



The Auk 115(1):209–214, 1998

Behavioral Interactions Between Golden-winged and Blue-winged warblers

JOHN L. CONFER¹ AND JEFFERY L. LARKIN²

Biology Department, Ithaca College, Ithaca, New York 14850, USA

The breeding range of the Golden-winged Warbler (*Vermivora chrysoptera*) has expanded in some regions and contracted in others for more than a century (Gill 1980). The decline of the Golden-winged Warbler often is attributed to loss of breeding habitat and/or interactions with the Blue-winged Warbler (*V. pinus*; Confer and Knapp 1977, 1981; Will 1986; Hands et al. 1989; Confer 1992a,b).

Golden-winged Warblers nest in early successional habitat. Abandoned farmland is the precursor of most its nesting habitat, although fires, lumbering, and powerline maintenance also create habitat (Hands et al. 1989). The decline of the Golden-winged Warbler is part of a widespread reduction in early successional species (Sauer et al. 1997) that is correlated with habitat loss. For example, abandonment of farmland in New Hampshire peaked about a century ago, and early successional habitat was most abundant from 1900 to 1955 (Litvaitis 1993). Since 1955, early successional habitat has decreased to nearly zero. Similar loss of habitat has occurred throughout the reforested northeastern United States, and the abundance of Golden-winged Warblers and other early successional birds has declined (Hill and Hagan 1991, Witham and Hunter 1992, Smith et al. 1993). At the other extreme, the rate of farmland abandonment has increased in Pennsylvania, Minnesota, and Wisconsin from 72,000 ha per year during 1925 to 1960 to 185,000 ha per year from 1960 to 1990 (Census of Agriculture 1935, 1992). Numbers of Golden-winged Warblers increased from 1980 to 1996 (Sauer et al. 1997). Within forested habitats, bird species turnover may continue as young forests mature (Holmes et al. 1986).

Rappole and McDonald (1994) speculated that Golden-winged Warblers (but not Blue-winged warblers) "have been seriously reduced in numbers as a result of winter-habitat loss. . . ." However, regional declines of Golden-winged Warblers began more than 90 years ago (Gill 1980), before loss of winter habitat was extensive, and their numbers are increasing in the northern portions of their range (Sauer et

al. 1997). Thus, the century-old pattern of regional expansion followed by decline does not correlate with recent changes in winter habitat.

In New England and central New York, Golden-winged Warblers were eliminated within 50 years of the arrival of Blue-winged Warblers (Gill 1980). This decline might be due to hybridization with Blue-winged Warblers, which is fairly common in regions of overlap (Gill 1997), or to competitive displacement of Golden-winged Warblers from optimal habitat (Will 1986). In this study, we conducted experimental removals and observed interspecific interactions to assess whether Blue-winged Warblers displace Golden-winged Warblers.

Study area and methods.—Study sites were north of Syracuse in Oswego County, north-central New York. Observations were obtained from 1988 to 1994 at a total of 21 sites. Eight sites were studied for four to six consecutive years. Usually, we visited sites three times a week from early May through early July and about twice a week in late July. During 1988 to 1990, one to two assistants and the senior author observed 10 to 15 male Golden-winged and Blue-winged warblers at eight sites each year. During 1991 to 1994, three to four assistants and the senior author observed 25 to 30 male Golden-winged Warblers and 15 to 20 male Blue-winged Warblers at 10 to 13 sites each year.

Farming began to decline in the region around 1940. Abandonment of farms continues today, producing an abundance of successional habitats ranging from fallow fields to young forests. Golden-winged Warblers began nesting in the area before 1950 (Benton 1950) and were fairly abundant by the mid-1950s (Scheider 1959). Blue-winged Warblers were absent in the mid-1950s but became moderately abundant by the early 1970s (Confer et al. 1991, Sauer et al. 1997).

We scored all interspecific interactions, even occasional long chases, as single events. Interactions and their scores (in parentheses) were as follows: flight into a tree or shrub where the male of the other species was located (+); in-flight pursuit (+); displacement from a perch (–); and departure by one male when another approached (–). About half of the interactions were scored as a tie, e.g. flight by one

¹ confer@ithaca.edu

² Present address: Department of Forestry, University of Kentucky, Lexington, Kentucky 40546, USA.

TABLE 1. Phenotypic identity of Golden-winged Warblers, Blue-winged Warblers, and hybrids (Brewster's Warblers and Lawrence's Warblers) for individuals with known nests in the study area.

Phenotype	<i>n</i>	%
Males^a		
Golden-winged Warbler	84	71
Blue-winged Warbler	30	25
Brewster's Warbler	3	3
Lawrence's Warbler	1	1
Total	118	100
Females		
Golden-winged Warbler	76	63
Blue-winged Warbler	32	26
Brewster's Warbler	12	10
Lawrence's Warbler	1	1
Total	121	100

^a Three bigamous males were counted only once.

male into a tree occupied by another male (+) and then retreat by the first male toward the area of origin (-).

In 1992 and 1994, we removed male Blue-winged Warblers whose territories were adjacent to those of male Golden-winged Warblers and observed if the Golden-winged Warblers expanded into the vacated territories. Pre-removal boundaries were determined by watching males for at least 1 h on each of three to four mornings over a period of five to eight days, starting within a few days of the arrival of both birds on the territory. After removal of the Blue-winged Warbler, we observed the male Golden-winged Warbler the next day and at two-day intervals thereafter for the next two weeks. Boundary determinations were enhanced by color-banding about 90% of all male Golden-winged Warblers and 50% of all male Blue-winged Warblers at our sites.

We removed Blue-winged Warblers if: (1) the territories of the Golden-winged Warbler and Blue-winged Warbler were contiguous or partially overlapping so that potential existed for significant expansion by the Golden-winged Warbler; (2) we knew the song posts of both males near the area of contact and were familiar with the boundaries of the entire territory of each species; and (3) both birds were unmated or without an active nest at the time of removal (expansion would be less likely after nesting had started). Territorial boundaries were mapped with a Trimble[®] global positioning system. A handheld rover was corrected for inaccuracies by use of a base station; replicate measurements differed by 2 to 5 m. Data from the global positioning system were then exported to Generic CADD[®] to determine territory size, amount of overlap between territories, and shifts in territory boundaries.

Results.—No Blue-winged Warblers were observed at our two northwesternmost sites during brief ob-

TABLE 2. Composition of Golden-winged Warbler (GW), Blue-winged Warbler (BW), and hybrid (Brewster's [BR] and Lawrence's [LA] warbler) pairs with known nests. Expected values for random pairings were derived from the product of the proportional abundance of male and female phenotypes presented in Table 1.

Pairing	Observed		Expected ^a		Difference (%) ^b
	<i>n</i>	%	<i>n</i>	%	
GW × GW	73	60.3	54.1	44.7	15.6
GW × BW	1	0.8	22.7	18.8	-18.0
BW × GW	2	1.7	19.3	16.0	-14.3
BW × BW	28	23.1	8.1	6.7	16.4
LA × BW	1	0.8	0.3	0.2	0.6
GW × BR	11	9.1	8.5	7.0	2.0
GW × LA	1	0.8	0.7	0.6	0.3
BR × BR	1	0.8	0.3	0.2	0.6
BR × GW	1	0.8	1.9	1.6	-0.7
BR × BW	2	1.7	0.8	0.7	1.0
Total	121	100	117	96	—

^a Potential but unobserved pairings omitted.

^b "Difference" is the observed frequency minus the expected random frequency.

servations in 1988. Yet, Blue-winged Warblers comprised 12% (*n* = 33) of the territorial males there from 1989 to 1991, and 33% (*n* = 47) of the territorial males from 1992 to 1994. In five years, the range over which Blue-winged Warblers were abundant advanced northward by about 33 km. Golden-winged Warblers comprised about 55% of the non-hybrid males (*n* = 172) at other sites where their relative abundance did not change during the study.

The phenotypes for warblers with known nests are shown in Table 1. Both species paired assortatively. Only three (2.5% of 121) pairings involved interspecific crosses between phenotypically pure birds compared with an expected 42 if pairings were random (Table 2). Of the phenotypically pure birds, 12 males (10.2% of 118) and 4 females (3.3% of 121) mated with hybrids. All 12 of the males (14.3% of 84) were Golden-winged Warblers, whereas none of 30 male Blue-winged Warblers mated with a hybrid, a statistically significant difference ($\chi^2 = 4.07$, *df* = 1, *P* < 0.05). Of the phenotypically pure females, three Blue-winged Warblers (9.4% of 32) and one Golden-winged Warbler (1.3% of 76) mated with hybrid males, again a statistically significant difference ($\chi^2 = 4.10$, *df* = 1, *P* < 0.05). Overall, hybridization was more frequent for phenotypically pure Golden-winged Warblers (8.1% of 160) than for Blue-winged Warblers (4.8% of 62), but the difference was not significant ($\chi^2 = 0.722$, *df* = 1, *P* > 0.10).

Return rates were determined with color-banded, territorial male Golden-winged Warblers. Only 38% (31 of 81) of these males returned the summer im-

mediately after banding, including three that were not detected the first summer after banding but were observed at the original site the second summer after banding. It seems most likely that these birds returned to the site vicinity in the first year but were not detected by us. Of the 31 males presumed or observed to have returned once after banding, 64% (16 of 25) returned a second time, and 60% (9 of 15) of these birds returned a third time. The return rate in the first year after banding was significantly lower than that for "repeat" returns ($\chi^2 = 6.3$, $df = 1$, $P < 0.01$).

Blue-winged Warblers were sufficiently abundant that we could hear or see them from within almost all of the Golden-winged Warbler territories. We quantified this proximity as the proportion of a Golden-winged Warbler territory that overlapped with a Blue-winged Warbler territory, plus the proportion of the shared boundary. Among all years and sites, proximity ranged from 25 to 69%. For the two northwestern sites, proximity was zero during the first two years of observation but increased to 16 to 35% in the later years.

We monitored behavioral interactions between male Golden-winged and Blue-winged warblers at the territories of 98 Golden-winged \times Golden-winged pairs. The intensity of our effort is indicated by the fact that we found the Golden-winged Warbler nest, determined the Blue-winged Warbler proximity, and measured the vegetative attributes at 68 of these territories. We detected a total of 87 interactions between Golden-winged and Blue-winged warblers that fit our criteria of dominance behavior. Most interactions occurred early in the breeding season before 5 June. By this date for all years, we tabulated 3,078 person-hours in the field and detected 87 instances of dominance, or 1 per 35 person-hours. Studies that focused on foraging males in 1988 and 1991 provided the best estimate of the frequency of dominance interactions. During these years, we detected 45 dominance interactions, or 1 per 16 person-hours. We detected no interactions between most of the adjacent Golden-winged Warbler and Blue-winged Warbler males. For statistical analyses, we summed data from all years to reduce the potential influence of individual males or sites and to obtain an adequate sample size. Golden-winged Warblers were dominant in more than half of the interactions we observed ($\chi^2 = 5.06$, $df = 1$, $P < 0.025$; Fig. 1).

Three pairs of adjacent male Golden-winged and Blue-winged warblers interacted repeatedly. These interactions included conspicuous vocalizations and flights that would have been easy for us to detect at other territories, assuming the behaviors were typical for the two species. Two instances of multiple interactions occurred near a Golden-winged Warbler nest. In one case, the males and females of both species arrived within two days of each other. The males established territories that overlapped by about 80%,

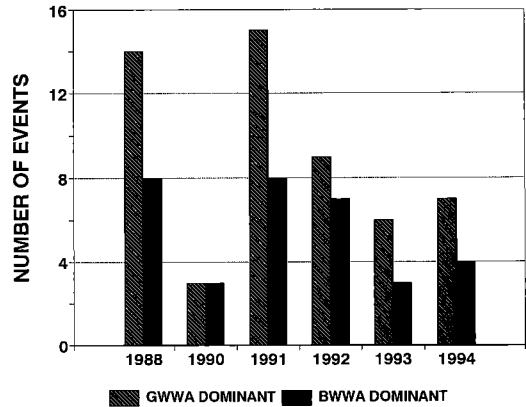


FIG. 1. Dominance interactions between male Golden-winged Warblers and Blue-winged Warblers recorded in north-central New York.

and sang frequently from adjacent trees. We never saw these males chase each other during 10 visits to the territories, except near the Golden-winged Warbler nest. On two dates the male Golden-winged Warbler chased the male Blue-winged Warbler for several minutes while giving loud type-II (after Gill and Lanyon 1964) songs after the Blue-winged Warbler approached within a few meters of the Golden-winged Warbler nest.

In another case, a male Golden-winged Warbler and a male Blue-winged Warbler foraged near each other without pursuit during the first few days after arrival. Five days after arrival, the male Golden-winged Warbler escorted a female conspecific and drove the male Blue-winged Warbler from the area of overlap. On three subsequent occasions, this color-banded male Blue-winged Warbler was seen near the Golden-winged Warbler female and her nest. In each case, the male Golden-winged Warbler chased the male Blue-winged Warbler. This Golden-winged Warbler ignored other males with adjacent or overlapping territories, becoming aggressive only after his mate arrived and only when a specific male Blue-winged Warbler was near the female. Thus, intense aggression appeared to occur only in relation to nest defense or mate guarding.

Because of our restrictive criteria for removal, we conducted only six removal experiments: two in 1992, and four in 1994. Golden-winged Warblers showed no expansion into territories of removed Blue-winged Warblers in four cases, trivial expansion in one case, and extensive expansion in only one case (Table 3).

At the Falanga site, we observed the Golden-winged Warbler in the vacated Blue-winged Warbler territory only once during eight visits within two weeks of the removal. Because this Golden-winged Warbler was seen there only briefly and was not sing-

TABLE 3. Change in territory size of Golden-winged Warblers after removal of male Blue-winged Warblers that had contiguous or overlapping territories.

Site	Date ^a	Pre-removal		Post-removal	
		Size ^b	Overlap ^c	Increase A ^d	Increase B ^e
Canning	23 May 92	0.59	0.00	0.00	0.00
Falanga	2 Jun 92	1.60	0.44	0.00	0.00
Peck	25 May 94	0.21	0.05	0.00	0.00
Hall	25 May 94	0.92	0.12	0.47 (51)	0.15 (31)
Power	25 May 94	1.60	0.00	0.00	0.00
M102	27 May 94	0.77	0.00	0.98 (126)	0.08 (8)

^a Date of removal of Blue-winged Warbler.

^b Initial size (ha) of Golden-winged Warbler territory.

^c Proportion of Golden-winged Warbler territory that overlapped with Blue-winged Warbler territory.

^d Increase in size (ha) of Golden-winged Warbler territory one week after removal (% increase in parentheses).

^e Increase in size (ha) of Golden-winged Warbler territory within vacated Blue-winged Warbler territory (% increase in parentheses).

ing, we do not believe that it expanded its territory into the Blue-winged Warbler territory.

At the Peck site, the Golden-winged Warbler used the same pre-removal song perches on the first, third, and sixth days after removal. Seven days after removal, another Blue-winged Warbler was detected in the vacated territory. After a week without expansion, the Golden-winged Warbler advanced its song posts by about 5 m toward the newly occupied territory. We interpret this as a response to contact with a new male Blue-winged Warbler, and not as a release from interference competition with the removed male.

At the M102 site, the Golden-winged Warbler expanded its territory by 126%, but only 8% of this expansion occurred within the territory of the removed Blue-winged Warbler. For objectivity, we drew territorial boundaries and estimated expansion by drawing straight lines between song posts. Actually, the vegetative boundary was concave between two shared song posts. If these song posts were connected by a concave line, the estimated expansion would have been zero. All of the real expansion occurred into the territory of a different pair of Blue-winged Warblers. These Blue-winged Warblers continued their nesting activities without any interaction with the Golden-winged Warblers. After the removal, a pair of "Brewster's" Warblers (i.e. both birds were hybrids) started incubation within the expanded territory of the Golden-winged Warbler. We detected no interactions between the Golden-winged Warbler and Brewster's Warbler males.

At the Hall site, the Golden-winged Warbler clearly expanded into the vacated Blue-winged Warbler territory. This territory was unusually large, partially because the song posts encompassed a large, unused grassy field. A large portion of the initial Golden-winged Warbler territory overlapped with the eastern portion of the Blue-winged Warbler territory. When both birds were within the area, they appeared to ignore each other. However, the Golden-winged Warbler frequently flew into the western

portion of the Blue-winged Warbler territory and always was chased out. On the morning following the removal, the Golden-winged Warbler expanded even beyond the western portion of the vacated territory.

Discussion.—If interference competition by Blue-winged Warblers is a limiting factor for Golden-winged Warblers, then dominance by Blue-winged Warblers must be sufficiently frequent and intense, and suitable habitat must be sufficiently limited, that Golden-winged Warblers are excluded from suitable nesting habitat. Our observations, however, indicate clearly that interactions between Golden-winged Warblers and Blue-winged Warblers are uncommon (one per 16 h). The rate of dominance interactions between these two species was even lower during a study in central Michigan (one per 24 h; Will 1986).

Will (1986) observed that the frequencies of interspecific and intraspecific aggression were virtually identical, suggesting that Blue-winged Warblers and Golden-winged Warbler treat each other as conspecifics. However, intraspecific territorial overlap does not occur in these species (Murray and Gill 1976, Confer and Knapp 1977, Will 1986), whereas interspecific overlap can be extensive. At our sites with about a 1:1 ratio of Golden-winged to Blue-winged warbler males, overlap ranged from 20 to 60%; in central Michigan, overlap averaged 49% of the Golden-winged Warbler territories (Will 1986). Despite the greater potential for interspecific aggression, intraspecific and interspecific aggression occur with the same frequency in these two species.

The absence of interspecific aggression between most males may account for the high overlap between the territories of Golden-winged and Blue-winged warblers (Confer and Knapp 1977, Will 1986). Murray and Gill (1976) commented that "As reported by Ficken and Ficken (1968) and by us elsewhere (Gill and Murray 1972), male Golden-winged and Blue-winged warblers by and large ignore each other."

The intense interactions at two Golden-winged Warbler nests do not support the hypothesis that interference competition for territorial space limits Golden-

winged Warblers. In one case, the territories overlapped substantially, and pursuit by the Golden-winged Warbler occurred only near the nest. In the second case, the male Golden-winged Warbler dominated the male Blue-winged Warbler and expanded into its territory. In contrast, Will (1986) observed that Blue-winged Warblers often dominate Golden-winged Warblers, and he speculated that Blue-winged Warblers drive Golden-winged Warblers from the drier sites that both species prefer.

Will (1986) monitored a total of 60 individuals at one site for three years. We observed more than four times as many males at a total of 21 sites. Our larger sample reduces the potential of biasing the results due to specific birds or site-specific factors. Only 54% of the territorial male Golden-winged Warblers, and 64% of the territorial male Blue-winged Warblers, had mates at Will's study site. We had evidence of pairing for 78% of the territorial male Golden-winged Warblers. Perhaps at Will's site, the high proportion of unmated male Golden-winged Warblers resulted in them encountering many females that were defended by dominant, mated Blue-winged Warblers.

Results from our removal experiments seemed conclusive. In five of six cases, Golden-winged Warblers showed no significant expansion into the territory of the removed Blue-winged Warbler. Only one new bird, a Blue-winged Warbler, moved into a vacated territory. Thus, at least in our study area, the removal experiments provided little evidence for the presence of unmated males looking for vacant breeding territories.

In summary, our results in north-central New York indicate that: (1) interactions between male Golden-winged and Blue-winged warblers are rare, (2) most adjacent males of the two species ignore each other, (3) Golden-winged Warblers dominate most of the few interspecific interactions that do occur, (4) Golden-winged Warblers generally do not expand into vacated Blue-winged Warbler territories, and (5) suitable nesting habitat is sufficiently abundant that there seem to be few males seeking territories by late May. We conclude that Blue-winged Warblers generally do not drive Golden-winged Warblers into inferior nesting habitat and that interference competition is not the cause of the decline of Golden-winged Warblers.

Hybridization by extrapair copulation or interspecific pair formation might affect population trends differently for these two species. The most common hybrid pairings in our area, pure male Golden-winged Warblers with hybrid females, and hybrid males with pure female Blue-winged Warblers, produce young with a preponderance of Blue-winged Warbler mitochondrial DNA (because inheritance of mitochondrial DNA [mtDNA] is matrilineal). Gill (1997) documented an asymmetrical transmission of mtDNA whereby most phenotypic Golden-winged Warblers and hybrids have Blue-winged Warbler mtDNA. However, an asymmetry in the transmission of mtDNA does not by itself explain why the

Golden-winged Warbler phenotype, which is controlled by the action of nuclear genes, often disappears in areas with hybridization. The asymmetrical transmission of mtDNA and its relationship to population change need further study.

Acknowledgments.—Many students provided invaluable and dedicated assistance during this study. In particular, this includes D. Coker, M. Armstrong, and P. Allen, who worked for two years. We are most grateful to the numerous landowners who provided access to their property. The administrators of Cornell's Biological Field Station, especially E. Mills, J. and J. Forney, and D. Green, provided a home base and collegial support. N. Rodenhouse, F. Gill, and L. Stenzler helped at our study sites. We are grateful for the reviews of R. Holmes, F. Gill, P. Hunt, L. Petit, and an anonymous reviewer. P. Hamill and the personnel of Planned Dynamics provided special assistance. Financial support came from the following: Ithaca College Provost's Research Grant, two grants from The Max McGraw Foundation, NSF-ROA supplement to grant BSR-8817950 to H. Pulliam and J. Dunning, Jr., National Geographic Society Grant 4302-90, NSF Grant and Supplement BSR-910781, NSF Mid-Career Fellowship 1991-92, and U.S. Fish and Wildlife Service Grant 14-48-0005-94-9046. Particular appreciation is due to K. Allaben-Confer, who tolerated prolonged absences for many summers and provided essential life support.

LITERATURE CITED

- BENTON, A. H. 1950. Bird population changes in a central New York county since 1870. *Kingbird* 1: 2-11.
- CENSUS OF AGRICULTURE. 1935. Vol. II. Government Printing Office, Washington, D.C.
- CENSUS OF AGRICULTURE. 1992. Vol. I. Geographic area series. Government Printing Office, Washington, D.C.
- CONFER, J. L. 1992a. Golden-winged Warbler (*Vermivora chrysoptera*). In *The birds of North America*, no. 20 (A. Poole, P. Stettenheim, and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- CONFER, J. L. 1992b. Golden-winged Warbler, *Vermivora chrysoptera*. Pages 369-383 in *Migratory nongame birds of management concern in the Northeast* (K. J. Schneider and D. M. Pence, Eds.). United States Fish and Wildlife Service, Newton Corner, Massachusetts.
- CONFER, J. L., D. COKER, M. ARMSTRONG, AND J. DORHERTY. 1991. The rapidly changing distribution of the Golden-winged Warbler (*Vermivora chrysoptera*) in central New York. *Kingbird* 41:5-10.
- CONFER, J. L., AND K. KNAPP. 1977. Hybridization and interactions between Blue-winged and Golden-winged warblers. *Kingbird* 27:181-190.

- CONFER, J. L. AND K. KNAPP. 1981. Golden-winged Warblers and Blue-winged Warblers: The relative success of a habitat specialist and a generalist. *Auk* 98:108–114.
- FICKEN, M. S., AND R. W. FICKEN. 1968. Territorial relationships of Blue-winged Warblers, Golden-winged Warblers, and their hybrids. *Wilson Bulletin* 80:161–172.
- GILL, F. B. 1980. Historical aspects of hybridization between Blue-winged and Golden-winged warblers. *Auk* 97:1–18.
- GILL, F. B. 1997. Local cytonuclear extinction of the Golden-winged Warbler. *Evolution* 51:519–525.
- GILL, F. B., AND W. E. LANYON. 1964. Experiments on species discrimination in Blue-winged Warblers. *Auk* 81:53–64.
- GILL, F. B., AND B. G. MURRAY, JR. 1972. Discrimination behavior and hybridization of the Blue-winged and Golden-winged warblers. *Evolution* 26:282–293.
- HANDS, H. M., R. D. DROBNEY, AND M. R. RYAN. 1989. Status of the Golden-winged Warbler in the north-central United States. United States Fish and Wildlife Service, Twin Cities, Minnesota.
- HILL, N. P., AND J. M. HAGAN III. 1991. Population trends of some northeastern North American landbirds: A half-century of data. *Wilson Bulletin* 103:165–182.
- HOLMES, R. T., T. W. SHERRY, AND F. W. STURGES. 1986. Bird community dynamics in a temperate deciduous forest: Long-term trends at Hubbard Brook. *Ecological Monographs* 50:201–220.
- LITVAITIS, J. A. 1993. Response of early successional vertebrates to historic changes in land use. *Conservation Biology* 7:866–873.
- MURRAY, B. G., JR., AND F. B. GILL. 1976. Behavioral interactions of Blue-winged and Golden-winged warblers. *Wilson Bulletin* 88:231–254.
- RAPPOLE, J. H., AND M. V. McDONALD. 1994. Cause and effect in population declines of migratory birds. *Auk* 111:652–660.
- SAUER, J. R., J. E. HINES, G. GOUGH, I. THOMAS, AND B. G. PETERJOHN. 1997. The North American Breeding Bird Survey home page, version 96.3. Patuxent Wildlife Research Center, Laurel, Maryland.
- SCHEIDER, F. 1959. Warblers in southern New York. *Kingbird* 9:13–19.
- SMITH, C. R., D. M. PENCE, AND R. J. O'CONNOR. 1993. Status of Neotropical migratory birds in the northeast: A preliminary assessment. Pages 172–188 in *Status and management of Neotropical migratory birds* (D. M. Finch and P. W. Stangel, Eds.). United States Forest Service General Technical Report RM-229, Newton Corner, Massachusetts.
- WILL, T. C. 1986. The behavioral ecology of species replacement: Blue-winged and Golden-winged warblers in Michigan. Ph.D. dissertation, University of Michigan, Ann Arbor.
- WITHAM, J. W., AND M. L. HUNTER, JR. 1992. Population trends of Neotropical migrant landbirds in northern coastal New England. Pages 85–95 in *Ecology and conservation of Neotropical migrant landbirds* (J. M. Hagan III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D.C.

Received 21 October 1996, accepted 29 May 1997.

Associate Editor: L. J. Petit

The Auk 115(1):214–221, 1998

Numts: A Challenge for Avian Systematics and Population Biology

MICHAEL D. SORENSON^{1,3} AND THOMAS W. QUINN²

¹Museum of Zoology, University of Michigan, 1109 Geddes Avenue, Ann Arbor, Michigan 48109, USA; and

²Department of Biological Sciences, University of Denver, Denver, Colorado 80208, USA

The development of the polymerase chain reaction (PCR) and dramatic improvements in technologies for DNA sequencing over the last decade have provided new opportunities in avian systematics (Mindell 1997) and the study of population genetic struc-

ture (e.g. Quinn 1992). For reasons associated with its rapid rate of evolution, haploidy, and maternal inheritance (e.g. Moore 1995, Zhang and Hewitt 1996), recent work has focused on mitochondrial DNA (mtDNA). Direct sequencing of PCR products amplified from extracts of genomic DNA has circumvented the need for purified mtDNA. Almost any material is now a workable source of DNA for PCR, including blood, feathers, eggshells, feces, and other tissues from live birds; skin, feathers, cartilage, and

³Present address: Department of Biology, Boston University, 5 Cummington Street, Boston, Massachusetts 02215, USA. E-mail: msoren@bu.edu