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FOREST FRAGMENTATION AFFECTS THE BEHAVIORAL RESPONSE OF AMERICAN REDSTARTS TO THE THREAT OF COWBIRD PARASITISM[1]

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Abstract. Defensive behavior of American Redstarts (*Setophaga ruticilla*) in response to models of a female Brown-headed Cowbird (*Molothrus ater*) and a control (*Spizella passerina, Passerella iliaca,* or *Melospiza melodia*) placed near their nests was investigated in fragmented and contiguous boreal forest of western Canada. Female redstarts usually discovered and responded first to models but males also participated in nest defense. Based upon several behavioral measures, which included distraction displays, close passes or striking the model, and alarm "chip" or "buzz" vocalizations, female redstarts reacted more intensely or aggressively to the cowbird model in fragmented compared with contiguous forested landscapes. We interpret these differences as evidence that redstarts are more familiar with cowbirds in fragmented landscapes because cowbirds are more common there and pose a greater threat to this host's reproductive success. Our findings have implications for interpretations of the demography of redstart populations and the fixation of antiparasite behavioral responses within populations. We suggest that tests using models provide a viable means of evaluating the influence of landscape matrix on the severity of cowbird exposure to host populations.

Key words: coevolution, host-parasite interactions, landscape fragmentation, Molothrus ater, *nest defense,* Setophaga ruticilla.

In areas of sympatry, American Redstarts (*Setophaga ruticilla*) are often a frequent host of the brood parasitic Brown-headed Cowbird (*Molothrus ater*) (Friedman and Kiff 1985). Like many other cowbird hosts, redstarts typically suffer reduced reproductive success as a result of being parasitized (May and Robinson 1985, Sherry and Holmes 1997), and the evolution of antiparasite strategies to reduce the likelihood of being parasitized are expected in this and other hosts (Rothstein 1990, Sealy et al., in press). Based upon acceptance of cowbird eggs at some nests and foster parents' feeding cowbird fledglings, cowbirds are known to parasitize American Redstarts successfully (Friedmann 1963, Sherry and Holmes 1997), and so one effective antiparasite strategy would be to prevent parasitism from occurring in the first place. This might be achieved through cryptic nest placement and furtive behavior about the nest (Hobson and Sealy 1989), but once discovered by a female cowbird, host nests may best be protected through nest defense. Previous studies have provided evidence that some passerine hosts recognize Brown-headed Cowbirds as a unique threat and manifest a variety of defensive or distraction behaviors that may reduce the chances of being parasitized (Sealy et al., in press).

Although the existence of nest defense behaviors in hosts of brood parasites is expected in populations historically sympatric with parasites, such behaviors are expected to be absent or much less frequent or intense in allopatric or recently sympatric populations (e.g., Davies and Brooke 1989, Soler and Møller 1990). Briskie et al. (1992) demonstrated that populations of Yellow Warblers (*Dendroica petechia*), long sympatric with Brown-headed Cowbirds at Delta Marsh, Manitoba, Canada, showed more overt nest defense behaviors in response to cowbird models presented near their nests than allopatric populations at Churchill, Manitoba. These authors attributed the persistence of such nest defense behaviors to continued introgression of genes from sympatric populations or to the low cost of such behaviors when parasites are rare. However, to date, few studies have investigated nest defense behaviors at smaller scales of geographic segregation of cowbirds and hosts or at the landscape scale (Freeman et al. 1990).

Prior to European settlement of North America, Brown-headed Cowbirds were associated primarily with short-grass prairies and were absent from contiguous forests and tall grass openings (Mayfield 1965). Landscape changes involving clearing and fragmentation of forests and the spread of agriculture have resulted in range expansion of cowbirds into areas where they have exploited new sources of food and new host species (Mayfield 1965, Rothstein 1994, Robinson et al. 1995). In forested landscapes, feeding areas are often spatially separated from breeding areas (Verner and Ritter 1983, Rothstein et al. 1984). Here, the penetration of cowbirds into host-rich forested areas is influenced by the relative proximity of open fields, livestock pens, horse corrals, and other disturbances associated with human activities (Darley 1982, Verner and Ritter 1983, Ariola 1986). The ability of cowbirds to commute between feeding and breeding areas sug-

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gests that even small openings in contiguous forest may provide access to large expanses of breeding habitat (Rothstein et al. 1984). However, remote forest openings are unlikely to attract Brown-headed Cowbirds (Coker and Capen 1995), and songbirds inhabiting large tracts of contiguous forest may rarely encounter cowbirds and, hence, be effectively isolated from them during breeding. Depending upon the extent of host natal dispersal among cowbird-free habitats and areas occupied by cowbirds, local host populations may or may not exhibit different degrees of nest defense responses to Brown-headed Cowbirds. Similarly, if antiparasite behaviors have a learned component (Smith et al. 1984, Hobson and Sealy 1989, Briskie et al. 1992), then the extent of dispersal of hosts with experience with cowbirds will determine whether cowbird-free areas can maintain nest-defense behaviors associated with sympatric populations.

Breeding American Redstarts are broadly distributed in North America and occur in contiguous as well as fragmented forest landscapes. In western Canada, redstarts occur in south-central regions in forest patches surrounded by agriculture where cowbirds are common. They also occur in contiguous mixedwood and deciduous stands within contiguous boreal forest where cowbirds are rare or absent. We examined the responses of American Redstarts to models of female Brown-headed Cowbirds and controls placed near their nests. We tested populations breeding in (1) forest fragments long isolated (> 50 years) by agriculture and with cowbirds regularly present and (2) contiguous forests with cowbirds either absent or occurring only recently and in low numbers. We tested the hypothesis that redstarts occurring in landscapes with frequent cowbird use show more overt nest defense behaviors than those occurring in landscapes where cowbirds are infrequent. This demographic study contrasts the effects of forest fragmentation and landscape change on host responses to the threat of cowbird parasitism. Because little is known about the nature of specific responses to cowbirds compared with other intruders near their nests, we also were interested in documenting the behavioral repertoire of redstarts associated with anti-brood-parasite strategies and the geographical consistency of these behaviors over a significant portion of their breeding range.

METHODS

We tested the responses of American Redstarts to models of a female Brown-headed Cowbird and a control species during June in large contiguous forest tracts near Dore Lake, Saskatchewan (54°46′N, 107°17′W; 1992) and Calling Lake, Alberta (55°15′N, 113°19′W; 1994, 1995), and in forest fragments near Riding Mountain National Park, Manitoba (50°50′N, 99°37′W; 1988), and Prince Albert National Park, Saskatchewan (53°52′N, 105°57′W; 1994, 1995). We chose two sites in each landscape type (fragmented vs. contiguous forest) in order to confirm more adequately any effects of treatment on host response. In the fragmented landscape, tests were conducted along the edges of park boundaries or in wooded fragments surrounded by agricultural land. These areas had been fragmented by agriculture for at least 50 years and cowbirds were observed frequently in the vicinity of these sites. The two sites located in the forested landscape were 20 to 100 km from nearest pastures or cultivated fields, and were in large tracts of boreal forest that were either contiguous or only recently exposed to logging activity. Although cowbirds range well into the boreal landscape of central Canada and, hence, our sites (Briskie et al. 1992, Semenchuk 1992, Smith 1996), they occur sporadically and primarily around permanent clearings, and we rarely detected them during our study.

During egg laying or early incubation, a freeze-dried model of a female cowbird was placed approximately 0.5 m from the nest and level with the nest rim. We recorded the response of redstarts returning to their nests during a 5-min test period from a blind positioned at least 30 min prior to testing or from cover 10–15 m from the nest. As a control, we presented either a freeze-dried Chipping Sparrow (*Spizella passerina,* used in Alberta 1994), Song Sparrow (*Melospiza melodia,* Alberta 1995), or Fox Sparrow (*Passerella iliaca,* Saskatchewan and Manitoba). These models were chosen because, with the exception of the Chipping Sparrow, they are similar in size to the female cowbird and all pose no threat to the host (Sealy et al., in press). The order of model presentation at each nest was random and we waited at least 20 min between trials at the same nest. All nests were tested only once. All behaviors were recorded onto a portable tape recorder and later transcribed. KAH made all observations at Saskatchewan (F-1: $n = 18$ trials, C-2: $n = 13$, see Fig. 1) and Manitoba (F-2: $n = 18$) sites, and M-AV made all observations at the Alberta site (C-1: $n = 16$).

As in Hobson and Sealy (1989), we scored the proximity and behavior of American Redstarts to the model for each 10-sec period within the trial as follows: (1) the distance of the focal bird from the model in one of three distance categories, < 2 m, 2–5 m, and > 5 m, (2) alarm calling ("chip" or "buzz" calls), (3) perch changes, (4) in view and perched, (5) close pass or hover over the model, (6) strikes model, (7) distraction display, (8) tail fan, (9) beak gape, and (10) out of sight or leaves area. Recording commenced when the host returned to within view (approximately 5 m) of the observer.

Distraction displays were similar to those described by Hobson and Sealy (1989) for Yellow Warblers at Delta Marsh, Manitoba, in 1988, and involved adults fluttering their wings rapidly or quivering them above their heads while moving along branches or dropping below the model, often to the ground. Distance categories together with "in view and perched," "distraction display," "tail fan," "beak gape," and "out of sight or leaves area" were analyzed as the number of 10-sec periods within trials that the bird was observed engaged in these behaviors. All other categories were quantified by counting the actual number of behaviors observed in a 5-min trial.

We made no assumptions about the distribution of behavioral responses and so used nonparametric tests throughout when testing for differences between models or study sites. Unless otherwise stated, tests are two-tailed and the assumed level of significance is $P < 0.05$. Whereas it is more appropriate to examine

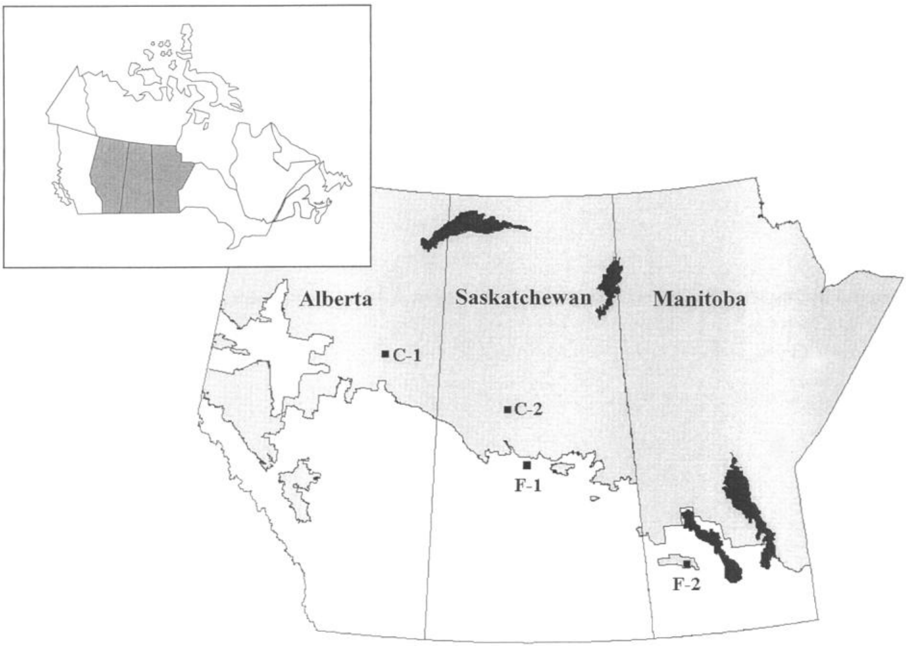

FIGURE 1. Location of study sites in Alberta, Saskatchewan, and Manitoba (C prefix refers to contiguous forest and F prefix refers to fragmented forest landscapes). Shaded area shows approximate extent of contiguous boreal forest as depicted by forest management license areas. Regions to the south of this consist largely of a highly fragmented agricultural landscape.

median responses when summarizing nonparametric data, previous studies using models have summarized responses as means (Hobson and Sealy 1989, Briskie et al. 1992, Sealy et al., in press), and we followed this convention to make our data readily comparable.

RESULTS

In all trials, female redstarts were the focal bird. However, in 9 trials, we also observed male redstarts near the nest, often joining in attacks or distraction displays. On these occasions, we noted the presence and general behavior of males but continued to focus our attention on females. For this reason, male response behaviors are not examined here.

Within each landscape type, we detected no difference in responses of American Redstarts to either cowbird or to control models within each landscape category (Mann Whitney *U*-tests, $P > 0.3$ in all cases), and so we pooled responses within landscapes for each model type. We detected no effect of landscape in responses of female redstarts to control models with the exception of a greater number of strikes against the control in fragmented compared with contiguous forest (Mann Whitney *U*-test; $P < 0.05$, Table 1). However, as measured by several behavioral categories, redstarts responded more aggressively toward the female cowbird model in fragmented landscapes than in contiguous forest (Table 1). Although redstarts spent a similar amount of time close to cowbird and control models in both landscapes, they changed perch more frequently in fragmented habitats in response to the cowbird model; this was related to more aggressive behaviors such as strikes, as well as distraction displays and associated behaviors, such as tail fanning and bill gaping. Redstarts also uttered more "chip" and "buzz" vocalizations in response to the cowbird model in fragmented compared with contiguous forests (Table 1).

DISCUSSION

We hypothesized that redstart populations would consistently exhibit more overt nest defense behaviors in fragmented forests than in extensively forested landscapes. This was indeed the case, even when extensive forest sites were relatively close (within 20 km) to fragmented forests with high cowbird abundance. Our results agree with the few previous studies investigating host defenses in sympatric and allopatric populations (Briskie et al. 1992). However, ours is the first study to reveal that such population differences also may be driven by landscape rather than larger-scale geographic effects contributing to differential distributions of cowbirds relative to their hosts. Our results emphasize the fact that forest fragmentation may influence the degree of sympatry of potential hosts with Brown-headed Cowbirds, and subsequently influence the establishment of antiparasite behaviors at the population level. These findings are surprising given the proximity of our contiguous forest sites to areas of high cowbird abundance. Data from the North American Breeding Bird Survey (available from the authors, Price et al. 1995) show a distinct peak in the abundance of cowbirds in the Great Plains, and relatively

TABLE 1. Differences in the responses of female American Redstarts between fragmented and contiguous forest landscapes to a model female Brown-headed Cowbird and a control model sparrow near the nest. Values are mean ± SE. Sample sizes given in parentheses and the *P*-value corresponds to the results of a Kruskall-Wallace test for differences between means.

Response variable[a]	*n*	Cowbird[b]		Sparrow		*P*
		Contiguous (29)	Fragmented (36)	Contiguous (29)	Fragmented (36)	
Distance from nest						
<2 m		28.0 ± 0.4	28.7 ± 0.2	27.1 ± 0.6	28.4 ± 0.2	0.34
2–5 m		1.9 ± 0.4	1.1 ± 0.2	2.7 ± 0.6	1.4 ± 0.2	0.25
5 m		0.14 ± 0.07	0.2 ± 0.1	0.14 ± 0.08	0.2 ± 0.1	0.80
Perch changes		5.9 ± 1.3A	21.6 ± 2.7B	7.0 ± 1.5A	5.6 ± 0.9A	<0.001
"Chip" calls		4.3 ± 1.3A	8.8 ± 1.3B	7.9 ± 2.9A	5.8 ± 1.8A	<0.03
"Buzz" calls		0.14 ± 0.09A	2.8 ± 0.6B	0A	0.08 ± 0.06A	<0.001
Sitting in nest		19.1 ± 1.9A	7.3 ± 1.7B	19.5 ± 2.0A	19.7 ± 1.5A	<0.001
Tail fan		9.1 ± 1.8A	15.8 ± 1.5B	6.7 ± 1.5A	3.2 ± 0.9C	<0.001
Beak gape		3.0 ± 0.8A	12.6 ± 1.3B	2.0 ± 0.7A	2.1 ± 0.6A	<0.001
Distraction display		0.07 ± 0.05A	10.9 ± 1.3B	0.04 ± 0.04A	1.1 ± 0.6A	<0.001
Close pass		0.7 ± 0.28A	1.9 ± 0.4B	0.9 ± 0.5A	0.3 ± 0.1A	<0.01
Strikes		3.2 ± 1.3A	13.1 ± 2.3B	0.6 ± 0.4C	0.5 ± 0.4C	<0.001

[a] Categories of distance, time spent sitting in nest and time spent giving distraction displays are given as mean number of 10-sec periods within trials that the bird was engaged in these behaviors. All other categories are given as the mean number observed in the 5-min trial.

[b] Results of Mann-Whitney *U*-Test corrected for ties where the same letter indicates no difference.

high abundances in agricultural areas throughout the continent. A rapid decrease in cowbird abundance is observed as one moves from the prairies of North Dakota to the boreal forest of Ontario. A similar northward decrease can be seen from the prairies of southern Alberta to the boreal forest of northern Alberta. In the Wood Thrush (*Hyocichla mustelina*), Hoover and Brittingham (1993) have shown that the increase in cowbird abundance from the Midwest to the northeast corresponds to a significant increase in parasitism levels. Our study indicates that the large-scale patterns in cowbird abundance and parasitism frequencies described above do not necessarily override effects of habitat configuration and landscape structure at the regional scale. The extensively forested landscapes in this study were located within 100 km of agricultural areas, at the southern edge of the boreal forest, and yet, they were characterized by significantly lower abundances of cowbirds than those recorded in nearby agricultural areas (Hannon and Villard, unpubl. data).

Our findings raise important questions about the relative importance of inherited and learned components of nest defense behavior, and the role of dispersal in the spread of these components. In Passerines, natal dispersal is substantially more extensive than breeding dispersal (Greenwood and Harvey 1982). Although the extent of natal dispersal movements is currently unknown for American Redstarts, their very low natal philopatry suggests that redstarts disperse over long distances in their first year (Lemon et al. 1996, Sherry and Holmes 1997). Hence, most of the dispersal between fragmented and contiguous boreal forests probably results from natal dispersal. The fact that females exhibited a lower response to cowbird models in contiguous forest sites suggests that either the learned component of nest defense behaviors dominates the inherited component, or that dispersal movements over the spatial scales considered here (20–100 km) are rare. The fact that adult female redstarts are relatively philopatric (Holmes and Sherry 1992, Lemon et al. 1996, Hobson and Bayne, unpubl. data) would further contribute to the differentiation of nest defense behaviors between the two landscape types. Even though redstart females were significantly more aggressive toward cowbird models in fragmented forests, there also was a relatively high variance among individuals within landscape types. Some females reacted aggressively, whereas others apparently ignored the model. High variance in host response to cowbird models or in nest defense in general has been noted by other researchers (Roell and Bossema 1982, Regelmann and Curio 1983, Sealy et al, in press). Such variation may be associated with intrinsic methodological problems or may genuinely reflect high interindividual behavioral differences. Dispersal of individuals between areas with cowbirds abundant and rare might contribute substantially to the variation in behaviors observed within any given area.

In this study, we have assumed that cowbirds were infrequent or absent in extensively forested landscapes. This assumption cannot be tested, however, because cowbird censuses for all of our sites are not available. However, data from northern Alberta indicate that, depending upon the year considered, cowbirds were 2.5 to 5.5 times less frequent in the contiguous forested landscape near Calling Lake than in an agricultural landscape 70 km to the south (S. Hannon, pers. comm.). Furthermore, previous studies investigating cowbird movements and frequency of parasitism support the assumption that cowbirds do not penetrate deep into extensively forested areas (Coker and Capen 1995). In the central Missouri Ozarks, an area with over 90% of the landscape forested, parasitism frequencies were 5% (Robinson et al. 1995). Similarly, Holmes et al. (1986) have never recorded instances of cowbird parasitism at the Hubbard Brook Experimental Forest in New Hampshire, an area of extensive contiguous forest. The recent large-scale lease of boreal forest to commercial logging in western Canada (Cummings et al. 1994, Stelfox 1995), together with the northward movement of agriculture and cattle grazing into previously forested regions, may result in cowbirds penetrating the remaining forest stands. The potential for penetration into the boreal mixedwood forest region is particularly serious because these areas are located close to regions of high cowbird abundance (North American Breeding Bird Survey data, available from the authors, Price et al. 1995).

Although models of cowbird intruders placed near nests cannot fully elicit the behavioral nest defense repertoire of hosts, this approach nevertheless has a number of advantages when conducted in a standardized fashion. As we have shown, this approach readily allows the comparison of nest defense behaviors among discrete populations (Sealy et al., in press). The distraction displays we recorded were consistent with those described previously and also involved a rich repertoire of gaping, bill snapping, crouching, and tail fanning (Ficken 1962). Reactions by redstarts to model cowbirds also involved behaviors recorded previously in actual encounters with live cowbirds (Sturm 1945, Ficken 1961). The "chip" vocalization we recorded apparently is a general alarm response used by redstarts in antagonistic encounters (Ficken 1962) and is similar to that recorded for Yellow Warblers responding to models of predators and cowbirds placed near their nests (Hobson and Sealy 1989, Gill and Sealy 1996). We are less certain whether the "buzz" vocalization we witnessed corresponds to alarm vocalizations previously described for this species ("screech," "hiss," or "snarl;" Hickey 1940, Ficken 1961, 1962). Hobson and Sealy (1989) described sitting in the nest as an antiparasite strategy of Yellow Warblers, a behavior that was usually accompanied by a "seet" vocalization. Further studies designed to identify whether redstarts emit a specific vocalization in response to cowbirds would be useful. Benson (1939) described redstarts sitting in their nests in response to live cowbirds but not to other species that came near their nests. We also detected this response most frequently in redstarts that occupied fragmented habitats.

Cowbirds are difficult to census in forests (Rothstein and Fleischer 1987), and their actual penetration into forests is difficult to quantify. Our study suggests that for some potential hosts, the use of behavioral trials with cowbird and control models, in addition to observed frequencies of cowbird parasitism, may provide a more powerful means of evaluating historical and contemporary influences of cowbirds in different landscapes. Our understanding of factors influencing behavioral responses in American Redstarts and other cowbird hosts also is elementary and there are multiple areas where further research is needed. In particular, it would be most useful to more carefully document the nature of both vocal and visual communication behaviors elicited by the cowbird. The causes of high variability of individual redstart responses to cowbirds and how much of the different responses to the cowbird model are learned versus genetic in origin also are extremely important areas of needed research. Finally, understanding the effect of cowbirds on host demography and the scale of movements of redstarts regionally will help elucidate the influence of forest fragmentation on the evolution of host-parasite interactions (Robinson et al. 1995).

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