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THE NORTH AMERICAN INVASION PATTERN OF THE SHINY COWBIRD

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Abstract.—Continuing a 90-yr trend of northward range expansion through the West Indies, the brood parasitic Shiny Cowbird (*Molothrus bonariensis*) appeared in the Florida Keys in 1985, and was first reported on the North American mainland in 1987. By 1991 the cowbird had been reported as far north as Maine, a displacement of 2300 km from its putative arrival point on the mainland. Shiny Cowbirds are permanent residents south of Tampa, Florida (28°N). Their numbers in southern Florida are augmented in the spring, apparently from the Greater Antilles. The cowbirds reinvade areas north of Tampa each spring in an explosive pattern. Most sightings have been along the Gulf and Atlantic coasts. The cowbirds disappear from the northern part of their range in the late autumn. The fat reserves of cowbirds collected in Florida in late summer were sufficient for flights greater than 400 km, and it is possible that cowbirds return to the Greater Antilles in the winter. Long-range movements of Shiny Cowbirds in North America support the hypothesis that the cowbird spread from South America unaided by human introductions.

EL PATRÓN DE INVASIÓN A NORTE AMÉRICA POR PARTE DE *MOLOTHRUS BONARIENSIS*

Sinopsis.—El tordo lustroso (*Molothrus bonariensis*) apareció en los Cayos de la Florida en 1985, y fue informado en tierra firme continental en 1987. Todo esto como continuación de su expansión territorial hacia el norte, que ha venido exhibiendo durante los últimos 90 años, a través de las Indias Occidentales. Para el 1991 el tordo había sido informado tan lejos como en Maine, un desplazamiento de 2300 km de su punto original de partida, en tierra firme. El tordo lustroso es un residente permanente del sur de Tampa (28°N). Sus números en la parte sur de Florida aumentan en la primavera, aparentemente con la llegada de aves de las Antillas Mayores. Cada primavera el ave reinvade áreas al norte de Tampa en un patrón explosivo. La mayoría de los avistamientos han sido a lo largo de las costas del Golfo y del Atlántico. No obstante, tarde en el otoño desaparecen de la parte norte de su extensión territorial. Las reservas de grasa de tordos coleccionados en Florida tarde en el verano han demostrado ser suficientes para viajar distancias mayores a los 400 km. Es posible que durante el invierno las aves regresen a las Antillas Mayores. Los movimientos de largas distancias de estas aves en los Estados Unidos apoyan la hipótesis de que el tordo se extendió desde América del Sur sin la ayuda del hombre.

Since about 1900 the Shiny Cowbird (*Molothrus bonariensis*), a brood parasite with generalized choice of hosts, has been expanding its breeding range northward through the Antilles from the region around the Guianas and Trinidad (Bond 1976, Post and Wiley 1977a). Its population growth and movement through the Lesser Antilles initially was gradual. But in

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mid-century, as the cowbird reached the larger islands of the Greater Antilles, its population size and range increased rapidly (Arendt and Vargas Mora 1984, Cruz et al. 1989, Post et al. 1990, Post and Wiley 1977a,b). By 1971 the cowbird had reached Mona Island, and by 1972, Hispaniola (Post and Wiley 1977a). It spread quickly through the Dominican Republic (Arendt and Vargas Mora 1984), appeared in north central Cuba in 1982 (Garrido 1984), and was first sighted in the Florida Keys in 1985 (Smith and Sprunt 1987). The purpose of this paper is to 1) document the early phase of the Shiny Cowbird's invasion of the North American mainland; 2) examine seasonal patterns of occurrence; and 3) estimate the flight ranges of individual cowbirds, to address the question of whether Shiny Cowbirds undertake periodic long-range movements between the Caribbean and the North American mainland.

METHODS

We obtained information on Shiny Cowbirds by reviewing the following journals published in 1985–1991: Alabama Birdlife, American Birds, Chat, Florida Field Naturalist, Migrant, Mississippi Kite, Oriole and Raven. We verified most extralimital reports by corresponding directly with observers. As a result of the similarity between female Shiny Cowbirds and female Brown-headed Cowbirds (*M. ater*), we include only reports of males at extralimital localities. For estimates of flock sizes, we include birds identified as males, females or juveniles of unknown sex.

We calculated flight ranges by using Pennycuick's (1989) computer program #1. Calculations were based on a wing span of 124 mm for male Shiny Cowbirds (Post, unpubl. data). The empty body mass and payload mass (fat) for a given wing size was estimated from a regression of weight on wing length (Mascher 1966). Weights and wing lengths (chords from wrist to wing tip) were from 80 male Shiny Cowbirds captured in mist nets during May–June in central and southern St. Lucia (map in Post et al. 1990). Twelve of 15 randomly-chosen St. Lucia males had no visible fat in their furcula (fat class = 0; Helms and Drury 1960); three had a trace of fat (fat class = 1). The relationship between weight (mean $\pm$ SD = 39.6 $\pm$ 2.8 g) and wing length (95.5 $\pm$ 2.8 mm) was estimated by: weight = 0.435 wing length $-$ 1.884. There was a significant positive correlation between weight and wing length ($r = 0.48$; $P < 0.001$). North American Shiny Cowbirds were weighed immediately after being shot. We estimated the expected weight of each individual by inserting its wing length in the above equation. Fat reserves were assumed to be the difference between expected and observed weights.

RESULTS

Shiny Cowbirds appeared in the central Florida Keys in 1985, but were not seen on the Florida mainland until 1987 (Smith and Sprunt 1987). The cowbird was first reported outside southern Florida in 1988, when one male appeared at Black Hammock Island, near Jacksonville, Florida (Table 1; Fig. 1). The latter record was 350 km from Fort DeSoto,

TABLE 1. Distribution and abundance of male Shiny Cowbirds in North America, January 1985–January 1991.

Year	Northernmost incursion	# of localities[a]		Estimated # seen		Range of dates	
		Total	North of Tampa, FL	Total	One locality	S of Tampa	N of Tampa
1985	Lower Matecumbe Key, FL	1	0	1	1	14 Jun.–1 Dec.	—
1986	Islamorada, FL	1	0	3	3	1 Jul.	—
1987	Flamingo, FL	1	0	5	5	5 May–30 Jun.	
1988	Black Hammock I., FL	8	1	35	7	25 Apr.–31 Dec.	22 Jun.–31 Aug.
1989	Aurora, NC	18	7	138	52	all year	1 May–16 Nov.
1990	New Bern, NC	28	21	109	28	all year	25 Apr.–15 Jul.

[a] Localities are at least 50 km apart.

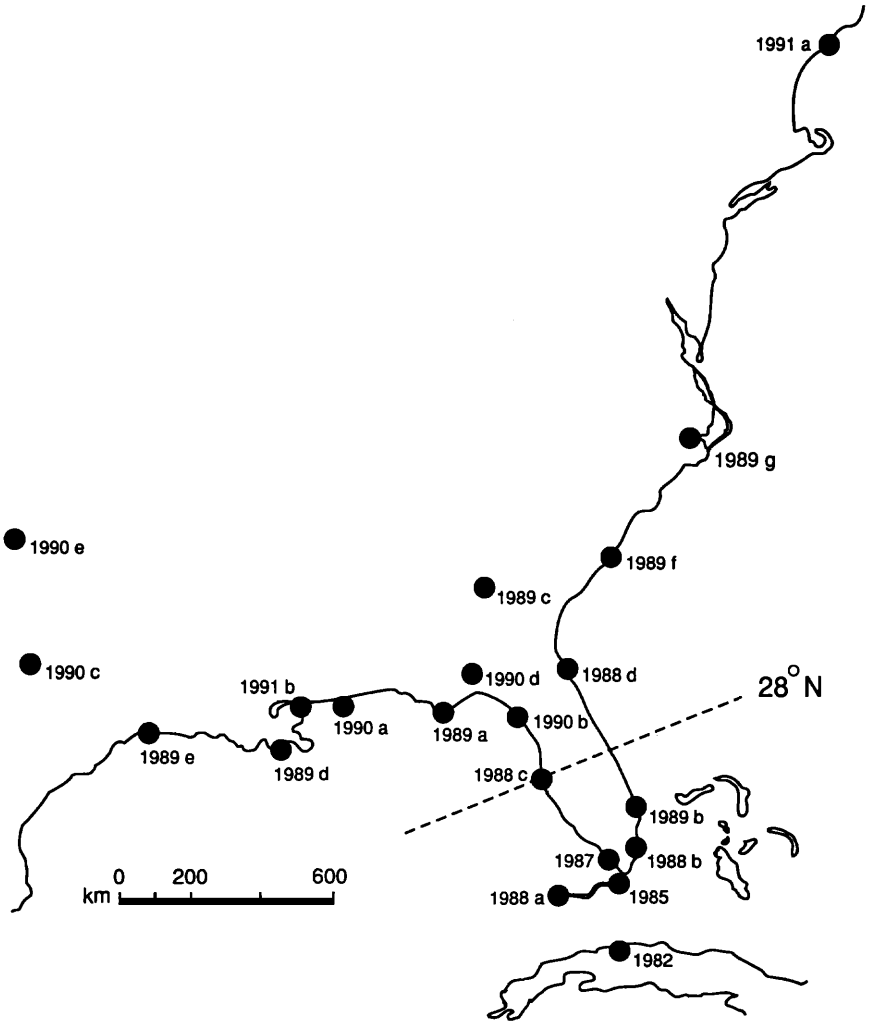

FIGURE 1. Localities of male Shiny Cowbirds in north central Cuba and United States, 1982–1991. Except for Flamingo, Florida, the first mainland locality, only range extensions of over 100 km are shown. The dashed line designates 28°N. For years with multiple localities, the lowest letter indicates the earliest record. Key to localities: 1982: Cardenas, Cuba; 1985: Lower Matecumbe Key, Florida (FL); 1987: Flamingo, FL; 1988a: Dry Tortugas, FL; 1988b: Homestead, FL; 1988c: Fort DeSoto, FL; 1988d: Black Hammock Island, FL; 1989a: Cape San Blas, FL; 1989b: Delray Beach, FL; 1989c: Warner Robbins, Georgia; 1989d: Port Fourchon, Louisiana; 1989e: Cameron, Louisiana; 1989f: Sullivan's Island, South Carolina; 1989g: Aurora, North Carolina; 1990a: Bon Secour, Alabama; 1990b: Levy County, FL; 1990c: Fort Hood, Texas; 1990d: Tallahassee, FL; 1990e: Winborn Spring, Oklahoma; 1991a: Monhegan Island, Maine; 1991b: Waveland, Mississippi.

Florida, the previous northernmost locality (Fig. 1). The Jacksonville sighting was not preceded by any substantial increase in population in southern Florida. We estimate that only 35 males were seen in Florida in 1988, and seven was the largest number seen at one place (Table 1).

Outside the winter period Shiny Cowbirds increased throughout southern Florida in 1989, and cowbirds appeared at seven locations north of Tampa, one as far north as Aurora, North Carolina (Fig. 1). The northward movement of the cowbird was accompanied by an increase in total numbers seen, and in the maximum number seen at one place (Table 1).

The trend toward population increase and range expansion continued in 1990, and the cowbird was seen at 21 localities north of Tampa, the northernmost being New Bern, North Carolina (Table 1; Fig. 1). But in 1990 fewer cowbirds were reported than in 1989 (Table 1). Possibly, this decrease is a result of uneven observer coverage, as the cowbird's novelty as a rare bird waned.

In 1991 male cowbirds continued to make erratic, long-range northward movements, which were not preceded by intermediate range consolidation. The northernmost record was on Monhegan Island, off central Maine, 1200 km from the previous northernmost locality, Aurora, North Carolina (Fig. 1). No Shiny Cowbirds were reported from the intervening Atlantic coastal region during the 18 mo between the two sightings, although this zone contains some of the most intensively monitored bird-watching sites in North America. Monhegan Island, Maine is 2340 km from Flamingo, Florida, where the species was first seen on the North American mainland (Fig. 1).

Most sightings of Shiny Cowbirds have been of one ($n = 30$) or two ($n = 15$) individuals. The largest groups have been in southern Florida (52 in the Dry Tortugas on 25 May 1989) and on the northern coast of the Gulf of Mexico (28 on Dauphin Island, 11 May 1990). The mean ($\pm$SD) size of the 10 largest flocks seen during April–July was 24.7 $\pm$ 15.6. In contrast, only individuals or small groups of cowbirds were reported after July (3.5 $\pm$ 3.3; $n = 10$).

By examining seasonal distribution during 1989–1991, the following pattern is discernible: Shiny Cowbirds are most common during April–July. In the fall, at the same time cowbirds disappear from areas north of Tampa, Florida, there is an overall reduction in cowbird numbers throughout their North American range, including even the southern Florida Keys (Fig. 2).

Eight male Shiny Cowbirds have been collected in North America as of February 1992. Fresh weights are available for four of the specimens (Table 2). A third-year male collected 30 Apr. 1991 on Sullivan's Island, South Carolina, had a slight amount of subcutaneous fat (fat class = 1; Helms and Drury 1960), and had a potential flight range of 231 km (Table 2). Two males collected at Ft. Pierce, Florida on 25 Jul. 1991 were extremely fat (fat class = 5). Their estimated flight ranges were 337–444 km (Table 2).

No female Shiny Cowbirds have been collected in North America. Two

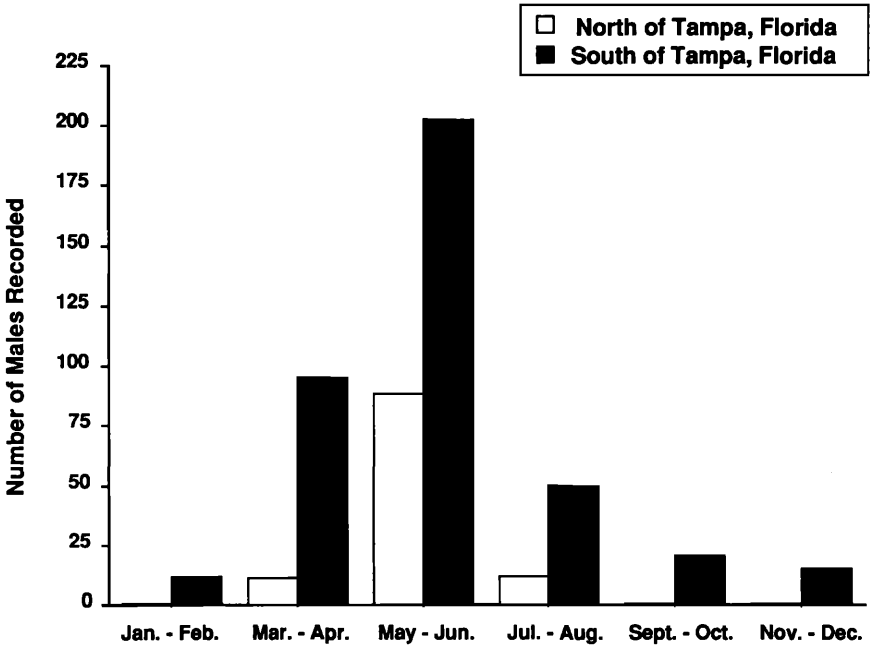

FIGURE 2. Seasonal pattern of occurrence of Shiny Cowbirds in North America. The open histograms show the number of Shiny Cowbirds recorded in each two-month period from January 1985 to December 1990 north of Tampa, Florida (28°N; see Fig. 1). The shaded histograms indicate the total number of cowbirds recorded south of Tampa during the same intervals.

of the males, one collected at Sullivan's Island, South Carolina, and the other at Fort Pierce, Florida, had adult nuptial (second alternate) plumages (Friedmann 1929), and thus were in their third year. Six of the specimens had first nuptial (first alternate) plumages, which are similar to adult nuptial, except in the retention of varying amounts of brown feathers.

Little is known about the behavior of Shiny Cowbirds in North Amer-

TABLE 2. Estimated flight ranges of male Shiny Cowbirds collected in North America. The payload mass (fat weight) is the difference between expected and observed weights. Procedures for calculating expected weights and flight ranges are in methods.

Date	Locality	Wing chord length (mm)	Weight (g)		Flight range (km)
			Expected	Observed	
30 Apr. 1991	Sullivan's I., SC	95.5	40.1	44.9	231
18 Jun. 1991	Sullivan's I., SC	100.0	41.6	32.0	0
25 Jul. 1991	Ft. Pierce, FL	95.0	39.4	46.5	337
25 Jul. 1991	Ft. Pierce, FL	93.0	38.6	48.0	444

ica. Males appear to be reproductively active at least during the period 30 April–25 July. Seven of the eight males collected at this time had enlarged testes. In Florida and South Carolina, we often heard male Shiny Cowbirds singing ("twitter song" of Friedmann 1929), usually when they were flying. Post also saw several males displaying to female Shiny Cowbirds on Sullivan's Island, South Carolina in 1991. On 26 May, one male in post-juvenal plumage and two female Shiny Cowbirds were loosely associated as they perched near a bird feeder. The male Shiny Cowbirds sang and made a low, swooping flight toward the two females, and attempted to land next to them. One of the females gave a rattle call (Friedmann 1929), and the two females moved away together. Brown-headed Cowbirds were also in the vicinity, but the Shiny Cowbirds did not approach them while feeding, nor when they moved to and from the feeding station. The male Shiny Cowbird once landed within 1 m of a male Brown-headed Cowbird. The two gave bill-ups (Friedmann 1929) while perched next to each other. The male also chased a juvenile European Starling (*Sturnus vulgaris*) about 25 m. During the chase, the cowbird sang and the starling emitted distress calls. Interspecific chasing by Shiny Cowbirds has been seen in Puerto Rico (Post, unpubl. data). Again, on 2 June, Post watched two male Shiny Cowbirds approach a female, which gave a rattle call, and moved away.

Sixteen reports mentioned habitats or feeding sites of Shiny Cowbirds; 10 of these were of individuals or groups at bird feeders, three on lawns, and two at feedlots. Only one individual was reported in a natural habitat: a male near Mahogany Hammock in Everglades National Park. Of the eight males collected, four were at bird feeders, two were captured in cowbird-control decoy traps and two were in a roost. The stomachs of the roosting birds were full of millet seeds, which were likely obtained at a bird feeder. Thus, all cowbirds collected in North America have been associated with provisioned food.

Shiny Cowbirds in North America join mixed-species roosts, a behavior that has been reported in the Caribbean (Post and Post 1988). On the evening of 25 Jul. 1991 Post watched two males in a roost in a small cattail marsh near Ft. Pierce, Florida (Post 1992). The two, one in second-year plumage and the other in full adult plumage, arrived at the roost about 1600 hours EST, after other blackbirds had already arrived. The others were Brown-headed Cowbird (170), Common Grackle (*Quiscalus quiscula*) (50) and Boat-tailed Grackle (*Q. major*) (30). Before they were collected, the male Shiny Cowbirds sat 2–3 m apart about 1 m above the water on cattail stems. Neither bird perched closer than 2 m to individuals of other roosting species. A third male Shiny Cowbird was in the roost at 0520 on 26 Jul. 1991. It also sat apart from other birds. It preened, sang, and left the roost at 0530 with a flock of other blackbirds.

A second roost was observed by McNair near Panama City, Florida on 3–4 May 1990. Two male Shiny Cowbirds settled with about 10 Red-winged Blackbirds (*Agelaius phoeniceus*) and 25 Brown-headed Cowbirds on a small shrub-covered island in a brackish pond. The Shiny Cowbirds

roosted in cattails on the edge of the island, and about 1.5 m above water. It was not determined how closely they associated with the other roosting species.

DISCUSSION

In addition to North America, Shiny Cowbirds are colonizing new areas of South America, aided by introductions west of the Andes (Johnson 1967, Long 1981) and by deforestation in the Amazon Basin (Ridgley and Tudor 1989). Their rapid increase in the Western Hemisphere parallels that of the Cattle Egret (*Bubulcus ibis*) and Brown-headed Cowbird, species which also have responded to clearing of forests for animal husbandry (Arendt 1988, Davis 1960, Friedmann 1929, Mayfield 1965, Rothstein et al. 1980, Siegfried 1978). Similarly, the Shiny Cowbird's success in spreading north through the Caribbean has depended on the availability of suitable feeding areas for adults as much as on opportunities for nesting (Post et al. 1990). Many of the Shiny Cowbirds seen in the United States have been at bird feeders. The abundance of feeding stations in North America may aid the cowbird's spread.

The Shiny Cowbird's invasion pattern of North America is characterized by erratic, long-range movements. The annual distribution pattern that has developed has the following features. 1) Although the cowbirds are permanent residents in Florida south of Tampa, their numbers are augmented each spring, possibly by movements from the Greater Antilles. 2) Cowbirds then appear to reinvade the northern part of their range, possibly from the Florida population center. 3) The annual reinvasion occurs in an explosive pattern, although most propagules are concentrated along the Atlantic and Gulf coasts. The cowbirds have penetrated farthest north along the Atlantic coast, although they are recorded more frequently along the northern Gulf of Mexico. 4) Shiny Cowbirds disappear from the northern part of their range in late fall, and few are seen north of Tampa in the winter. 5) It is not yet possible to relate the movement patterns of the Shiny Cowbird to extrinsic factors such as food or host availability.

The Shiny Cowbird differs from species of passerines that have been introduced to Florida and the West Indies (reviewed in Long 1981) in its tendency to make repeated long-range movements. The physiological condition of the two Shiny Cowbirds collected at Ft. Pierce, Florida in late July indicates that they were capable of flights of up to 444 km, which, had they departed from the Miami area, would have put them in range of Cuba. The limited data that we have suggest that, compared with Shiny Cowbirds examined in St. Lucia, the fat reserves of cowbirds collected in Florida are adaptations for long-range dispersal.

All Shiny Cowbirds that have been collected in the West Indies and North America belong to the smallest subspecies, *M. b. minimus*. This form was initially confined to the tropics (Hellmayr 1937). Tropical, continental populations of *minimus* are not known to migrate (Friedmann 1929). South Temperate Zone Shiny Cowbirds are at least partially

migratory, however (Friedmann 1929, Hudson 1920). Thus it is possible that the long-range dispersal behavior of Shiny Cowbirds in North America will develop into a pattern of periodic migration.

Large gaps in the Caribbean distribution of the Shiny Cowbird led Bond (1976) to suggest that its spread to the Greater Antilles was abetted by human introductions. This idea was supported by information that the species had been popular as a cage bird on some islands (Bond 1976). Others, working in Puerto Rico and Mona Island (Post and Wiley 1977a), agreed with Bond's interpretation. But the pattern of the Shiny Cowbird's invasion of North America lends support to the alternative view, that the species spread unaided through the Caribbean. The distance between southern Martinique, the probable northern limit of its breeding distribution in the Lesser Antilles (Post et al. 1990) and eastern Puerto Rico is 675 km, well within the range of the species' movements in North America. Further, information from the Lesser Antilles may help explain why the cowbird has not been seen on many islands, although suitable hosts are available. The cowbird's abundance in St. Lucia, and scarcity on Martinique, may be related to availability of suitable feeding sites such as stockyards, rather than to nesting opportunities (Post et al. 1990). Although cowbirds may have landed on the small islands of the Lesser Antilles north of Martinique, they may not have stayed because provisioned food was not available.

The arrival of Shiny Cowbirds in North America presents a unique opportunity to study the colonization of a continent by a brood parasite. The invasion process is made especially interesting by the presence of another cowbird that is also a host generalist. A potential problem for studies of Shiny Cowbird population growth is that of differentiating their eggs, fledglings and females from those of Brown-headed Cowbirds. This will make it difficult to study host choice in areas where the two cowbirds co-occur. As of February 1992, we know of no substantiated report of parasitism by Shiny Cowbirds in North America. We believe that confirmation cannot be based on sight records, but will require collection of Shiny Cowbird eggs or fledglings.

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