we found almost the entire spectrum of louse genera known to occur on host species when we collected lice from a sample of 244 cowbird fledglings. The 44 cowbird fledglings with lice carried 11 species from 6 genera. In many cases, these lice apparently become established on adult cowbirds. Of 219 adult cowbirds that we trapped, 45 carried lice that represented 6 species and 5 genera. We also collected lice from 45 of 320 trapped individuals of 11 passerine host species, and they carried 13 species of lice from 7 genera.

Ewing (1933) concluded that Brown-headed Cowbirds carried only lice specific to cowbirds,

not those of the foster parents, but his findings were constrained because he worked only with museum skins and only with adult cowbirds, not with live fledglings and adults as we did in our study. It is likely that many louse species transfer to cowbird fledglings, but not all of them survive long enough to be collected on adult cowbirds. We believe that our finding of 14 species of lice in 7 genera from Brown-headed Cowbirds represents a conservative number. Because cowbirds parasitize more than 200 species of passerines, the potential contrast in louse species richness between cowbirds and any one avian host species may be even more exaggerated. We are confident that more intensive collecting of lice from Brown-headed Cowbirds will greatly expand the list of louse species and that equally intensive collecting from large numbers of cowbird host taxa will offer much more limited species richness. We recommend that lice be collected from cowbirds and hosts at long-term field sites where cowbirds can be examined in the nests of hosts just before or after they fledge. The results from such studies would further clarify the validity of using lice as a tool to identify cowbird hosts.

Parasite species richness generally increases with larger sample sizes of hosts (Price 1980, Lafferty et al. 1994, Walther et al. 1995), and this appears to be true up to a point when sampling lice from passerines (R. D. Price unpubl. data). Very few studies of the lice carried by passerines have examined a sample size as large as ours, but those that have done so have reported two to five louse species on individual avian species. In previous work on icterids, Starks (1951) examined 210 Red-winged Blackbirds and found 5 louse species, and Cooper et al. (1975) examined 90 Common Grackles and found 1 louse species. Two previous studies of adult Brown-headed Cowbirds reported 5 louse species on 155 individuals (Geist 1935) and 3 louse species on 187 individuals (Starks 1951). In another study, Ash (1960) found 2 louse species on 704 Blue Tits (*Parus caeruleus*) and 3 louse species on 173 Great Tits (*Parus major*). He also found 2 louse species on 665 White Wagtails (*Motacilla alba*).

The relationship between louse species diversity and host sample size can best be addressed in studies that examine a large sample size of each passerine host. Our simulations confirmed that the group of cowbird fledglings we examined carried significantly more louse species than the potential hosts examined, despite the smaller sample size of hosts relative to cowbirds.

The survey technique reported here provides a partial assessment of local parasitism patterns. Of 44 fledgling cowbirds that carried lice, 11 were linked with their probable avian foster parents (Red-winged Blackbird and Wood Thrush) and 18 were linked with one of two possible hosts. Cowbird fledglings can be trapped and de-loused effectively in large numbers. Trapping is easiest at a site where a feeding flock has congregated, and such a flock can be baited near an assemblage of species that is parasitized by cowbirds (Hahn and Fleischer 1995).

The prevalence of lice infestation in an assemblage of avian species usually is well below 100% (Marshall 1981); we found lice on 36.7% of 30 host species and on 14.1% of 320 individual host birds. No data are available on the synchrony of infestation patterns among passerines in a single locality, but the prevalence, intensity, and abundance of lice on different passerine host species may not be similar in a particular breeding season. The principal transmission of lice to new hosts is vertical, i.e. from parents to offspring in the nest (Tompkins and Clayton 1999), although lice also can be transferred between individuals during copulation and brooding (Marshall 1981).

Little is known about transfer of lice between individual birds at a roost (Skutch 1961), but it seems unlikely that roosting blackbirds, particularly at summer roosts, come into the prolonged physical contact required to facilitate transfer of lice. In future studies like ours, however, a search should be made to see whether local blackbird roosts are present, and if so, whether the roosts include fledgling and adult cowbirds.

The incomplete state of louse taxonomy requires that anyone using our technique obtain a reference collection of lice from cowbird fledglings and local host species. Price's (1975) study of *Menacanthus eurysternus* demonstrates how much revision of older records of passerine lice can be required once comprehensive taxonomic work is undertaken. Lice from cowbird fledglings can be identified by a skilled taxonomist and linked to particular host spe-

cies, the principal difficulty being the scarcity of skilled taxonomists that study avian lice.

Host specificity of avian lice is the central concept behind the use of lice as indicators of cowbird hosts, as well as the use of lice to elucidate the phylogeny of their hosts (Marshall 1981, Clayton 1990, Tompkins and Clayton 1999). Although Wheeler and Threlfall (1986) speculated that passerine lice are less host-specific than lice that parasitize other avian orders, the data are not yet sufficient to draw firm conclusions. Our finding of a rich louse fauna on adult cowbirds supports the interpretation that lack of opportunity for parasite transfer because of physical isolation of individual birds has been the fundamental factor in the host specificity of lice observed in certain avian orders (Price and Beer 1963, Wheeler and Threlfall 1986, Clayton 1990, Clayton et al. 1992). Our survey technique provides a partial assessment of local patterns of brood parasitism that will be useful at sites where no other information on parasitism patterns by cowbirds is available. The accuracy of using lice to infer foster parents of young cowbirds will improve as the taxonomy of passerine lice receives additional study.

ACKNOWLEDGMENTS

We thank R. L. Jachowski for research support of unconventional ideas. DCH thanks D. H. Clayton for early encouragement and guidance throughout the study. R. Dalgleish provided helpful guidance on collection technique, D. K. Dawson allowed us to work with the songbirds she netted, and J. S. Hatfield and M. Kramer provided essential statistical consultation and analyses. We particularly thank M. Kramer for kindly carrying out simulation procedures. We appreciate equipment and supplies provided by W. N. Beyer, M. J. Melancon, M. C. Perry, and D. W. Sparling. B. Keyworth provided essential field assistance, and C. Peltzman provided technical assistance in several aspects of the work. This paper benefitted from comments by S. I. Rothstein, K. D. Lafferty, J. Loye, R. L. Jachowski, M. Kramer, J. S. Hatfield, and D. H. Clayton.

LITERATURE CITED

ASH, J. S. 1960. A study of the Mallophaga of birds with particular reference to their ecology. Ibis 102:93–110.

BUSH, A. O., K. D. LAFFERTY, J. M. LOTZ, AND A. W. SHOSTAK. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. Journal of Parasitology 83:575–583.

CLAY, T. 1951. The Mallophaga as an aid to classification of birds with special reference to the structure of feathers. Pages 207–215 *in* Proceedings of the Xth International Ornithological Congress (S. Hörstadius, Ed.). Uppsala, 1950. Almquist and Wiksell, Uppsala, Sweden.

CLAYTON, D. H. 1990. Host specificity of *Strigiphilus* owl lice (Ischnocera: Philopteridae), with the description of new species and host associations. Journal of Medical Entomology 27:257–265.

CLAYTON, D. H., R. D. GREGORY, AND R. D. PRICE. 1992. Comparative ecology of Neotropical bird lice (Insecta: Phthiraptera). Journal of Animal Ecology 61:781–795.

CLAYTON, D. H., AND D. M. TOMPKINS. 1995. Comparative effects of mites and lice on the reproductive success of Rock Doves (*Columba livia*). Parasitology 110:195–206.

COOPER, C. L., J. E. MADDEN, AND J. L. CRITES. 1975. Arthropod parasites of the Common Grackle in Ohio. Journal of Medical Entomology 12:262.

DIXON, P. 1993. The bootstrap and the jackknife: Describing the precision of ecological indices. Pages 290–318 *in* Design and analysis of ecological experiments (S. M. Scheiner and J. Gurevitch, Eds.). Chapman and Hall, New York.

EWING, H. E. 1933. Some peculiar relationships between ectoparasites and their hosts. American Naturalist 67:365–373.

FOWLER, J. A., AND S. COHEN. 1983. A method for the quantitative collection of ectoparasites from birds. Ringing and Migration 4:185–189.

FRIEDMANN, H., L. F. KIFF, AND S. I. ROTHSTEIN. 1977. A further contribution to knowledge of the host relations of the parasitic cowbirds. Smithsonian Contributions to Zoology 235:1–75. Washington, D.C.

GEIST, R. M. 1935. Notes on the infestation of wild birds by Mallophaga. Ohio Journal of Science 35: 93–100.

HAHN, D. C., AND R. C. FLEISCHER. 1995. DNA fingerprint similarity between female and juvenile Brown-headed Cowbirds trapped together. Animal Behaviour 49:1577–1580.

HAHN, D. C., AND J. S. HATFIELD. 1995. Parasitism at the landscape scale: Cowbirds prefer forest. Conservation Biology 9:1415–1424.

HAHN, D. C., J. A. SEDGWICK, I. S. PAINTER, AND N. J. CASNA. 1999. The spatial and genetic basis of cowbird host selection. Pages 204–217 *in* Research and management of the Brown-headed Cowbird in western landscapes (M. L. Morrison, L. S. Hall, S. K. Robinson, S. I. Rothstein, D. C. Hahn, and T. D. Rich, Eds.). Studies in Avian Biology No. 18.

HOPKINS, G. H. E. 1942. The Mallophaga as an aid to the classification of birds. Ibis 6:94–106.

KELLOGG, V. L. 1913. Distribution and species-forming of ectoparasites. American Naturalist 47:129–158.

LAFFERTY, K. D., D. T. SAMMOND, AND A. M. KURIS. 1994. Analysis of larval trematode communities. Ecology 75:2275–2285.

LEE, P. L. M., AND D. H. CLAYTON. 1995. Population biology of swift (*Apus apus*) ectoparasites in relation to host reproductive success. Ecological Entomology 20:43–50.

MAGURRAN, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, New Jersey.

MALCOMSON, R. O. 1960. Mallophaga from birds of North America. Wilson Bulletin 72:182–196.

MARSHALL, A. G. 1981. The ecology of ectoparasitic insects. Academic Press, London.

PRICE, P. W. 1980. Evolutionary biology of parasites. Princeton University Press, Princeton, New Jersey.

PRICE, R. D. 1975. The *Menacanthus eurysternus* complex (Mallophaga: Menoponidae) of the Passeriformes and Piciformes (Aves). Annals of the Entomological Society of America 68:617–622.

PRICE, R. D. 1977. The *Menacanthus* (Mallophaga: Menoponidae) of the Passeriformes (Aves). Journal of Medical Entomology 14:207–220.

PRICE, R. D., AND J. R. BEER. 1963. Species of *Colpocephalum* (Mallophaga: Menoponidae) parasitic upon the Falconiformes. Canadian Entomologist 95:731–763.

ROBBINS, C. S., J. R. SAUER, R. S. GREENBERG, AND S. DROEGE. 1989. Population declines in North American birds that migrate to the Neotropics. Proceedings of the National Academy of Sciences USA 86:7658–7662.

ROBINSON, S. K., J. P. HOOVER, AND R. JACK. 2000. Cowbird parasitism in fragmented landscapes: Effects of tract size, habitat, and abundance of hosts. Pages 280–297 *in* Ecology and management of cowbirds and their hosts (J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, Eds.). University of Texas Press, Austin.

ROTHSTEIN, S. I., AND S. K. ROBINSON. 1994. Conservation and coevolutionary implications of brood parasitism by cowbirds. Trends in Ecology and Evolution 9:162–164.

SEALY, S. G., D. G. MCMASTER, AND S. A. GILL. 2000. Yellow Warbler nest attentiveness before sunrise: Anti-parasite strategy or onset of incubation. Pages 169–177 *in* Ecology and management of cowbirds and their hosts (J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, Eds.). University of Texas Press, Austin.

SKUTCH, A. F. 1961. The nest as a dormitory. Ibis 103a:50–70.

STARKS, K. J. 1951. A study of ectoparasites of the cowbird and the red-wing. M.S. thesis, University of Oklahoma, Norman.

THOMPSON, F. R., AND W. D. DIJAK. 2000. Differences in movements, home range, and habitat preferences of female Brown-headed Cowbirds in three midwestern landscapes. Pages 100–109 *in* Ecology and management of cowbirds and their hosts (J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, Eds.). University of Texas Press, Austin.

TOMPKINS, D. M., AND D. H. CLAYTON. 1999. Host resources govern the specificity of swiftlet lice: Size matters. Journal of Animal Ecology 68:489–500.

WALTHER, B. A., P. COTGREAVE, R. D. PRICE, R. D. GREGORY, AND D. H. CLAYTON. 1995. Sampling effort and parasite species richness. Journal of Parasitology 83:570–583.

WHEELER, T. A., AND W. THRELFALL. 1986. Observations on the ectoparasites of some Newfoundland passerines (Aves: Passeriformes). Canadian Journal of Zoology 64:630–636.

WIENS, J. A. 1963. Aspects of cowbird parasitism in southern Oklahoma. Wilson Bulletin 75:130–138.

Associate Editor: S. I. Rothstein

APPENDIX. Observed versus expected species diversity of lice found on potential hosts of Brown-headed Cowbirds. We found 6 and 11 species of lice on adult and fledgling cowbirds, respectively (expected value = 10.799).

Host species	n	No. of lice species	
		Observed	Expected
Chipping Sparrow	2	0	0.4137
Yellow-breasted Chat	2	0	0.4137
Field Sparrow	2	0	0.4137
Yellow Warbler	2	0	0.4137
House Finch	2	0	0.4137
Worm-eating Warbler	2	0	0.4137
Acadian Flycatcher	3	0	0.5769
Eastern Phoebe	3	1	0.5769
Chestnut-sided Warbler	4	0	0.7663
Indigo Bunting	4	1	0.7663
Least Flycatcher	4	0	0.7663
Northern Parula	4	0	0.7663
Blue-winged Warbler	4	0	0.7663
Eastern Wood-Pewee	5	0	0.9712
Carolina Wren	5	0	0.9712
Prairie Warbler	5	0	0.9712
Veery	6	1	1.1358
White-eyed Vireo	7	0	1.3160
Wood Thrush	7	2	1.3160
Scarlet Tanager	8	0	1.4726
Eastern Towhee	8	1	1.4726
Common Grackle	9	2	1.6349
Hooded Warbler	9	0	1.6349
Northern Cardinal	10	0	1.7639
American Redstart	14	1	2.3555
Black-and-white Warbler	23	0	3.5229
Ovenbird	33	1	4.4999
Red-winged Blackbird	33	4	4.4999
Common Yellowthroat	38	3	4.9456
Red-eyed Vireo	62	2	6.6138