

- Grubb, Jr., T. C. 1987. Changes in the flocking behavior of wintering English titmice with time, weather, and supplementary food. *Anim. Behav.* 35:794-806.
- Grubb, Jr., T. C., and D. A. Cimprich. 1990. Supplementary food improves the nutritional condition of wintering woodland birds: evidence from ptilochronology. *Ornis Scand.* 21:277-281.
- Szekeley, T., T. Tzep, and T. Juhasz. 1989. Mixed species flocking of tits (*Parus* spp.): a field experiment. *Oecologia* 78:490-495.
- Wedeking, P., J. L. Huie, and H. B. Suthers. 2001. Utilization of a limited preferred food resource by Blue Jays (*Cyanocitta cristata*). *N. Am. Bird Bander* 26:41-49.
- White, G. C. 1996. NOREMARK: population estimation from mark-resighting surveys. *Wildl. Soc. Bulletin.* 24:50-52.
- Wilson, Jr., W. H. 1994. The distribution of wintering birds in central Maine: the interactive effects of landscape and bird feeders. *J. Field Ornith.* 65: 512-519.
- Wilson, Jr., W. H. 2001. The effects of supplemental feeding on wintering Black-capped Chickadees (*Poecile atricapilla*) in central Maine: population and individual responses. *Wilson Bull.* 113: 65-72.
- Withers, P. C. 1992. Comparative animal physiology. Saunders College Publishing, Philadelphia, PA.
- Yunick, R. P. 1997. Measuring sugar water consumption to monitor fluctuations in hummingbird abundance. *N. Am. Bird Bander* 22:114-115.

Returns, Repeats and Observations of Wilson's Warblers and Other Neotropical Migrants Wintering in a Costa Rican Cloud Forest

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ABSTRACT

In a cloud forest in the Cordillera de Talamanca, Costa Rica, six species of Neotropical migrant songbirds were banded and color-marked during eight 2-3 week mist-netting periods between Jan and early May, 1987-1993. Returns, repeats, and observations of behavior suggested that some Wilson's Warblers (*Wilsonia pusilla*) defended territories. Nine of 43 Wilson's Warblers were banded in the last year of the study, leaving a possible 34 returns. Twelve of 34 (35.3%) returned in subsequent years. One of five banded Golden-winged Warblers (*Vermivora chrysoptera*) was seen up to two weeks later in the year of banding, and one of two banded Summer Tanagers (*Piranga rubra*) was sighted four and five years

later. Individuals of three additional species were assumed to be migrating and were not recaptured or seen again.

INTRODUCTION

Individuals of many species of migratory birds not only return to reoccupy the nest sites or territories they held during the previous breeding season (Emlen 1975), but also return in successive years to the same location on the "wintering" grounds (Moreau 1969, Rappole 1995). The Wilson's Warbler (*Wilsonia pusilla*) is among the Neotropical migratory species known to be faithful to the winter quarters, based on banding conducted over several years in Belize (Nickell 1968), El Salvador (Thurber and Villeda 1980) and Mexico (Ely et al 1977, Rappole and Warner 1980). Returns, repeats, and sightings of banded and color-marked Wilson's Warblers in a cloud forest in Costa Rica add another locality to which this species returns in winter; and they also suggest that some individuals are sedentary until they depart in spring.

Wilson's Warblers and Black-throated Green Warblers (*Dendroica virens*) were the most common Neotropical migrants on the study area, but additional species of migrants were recorded on or adjacent to the site. Wilson's Warblers were netted readily because many foraged and interacted with one another and other species in second growth vegetation, low enough to be netted; but no Black-throated Green Warblers were captured as individuals foraged above the nets in the middle-to-upper canopy of mainly second-growth forest. Five Golden-winged Warblers (*Vermivora chrysoptera*) and two Summer Tanagers (*Piranga rubra*) were banded and later sighted. Individuals of the Western Wood-Pewee (*Contopus sordidulus*), Swainson's Thrush (*Catharus ustulatus*), and Mourning Warbler (*Oporornis philadelphia*) species were banded but not recaptured or seen again.

METHODS

Study area - During a study of distress calls of cloud forest birds (Neudorf and Sealy 2002), migrants were captured and observed within a 30-ha preserve of lower montane rain forest (Tosi 1969, Kappelle et al. 1992) on the Caribbean slope just below the continental divide (9°42' N, 83°54' W; 2300 m elev.) at the northwestern end of the Cordillera de Talamanca, Provincia Cartago, Costa Rica. The area is about 4 km from El Cañón off Km 58 of the Pan American Highway. Decades earlier a portion of the forest had been selectively logged and second growth was extensive. The preserve abutted a pasture on one side, forest that was being logged for charcoal production on two sides, and the fourth side was continuous with the Río Macho forest preserve that eventually merged with the Refugio Nacional de Fauna Silvestre Tapantí. Several tributaries of the Río Macho ran along and through the study area. About 4 km of trails penetrated the area and provided access to adjacent areas where additional observations were made. Mist nets were set along about 700 m of trails and in clearings, in various habitats. Some net sites were permanent across netting periods, whereas others were rotated every 4 - 5 days.

Banding - Birds were banded with United States Fish and Wildlife Service (USFWS) bands and given unique combinations of colored celluloid

bands. Banding was conducted during eight netting periods from 1987 to 1993 on the following dates: 17 Jan - 6 Feb (740 net-hr) and 29 Apr - 9 May 1987 (489.5 net-hr), 20 - 31 Mar (657.5 net-hr) and 29 Jul - 6 Aug 1988 (443 net-hr), 10 - 21 Feb 1990 (1001.5 net-hr), 18 - 29 Jan 1991 (893 net-hr), 25 Apr - 5 May 1992 (997.5 net-hr), and 9 - 17 Feb 1993 (922 net-hr), for a total of 6,144 net-hr that spanned most of the second half of the dry season (mid-Jan through early May). Six to 10 nets were operated from about 06:00 to 16:30 CDT on most days and usually were checked every 20 min. Nets were not operated when it was raining or too windy. Returns and repeats of banded birds were supplemented by sightings of marked individuals. Color-marked Wilson's Warblers and Summer Tanagers were recorded occasionally by Paula and Steve Friedman (hereafter Friedmans) when I was not on the study area. Observations of migrants and other birds also were made during each netting period and between 13 Mar and 2 Apr 1986, a period when no banding occurred.

I distinguished male Wilson's Warbler from females on the basis of the criteria presented by McNicholl (1977) and the U.S. Fish and Wildlife Service and Canadian Wildlife Service (1980). I designated as males individuals with distinct black "caps" and those with black especially evident in the anterior part of the crown (categories 3 and 4 of Weicker and Winker 2002) and as females those with caps sprinkled with black feathers, or no caps (categories 1 and 2). I may have mis-sexed six individuals that fell into categories 2 and 3 and they are treated here as unknown sex. In a recent paper, Weicker and Winker (2002:68) showed that "males have larger caps on average, but there is an intergradation between the sexes." I measured the discrete caps, made notes on the distribution of black feathers in the crowns of other individuals, and designated some as having "no caps" (category 1).

Hostile Interactions - Every time I saw a migrant chasing, being chased, or being attacked by an individual of the same or another species, I attempted to record the species that initiated the chase and the species that was being chased.

SPECIES ACCOUNTS

Wilson's Warbler - This species was the most common Neotropical migrant on the study area, as elsewhere at this and higher elevations in this mountain range (Wolf 1976, Stiles and Skutch 1989). Forty-three individuals were banded and color-marked (22 males, 15 females, 6 unknown sex) through 1993. As nine were banded in 1993, the last year of banding, 34 individuals could have been recorded as returns (Table 1). Of these, 10 were recaptured and two more were sighted in one or more of the subsequent six years, for a total of 12 returns (35.3%; 6 males, 5 females, 1 unknown sex; Table 1). This frequency of return is high. By contrast, 3 of 49 (6.1%) Wilson's Warblers banded in southern Mexico returned in one of five subsequent years (Ely et al. 1977). Thurber and Villeda (1980) recaptured eight Wilson's Warblers at the same sites in El Salvador after one or more intervening breeding seasons.

Returning birds were captured or sighted two or more times at or near the original capture site after one ($n = 8$), two (1), five (2), and six (1) intervening breeding seasons (Table 1). In 1987, time between banding and last sighting was 106 d for female 1750-53905 (banded 21 Jan, last sighted 7 May), 94 d for female -53909 (30 Jan, 4 May), 92 d for male -53910 (30 Jan, 2 May), and 88 d for female -53911 (30 Jan, 28 Apr). Each individual was sighted 15 - 20 m from its original banding site. At the site where female -53905 was seen on 6 May and for the last time on 7 May, an unbanded female was present on 9 and 10 May.

Sightings of marked birds, not necessarily the same individuals, spanned about 220 d from late Sep to early May. Although lone unbanded males were sighted earlier (19 Sep 1991, 26 Sep 1992, and 22 Sep 1993), the first banded male (-53902) was sighted on 29 Sep 1991. This male, banded on 20 Jan 1987, was also seen 31 Mar 1987 (singing), 28 Mar 1991, 30 Sep 1991, and for the last time on 2 Jan 1992 (Table 1). The latest sighting of a marked bird was, as noted above, female -53905 on 7 May 1987. In addition to the late Apr and early May 1987 sightings, in 1992 male -53941 was seen and heard singing on 4 May and two or three unbanded individuals were seen daily in late Apr through 5 May. Sample sizes were

small but most individuals that lingered into May were females. South of my study area, at the higher elevation of the Cerro de la Muerte, Wolf (1976) recorded the earliest Wilson's Warbler on 2 Sep [1966] and the last bird on 25 May [1967], but heard no singing.

Stiles and Skutch (1989) stated that Wilson's Warblers occur in Costa Rica from mid-Sep through mid-May. Thurber and Villeda (1980) considered Neotropical migrants captured between 15 Nov and 15 Feb to be winter residents and individuals encountered before and after those dates to be transients. Recaptures and sightings in my study area reveal that winter residents occupy most of this period. Unbanded birds observed during the early and late parts of this period may be transients, although the presence of marked individuals until at least early May confirms that some individuals linger on the wintering area before departing in spring and should not be assumed to be transients. Winter residents likely co-occur for brief periods with transients during their migrations.

Sightings suggest some Wilson's Warblers defended territories. Of the four males and five females color-marked between 20 and 30 Jan 1987, two males and all of the females were located several times feeding singly in the same locations. Individuals perch-gleaned insects or other small invertebrates off the surfaces of stems and leaves and occasionally aerial hawked flying prey (see also Wolf 1976). Aggressive interactions also suggest territorial defense. During four hours of observations of five marked birds in 1987, nine chases resulted as foraging individuals approached other individuals: five times the same male chased at least three different males, twice a male chased different females, and two females chased unidentified individuals. Powell (1980) also recorded Wilson's Warblers behaving agonistically against conspecifics and he suggested that the birds defended areas of several meters surrounding themselves, although the shortness of typical chases did not support a conclusion of true territoriality (see also Moynihan 1962, Wolf 1976) Wolf (1976) did not hear any singing.

Wilson's Warblers also interacted with other species on the site, both tropical residents and migrants. Twice in Mar 1986 male Wilson's

Table 1. Returns of Wilson's Warblers after Intervening Breeding Seasons*

USFWS Band Number	Sex	Date First Captured	Date Last Encountered	Number of Days Encountered
1750 -53902	M	20 Jan 87	02 Jan 92	5
-53905	F	21 Jan 87	29 Feb 88	7
-53906	M	23 Jan 87	24 Mar 88	2
-53907	M	23 Jan 87	27 Jan 88	4
-53909	F	30 Jan 87	20 Jan 88	7
-53910	M	30 Jan 87	13 Apr 92	4
-53911	F	30 Jan 87	09 Feb 93	6
-53921	F	10 Feb 90	19 Jan 91	2
-52923	M	12 Feb 90	25 Jan 91	3
-53924	F?	12 Feb 90	19 Jan 91	2
-53929	M	19 Feb 90	03 May 92	2
-53939	F	29 Apr 92	16 Feb 93	2

* Number banded in 1987 = 12, 1988 = 4, 1990 = 12, 1991 = 3, 1992 = 3, and 1993 = 8. The last encounters of females -53905 and -53709 and male -53907 were sightings, the rest were recaptures. Female -53721 had an injured but healed leg when banded.

Warblers supplanted larger Black-billed Nightingale-Thrushes (*Catharus gracillirostris*), and in 1986 and 1987 individual female Wilson's Warblers, foraging near the orange flowers of a species of *Bomarea*, were chased by a male Magnificent Hummingbird (*Eugenes fulgens*). Of 28 mixed-species foraging flocks observed on the study area and adjacent woodlands in 1987, single Wilson's Warblers were observed participating in two (7.1%) flocks that foraged along the edge of second-growth habitat. They moved with the flock, however, only a few meters before dropping out and remained behind when the flocks moved on (see also Buskirk et al. 1972, Powell 1980). One of the flocks, observed on 18 Mar 1986, in which a Wilson's Warbler participated, was comprised of Sooty-capped Bush-Tanager (*Chlorospingus pileatus*, $n = 5$ individuals), Buffy Tuftedcheek (*Pseudocolaptes lawrencii*, 1), Black-and-Yellow Phainoptila (*Phainoptila melanoantha*, 1), Flame-throated Warbler (*Parula gutturalis*, 1), and Collared Redstart (*Myioborus torquatus*, 2). Stiles (1983) noted that Wilson's Warblers regularly participated in mixed flocks at the mid-elevations (see also Mlecko 1968, Buskirk et al. 1972, Buskirk 1976) but less so at higher elevations.

Golden-winged Warbler - This species was uncommon and not encountered every year. There is no evidence from other studies (Loftin et al. 1966, Loftin 1977) that Golden-winged Warblers return to their previous winter quarters (see also Rappole 1995). Of five individuals banded (2 males, 3

females), none was recorded in a subsequent year. Banded on 17 Jan 1987, male -53901 was recaptured on 23 Jan, about 50 m from the original net site and a female banded on 20 Jan 1991 was recaptured on 22 Jan at 07:35 and again at 14:45, about 100 m from the capture site. The others were banded on 20 Jan 1987 (female), 30 Mar 1988 (male), and 20 Jan 1991 (female).

Unbanded males were observed foraging alone on 27 Mar 1986, 19 Jan 1987, and 22 Mar 1988. Several days after banding, male -53901 was sighted moving and foraging with a mixed-species flock, about 100 m from the original banding site. The other flock members were Sooty-capped Bush-Tanager (3), Ruddy Treerunner (*Margarornis rubiginosus*, 2), Barred Becard (*Pachramphus versicolor*, 1), Flame-throated Warbler (2), and Spangle-cheeked Tanager (*Tangara dowii*, 2). In Panamá, Buskirk et al. (1972) inferred from observations of unmarked Golden-winged Warblers that the warblers were "followers" of foraging flocks, recorded repeatedly with a particular flock. Mlecko (1968) and Powell (1979) similarly concluded this from observations at lower elevations in Costa Rica.

Summer Tanager - An adult male was banded on 30 Jan 1987 and seen two days later near the capture site. A second-year male, molting extensively on the head and body, was banded on 30 Mar 1988 and seen within 40 m of the original banding site on 6 Mar 1992 and on 29 Jan 1993 (Friedmans, pers. comm.), four and five years later, respectively. Unbanded males in adult plumage were sighted on 28-31 Jan and 5 Feb 1987 in about the same location, 21 and 23 Mar 1988 (sightings about 500 m apart) and 19 Feb 1990. Unbanded second-year males were sighted on 2 Feb 1987 and 21 - 22, 26 and 29 Mar 1988 (possibly the same

individual). Each foraged alone at the edge of second growth. The irregularity of sightings suggests that individuals wandered widely and did not establish territories. Although one Summer Tanager returned four and five years after banding, it was not recaptured or seen earlier.

There are three other reports of Summer Tanagers returning to their previous winter quarters. A female banded in Honduras was recaptured at the same site two years later (Nickell 1968). Two of 61 birds banded in Panamá were recaptured one year later (Loftin et al. 1966). Another bird, banded on 15 Oct 1965, was recaptured two years later, and one captured on 18 Mar 1967 returned the following year (Loftin 1977). Neither of the two Summer Tanagers banded by Warkintin and Hernández (1996) in Costa Rica was recorded in a subsequent year.

DISCUSSION

Following Rappole et al.'s (1992) definition of a winter resident, a bird with a documented stay on a site of more than 30 d, several Wilson's Warblers qualified as winter residents on the study area. Indeed, some were present for about 100 d. When different individuals were considered, the on-site residency was about 220 d, with arrival in late Sep and departure in early May. This is longer than the 175 d on site reported for Wilson's Warblers in Veracruz, with an arrival in early Nov and departure in late Apr. There, the earliest arrival and latest departure for an individual was 148 d (Rappole et al. 1992) and territories were occupied up to 140 d (Rappole and Warner 1980, Rappole et al. 1992). Karr (1971) also reported long-term site tenacity of an individual Kentucky Warbler (*O. formosus*) in a Panamanian forest.

Other studies found that some species defended habitat patches only for a portion of the winter, possibly during the dry season; and some individuals were identified as floaters that wandered about the site (Rappole et al. 1989, Mabey and Morton 1992). In addition to observations of behavior of marked birds, defense of territories was suggested when captured wintering birds returned to their presumed territories after being released 2 km away (Rappole et al. 1989). In the present study, although some

Wilson's Warblers were not encountered after banding, which suggests that they did not defend a habitat patch and perhaps moved around, others were engaged in chases, periodically sang, and exhibited site fidelity across years. These behaviors, among the six that Rappole (1995:39) listed as evidence for territoriality in wintering songbird migrants, suggest that some Wilson's Warblers defended territories during the second part of the wintering season.

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LITERATURE CITED

- Buskirk, W.H. 1976. Social systems in a tropical forest avifauna. *Amer. Nat.* 110:293-310.
- Buskirk, W.H., G.V.N. Powell, J.F. Wittenburger, R.E. Buskirk, and T.U. Powell. 1972. Interspecific bird flocks in tropical highland Panama. *Auk* 89: 612-624.
- Ely, C. A., P. J. Latas, and R. R. Lohofener. 1977. Additional returns and recoveries of North American birds banded in southern Mexico. *Bird-Banding* 48: 275-276.
- Emlen, S.T. 1975. Migration: orientation, and navigation. Pp. 129-219 *In* Avian biology, Vol. V. D.S. Farner, J.R. King, and K.C. Parkes [eds.]. Academic Press, London.
- Kappelle, M., A.M. Cleef, and A. Chaverri. 1992. Phytogeography of Talamanca montane *Quercus* forests, Costa Rica. *J. Biogeogr.* 19:299-315.

- Karr, J.R. 1971. Wintering Kentucky Warblers (*Oporornis formosus*) and a warning to banders. *Bird-Banding* 42:299.
- Loftin, H. 1977. Returns and recoveries of banded North American birds in Panama and the tropics. *Bird-Banding* 48:253-258.
- Loftin, H., D. T. Rogers, Jr., and D. L. Hicks. 1966. Repeats, returns and recoveries of North American migrant birds banded in Panama. *Bird-Banding* 37:35-44.
- Mabey, S. E. and E. S. Morton. 1992. Demography and territorial behavior of wintering Kentucky Warblers in Panama. Pp. 329-336 *In* Ecology and conservation of Neotropical migrant landbirds. J. M. Hagan III and D. W. Johnston [eds.]. Smithsonian Inst. Press, Washington, D.C.
- McNicholl, M. K. 1977. Measurements of Wilson's Warblers in Alberta. *N. Am. Bird Bander* 2: 108-109.
- Mlecko, B. E. 1968. Notes on the birds of Costa Rica with special emphasis on flocking. *Proc. Iowa Acad. Sci.* 75:457-462.
- Moreau, R.E. 1969. The recurrence in winter quarters (Ortstreue) of trans-Saharan migrants. *Bird Study* 16:108-110.
- Moynihan, M. M. 1962. The organization and probable evolution of some mixed species flocks of Neotropical birds. *Smithsonian Misc. Coll.* 143:1-140.
- Neudorf, D. L. and S. G. Sealy. 2002. Distress calls of birds in a Neotropical cloud forest. *Biotropica* 34:118-126.
- Nickell, W. P. 1968. Return of northern migrants to tropical winter quarters and banded birds recovered in the United States. *Bird-Banding* 39:107-116.
- Powell, G.V.N. 1979. Structure and dynamics of interspecific flocks in a Neotropical mid-elevation forest. *Auk* 96:375-390.
- Powell, G.V.N. 1980. Migrant participation in Neotropical mixed species flocks. Pp. 477-483 *In* A. Keast and E.S. Morton [eds.] Migrant birds in the Neotropics; ecology, behavior, distribution, and conservation. Smithsonian Inst. Press, Washington, D.C.
- Rappole, J.H. 1995. The ecology of migrant birds. Smithsonian Inst. Press, Washington, D.C.
- Rappole, J.H. and D.W. Warner. 1980. Ecological aspects of migrant bird behavior in Veracruz, Mexico. Pp. 353-393 *In* A. Keast and E.S. Morton [eds.] Migrant birds in the Neotropics; ecology, behavior, distribution, and conservation. Smithsonian Inst. Press, Washington, D.C.
- Rappole, J.H., E.S. Morton, and M.A. Ramos. 1992. Density, philopatry, and population estimates for songbird migrants wintering in Veracruz. Pp. 337-344 *In* J.M. Hagan III and D.W. Johnson [eds.] Ecology and conservation of Neotropical migrant landbirds. Smithsonian Inst. Press, Washington, D.C.
- Rappole, J.H., M.A. Ramos, and K. Winker. 1989. Wintering Wood Thrush movements and mortality in southern Veracruz. *Auk* 106: 402-410.
- Stiles, F.G. 1983. Birds. Pp. 502-544 *In* D.H. Janzen [ed.] Costa Rican natural history. University of Chicago Press, Chicago, IL.
- Stiles, F.G. and A.F. Skutch. 1989. A guide to the birds of Costa Rica. Comstock Pub. Assoc., Ithaca, NY.
- Thurber, W.A. and A. Villeda. 1980. Wintering site fidelity of migrant passerines in El Salvador, Central America. *N. Am. Bird Bander* 5:131-135.
- Tosi, J., Jr. 1969. Ecological map of Costa Rica. Tropical Science Center, San José, Costa Rica.
- U.S. Fish and Wildlife Service and Canadian Wildlife Service. 1980. Bird banding manual. Vol. 2: North American bird banding techniques. Canadian Wildlife Service, Ottawa.
- Warkentin, I.G. and D. Hernández. 1996. The conservation implications of site-fidelity: a case study involving Nearctic-Neotropical migrant songbirds wintering in a Costa Rican mangrove. *Biol. Conserv.* 77:143-150.
- Weicker, J.J. and K. Winker. 2002. Sexual dimorphism in the birds from southern Veracruz, Mexico, and other localities. III. Wilson's Warbler. *J. Field Ornithol.* 73:62-69.
- Wolf, L. 1976. Avifauna of the Cerro de la Muerte region Costa Rica. *Am. Mus. Novit.* 2606:1-37.