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Utilization of a new host in the screaming cowbird *Molothrus rufoaxillaris*, a host specialist brood parasite: host switch or host acquisition?

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Abstract The screaming cowbird *Molothrus rufoaxillaris* has been long known as a host specialist brood parasite. However, in the past years, the utilization of two new hosts has been documented. We examined the variation in mitochondrial control region sequences from screaming cowbird chicks found in the nests of two hosts, the bay-winged cowbird (*Agelaioides badius*), which is its regular host, and the chopi blackbird (*Gnorimopsar chopi*), which is a new host, in Formosa Province, Argentina. If a group of females switched to this new host, we expected to find an association between host use and haplotype frequency distribution, indicating the presence of host-specific female lineages, whereas we expected no such association if the cowbird population incorporated this new host and females use both hosts simultaneously. Haplotype frequency distributions differed between cowbird chicks from the nests of both hosts. This indicates that nest choice by females of this brood parasite is not random and that they preferentially parasitize the nests of the same host species.

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Introduction

Interspecific brood parasitism is a reproductive strategy in which the parasite lays its eggs in the nest of another species, the host, which performs all the parental care. In birds, this strategy is present in approximately 90 species and evolved independently at least seven times (Rothstein and Robinson 1998; Sorenson and Payne 2005). One appearance of this reproductive behavior occurred within the New World icterine blackbirds, and the screaming cowbird (*Molothrus rufoaxillaris*) is the most specialized parasite within this group (Ortega 1998). For a long time, it has been thought to use a single host species, the bay-winged cowbird (*Agelaioides badius*), throughout its entire distribution (Friedmann 1929, 1963). However, in the last years, recordings of two new host species have been documented: the chopi blackbird (*Gnorimopsar chopi*) in northern Argentina and southeast Brazil (Sick 1985; Fraga 1996; Di Giacomo 2005) and the brown-and-yellow marshbird (*Pseudoleistes virescens*) in Buenos Aires Province, Argentina (Mermoz and Reboreda 1996; Mermoz and Fernandez 2003). The interactions between the screaming cowbird and its main host, the bay-winged cowbird, are a good example of the evolutionary arms race that arises between parasites and hosts in which the host evolves antiparasitic defenses to decrease the costs of parasitism that in turn select for counter-defenses in the parasite (Davies et al. 1989; Davies and de Brooke 1989; Rothstein 1990; Rothstein and Robinson 1998; Davies 2000). In this system, hosts (bay-winged cowbirds) do not feed chicks that look unlike their own (Fraga 1998; De Mársico, personal communication) and parasites (screaming cowbirds) evolved mimetic chick plumage and calls (Fraga 1979, 1998) to deceive them.

The first description of a parasite chick in a chopi blackbird nest stems from the beginning of the nineteenth century (Fraga 1996), but due to the high specialization of the screaming cowbird in parasitizing the bay-winged cowbird, it was thought that alternative hosts were only used in areas where bay-winged cowbirds were absent (Sick 1985). However, later studies showed that both hosts are used in the same areas, although parasitism rates in the bay-winged cowbird always exceed 80% (Hoy and Ottow 1964; Mason 1980; Jaramillo 1993; Fraga 1998), whereas in the brown-and-yellow marshbird, they go from 5% to 20% (Mermoz and Reboreda 1996; Mermoz and Fernandez 2003), and in the chopi blackbird they reach 55% (Di Giacomo 2005).

If the screaming cowbird was historically a specialist brood parasite that only used the bay-winged cowbird as host, two alternative hypotheses may account for the present host use. On the one hand, a few individuals may have switched host, giving rise to a new population that only uses the alternative host or, alternatively, screaming cowbird females may have incorporated the new host, originating a population that uses both hosts simultaneously.

The aim of this study was to analyze host use by screaming cowbird females in an area where they parasitize chopi blackbirds and bay-winged cowbirds. In order to do this, we used a rapidly evolving, maternally inherited molecular marker, the mtDNA control region, and determined control region haplotype distributions between screaming cowbird chicks found in the nests of both hosts. We expected to find genetic differences among chicks raised by different hosts if individual females are host specialists and if female chicks raised in the nest of a particular host have a strong tendency to parasitize that same host as adults. On the contrary, we expected no pattern of genetic differentiation if females are host generalists or differ in host use with their mothers. In doing so, we assume that host fidelity has a detectable effect on the genetic structure of cowbird populations. In the presence of host switch, we expect to find fewer haplotypes in the population of females that uses the new host. Alternatively, if host switch has not been recent, haplotype number might not be reduced, but we expect to find haplotypes that are exclusively found in the new host.

Materials and methods

Cowbird samples

Samples were collected from screaming cowbird eggs or nestlings found in the nests of two hosts in Reserva El Bagual, Formosa Province, Argentina (26°10′ S, 58°56′ W) during two breeding seasons (October–February 2005–2006 and 2006–2007). Samples were collected from bay-winged cowbird nests (N=27) and from wooden nest boxes used by chopi blackbirds (N=31). We collected one or two samples from each chopi blackbird nest, whereas samples collected from bay-winged cowbird nests ranged from one to five. All sampled nests were maximally 5 km apart, a distance that can easily be covered by screaming cowbirds. Bay-winged cowbird nests were found in between two areas of nest boxes used by chopi blackbirds.

Cowbird samples were obtained from host nests either as eggs or as blood taken from nestlings. Freshly laid eggs were artificially incubated to obtain some embryonic development prior to DNA extraction (Strausberger and Ashley 2001), and eggs found with some degree of incubation were directly processed. Embryonic tissue was extracted from the eggs and stored in dimethyl sulfoxide buffer for posterior genetic analysis. Blood samples (20–50 μL) were taken via wing venipuncture of nestlings and stored in lysis buffer.

We also took samples of adult individuals to assess the mtDNA haplotype variation of the screaming cowbird population. Individuals were captured with mist nets during August 2005 (N=17) and 2006 (N=16) and banded before release. Blood samples were taken using the same methodology used in nestlings.

mtDNA analyses

To assess mtDNA variation, we sequenced a 1,200-bp fragment of the control region using two sets of primers: GSL-GLU and GSH-12s (Gibbs et al. 1997) and MBO-L1 and MBO-H2 (Mahler et al. 2007). For 48 individuals sequenced, only the first segment of the mtDNA region, corresponding to the fragment amplified by the second pair of primers, showed nucleotide variation. Therefore, we only sequenced the 600-bp fragment amplified with MBO-L1 and MBO-H2 for the remaining 43 individuals. DNA was extracted from blood and tissue samples with a standard ethanol protocol (Miller et al. 1988). Polymerase chain reaction amplifications for both sets of primers were performed in 10-μL reaction volumes using 50–100 ng of DNA template, 0.5 μM forward and reverse primers, 0.25 mM dNTPs, 2.5 mM $MgCl_2$, and 0.25 U of Invitrogen Taq-Polymerase. Annealing temperatures were set at 50°C and repeated for 30 cycles. Amplified products were sequenced on an Applied Biosystems Model 3100 Genetic Analyzer using ABI Big Dye™ Terminator Chemistry. Nucleotide sequences have been deposited in the European Molecular Biology Laboratory gene bank under accession numbers EU199785–EU199795.

Data analysis

The sequences were compiled in Bioedit v.7.0.5.3 software (Hall 1999) and aligned using Clustal W (Thompson et al. 1994). To control for unintentional amplification of nuclear pseudogenes (Sorenson and Fleischer 1996), sequences were checked carefully for double peaks. Additionally, blood samples yielded the same haplotypes as embryonic samples where the ratio of mitochondrial/nuclear genomes is manyfold higher than in avian erythrocytes. Phylogenetic relationships among mtDNA haplotypes were inferred using maximum parsimony, as implemented in TNT (Goloboff et al. 2003). Exact searches were performed using the "implicit enumeration" option.

The program Arlequin v.2.0 (Schneider et al. 2000) was used to test for population structure using as data input the sequences of the different mtDNA haplotypes and their frequencies in cowbird chicks from the nests of each host. Genetic differentiation of screaming cowbirds between host species was assessed using the exact probability test (Raymond and Rousset 1995) and analysis of molecular variance (AMOVA) (Excoffier et al. 1992), which partitions total variance into within-group versus between-group components (Hudson et al. 1992), through Φ_{ST} that takes into account both haplotype frequencies and molecular pairwise differences. Significance levels were determined using permutation procedures as implemented in Arlequin.

Results

A 600-bp variable segment of the mtDNA control region was sequenced from 58 screaming cowbird eggs or nestlings found in the nests of two different hosts and from 33 screaming cowbird adults. A total of nine nucleotide sites varied among individuals, resulting in 11 different haplotypes (H1–H11; Table 1). Three of them (H4, H8, and H11) were rare and were only found in adults. Phylogenetic relationships among the different haplotypes yielded ten most parsimonious networks that differed in the position of a few connections (Fig. 1). The number of mutations between directly related haplotypes was small, showing a difference of only 1 bp in the majority of the cases (Fig. 1). This indicates that haplotype divergence is relatively recent in this population in evolutionary terms.

Haplotype frequency distributions differed between screaming cowbird adults and chicks for one of the tests (Φ_{ST}=0.004, P=0.26; exact test: P=0.04), which could be a consequence of a sampling bias including multiple offspring of a few females. Therefore, we excluded all the nestlings but one that were found in the same nest and shared the same haplotype. Samples coming from bay-winged cowbird nests were reduced from 27 to 22 and those coming from chopi blackbird nests were reduced from 31 to 27 (Table 1; Fig. 1). After this elimination, haplotype frequency distributions did not differ between screaming cowbird adults and chicks in any of the tests (Φ_{ST}=0.002, P=0.3; exact test: P=0.1), indicating that chicks were a random sample of the adult population.

Haplotype frequency distributions were significantly different between screaming cowbird chicks found in the nests of bay-winged cowbirds and chopi blackbirds (Φ_{ST}=0.05, P=0.04; exact test: P=0.001; Fig. 1). Some of the haplotypes were only present in individuals found in the nests of chopi blackbirds (H5, H9) or bay-winged cowbirds (H2, H6, and H7), while others were present in individuals from the nests of both hosts (H1, H3, and H10). For these latter haplotypes, except for H3, the number of individuals was not equal between hosts, being H1 most frequently found in chopi blackbirds and H10 in bay-winged cowbirds

Table 1 mtDNA control region variation of 91 screaming cowbird samples

Haplotype	50	54	95	106	204	216	267	269	472	Frequency (%)	Bay-winged cowbird	Chopi blackbird
H1	T	C	T	A	A	C	G	G	G	55	9	21
H2	C	.	.	.	.	.	.	.	.	4	4	0
H3	.	T	.	.	.	.	.	.	.	8	5	2
H4	.	.	.	.	G	.	.	.	.	2	0	0
H5	.	.	.	.	.	.	T	.	.	7	0	5
H6	.	.	.	.	.	.	T	A	.	7	3	0
H7	.	T	C	.	.	.	A	.	.	3	2	0
H8	.	.	.	G	.	.	A	.	.	1	0	0
H9	.	T	.	.	.	.	T	A	.	5	0	2
H10	.	T	.	.	.	.	A	.	A	7	4	1
H11	.	.	.	.	.	T	.	.	.	1	0	0

Base positions for the variable sites that define haplotypes are relative to the beginning of the 600-bp mtDNA sequence. Dots represent identical bases to the first sequence. The last two columns show the number of screaming cowbirds of each haplotype found in the nests of both hosts

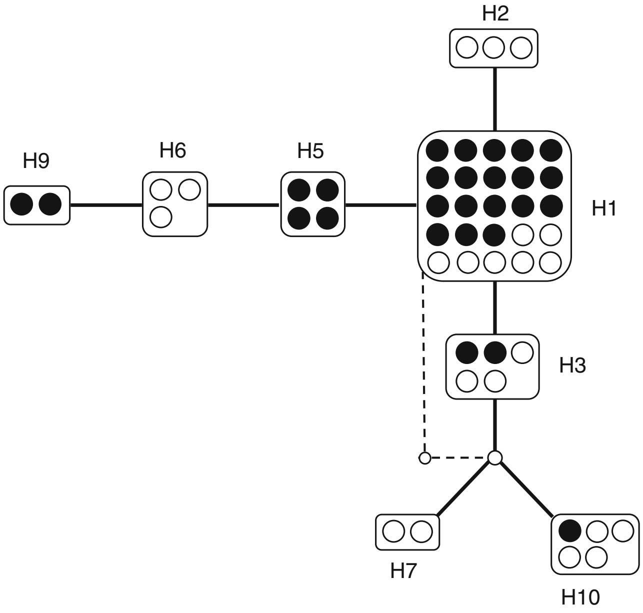

Fig. 1 Unrooted maximum parsimony network for eight haplotypes found in screaming cowbird nestlings (eggs/chicks). *Circles within boxes* represent the 49 individuals found in nests of both hosts (*black* chopi blackbird, *white* bay-winged cowbird). The number of line segments connecting the boxes gives the number of nucleotide differences between two haplotypes. Alternative connections defining other equally parsimonious trees are shown by *dotted lines*

(Fig. 1). The AMOVA attributed 6% of the variation to differences between hosts. Ninety-four percent of the variation was found between individuals found in the same host's nests.

Discussion

We found genetic differences between screaming cowbird chicks found in nests of two host species that coexist in northern Argentina. Our findings suggest that screaming cowbird females do not choose nests to lay their eggs randomly.

Female preference for particular host species has been found in several host generalist brood parasites. This preference may target only one host, like in the common cuckoo (*Cuculus canorus*; Gibbs et al. 2000), or a group of hosts, like in the molothrine species (Post and Wiley 1977; Cruz et al. 1995; Ellison et al. 2006; Mahler et al. 2007), where only a couple of hosts are used although other suitable hosts are available in the same area. Imprinting to morphological, behavioral, or ecological factors seems to be a widespread mechanism that accounts for nonrandom host choice in brood parasites (de Brooke and Davies 1991; Teuschl et al. 1998; Payne et al. 1998, 2000; Vogl et al. 2002). It might also explain host preference in screaming cowbird females, although we do not know what character of the host generates the imprinting.

In the group of Icterid brood parasites, comprised of five species, host specialization seems to be the ancestral state, retained in the screaming cowbird, which is the basal species of the clade, whereas the remaining four species acquired a host generalist behavior (Lanyon 1992). This view has been challenged by Rothstein and collaborators (2002) who suggested that host generalism can be considered as the plesiomorphic state in this group and that increased specialization in screaming cowbirds occurred due to longer coevolutionary periods with the host. Therefore, screaming cowbirds would have become bay-winged cowbird specialists over time by ceasing to use the nests of other hosts that evolved defenses against parasitism. Our haplotype distribution pattern can be explained by both evolutionary pathways, implying, in the first case, a recent switch to chopi blackbirds by females belonging to haplotypes H1, H3, H5, H9, and H10 (Fig. 1) and, in the second case, an evolutionary coexistence of females that use both hosts. In this latter scenario, switches in host use also have been present, with a switch to bay-winged cowbirds in H6 and a reversal to chopi blackbirds in H9, as well as changes in host use in H3 and H10. Due to the perfect mimetism of screaming cowbird chick plumage with bay-winged cowbird plumage, we think that it is more probable that chopi blackbirds began to be used as hosts recently. If chopi blackbirds had been used along evolution, we should find chicks that do not show mimetism with bay-winged cowbirds, stemming from a lineage historically associated to chopi blackbirds.

As expected by a host-switching scenario, several haplotypes are unique to one host species. It is possible that, if the number of samples increases, these unique haplotypes appear in the nests of the other host. However, the highly unequal distribution of hosts for one particular haplotype suggests that nest choice is not random and that females tend to parasitize one of the two available hosts. It could also be argued that the pattern found in this study arises from the distribution of genetically related individuals, with more related individuals being found in the same area, which also corresponds to the availability of nests of one host. Our study area includes the nests of both host species, with the nests of bay-winged cowbirds lying in between the nests used by chopi blackbirds. Hence, the haplotype frequency distributions between hosts cannot be explained by the geographical distribution of screaming cowbirds.

The use of chopi blackbird nests by screaming cowbird females of multiple haplotypes implies that host switch occurred many times and that it was not a unique evolutionary event. The colonization of the chopi blackbird as host may have occurred after the “mistake” of these females when depositing their eggs, a mechanism that has been suggested for other parasitic species (Davies 2000; Payne et al. 2002; Sorenson et al. 2003). After the chopi blackbird raised the offspring of these females successfully, it was subsequently parasitized by their daughters, giving rise to a group of chopi blackbird-specialized females. A possible feature that turns the chopi blackbird into a successful host is that it is a cooperative breeder. Remarkably, the other two known hosts of the screaming cowbird, the bay-winged cowbird (Fraga 1998) and the brown-and-yellow marshbird (Mermoz and Reboreda 1996; Mermoz and Fernandez 2003), are also cooperative breeders, which would indicate that competition for food with nestmates may be critical for screaming cowbirds (De Mársico and Reboreda 2008). The question that remains unanswered is why chopi blackbirds were not used earlier by screaming cowbirds. One possible explanation is that imprinting is very strong in this species, limiting host-switching events, as was suggested by Ellison et al. (2006). The increase in host number in the derived cowbird species might be related to the expansion to new areas containing new potential hosts (Rothstein et al. 2002), added to a relaxation in the imprinting process, thus allowing the colonization of new host species. Therefore, the acquisition of a host generalist behavior in this group might have arisen as a consequence of a modification in the imprinting mechanism.

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