WINTER SITE FIDELITY OF PRAIRIE WARBLERS IN THE DOMINICAN REPUBLIC

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Abstract. Wintering Prairie Warblers (*Dendroica discolor*) were studied in pine forest, desert thorn scrub, and desert wash habitats of the Sierra de Bahoruco, Dominican Republic from October–April 1996–1998 and January–February 1999. We used mist netting, color banding, and extensive resighting of color-banded birds to quantify habitat-specific demographies, site fidelity, and fitness indices. Males predominated early in the season in pine habitat while females predominated in the desert. Sex ratios were more equal through the drier months of late winter although females continued to be more frequent in the desert. Adult birds predominated throughout all habitats and time periods. Nonterritorial wanderers were far more common in desert habitats than in pine forest, and females predominated among these wanderers. Site persistence was moderately high, but variable between habitats and time periods, and was significantly lower in the drier months in thorn scrub than it was in the desert wash or pine forest. Annual return rates were generally high and did not vary significantly among years. Birds showed significant declines in pectoral-muscle-mass scores in both of the desert habitats but not in the pine forest. Data presented here emphasize the importance of dry-season events and habitat heterogeneity in the winter ecology of migratory birds.

Key words: demographics, Dendroica discolor, *Hispaniola, Neotropical migrants, Prairie Warbler, site fidelity, winter ecology.*

Fidelidad al Territorio Invernal de *Dendroica discolor* en la República Dominicana

Resumen. En los meses de octubre a abril de 1996 a 1998 y enero y febrero de 1999, investigamos a *Dendroica discolor* en el bosque de pino, en los matorrales del desierto y en el arroyo seco de desierto en la Sierra de Bahoruco, República Dominicana. Para llevar a cabo esto, se utilizaron redes ornitológicas y anillos colorados. Se realizó una revisión extensiva de las aves anilladas para cuantificar la demografía en los tres hábitats, la fidelidad al territorio invernal, y los índices de aptitud ("fitness"). Al comenzar el invierno, los machos predominaron en el bosque de pino mientras que las hembras lo hicieron en el desierto. La proporción entre los machos y las hembras mantuvo una mayor igualdad entre los sexos en los meses más secos del invierno, aunque hay que considerar que las hembras predominaban en el desierto. Se observó que las aves adultas predominaban en los tres hábitats durante todo el período investigado. Las aves sin territorio eran más comunes en el desierto y eran mayormente hembras. La fidelidad al lugar fue moderadamente alta pero variable entre los hábitats y los períodos y fue significativamente más baja en los meses secos en los matorrales del desierto que en los arroyos secos y los bosques de pino. La tasa anual de retorno de esta especie fue generalmente alta y no varió significativamente entre años. La masa de los músculos pectorales bajó significativamente en las aves que se encontraban en los matorrales del desierto y en el arroyo seco pero no en los bosques de pino. Los datos mencionados aquí acentúan la importancia de eventos que ocurren en la época seca del período invernal y de la heterogenidad del hábitat en la ecología invernal de las aves migratorias.

INTRODUCTION

Understanding winter limitation of populations of Neotropical migratory birds is fundamental to their ecology and conservation. Fretwell's

(1972) Ideal Despotic Distribution model predicts that habitat of optimal suitability will fill with birds before habitat of lower suitability, and that settlement of subsequent individuals will be constrained by intraspecific territorial behavior. Fitness variation results because fitness is expected to decline either with increased density of birds in a habitat or with variation between optimal and suboptimal habitats. Fitness may also vary with sex or age class (i.e., Holmes et al. 1989, Wunderle 1995), and between territo-

rial birds and nonterritorial wanderers (Marra et al. 1993, Rappole and McDonald 1994).

Habitat-specific demographies are needed to assess the operation of the Ideal Despotic Distribution model within winter populations of migratory birds. Sherry and Holmes (1995) and Latta and Baltz (1997) summarized evidence for winter limitation of migrant species through age and sex-specific survival characteristics and site fidelity across an array of habitats, suggesting that differences in habitat quality limit populations. Most available data, however, are restricted to two species of migrants, the Black-throated Blue Warbler (*Dendroica caerulescens*) and the American Redstart (*Setophaga ruticilla*). Marra et al. (1998) went further and used habitat-specific isotopic markers to link winter habitat quality with arrival schedules on breeding grounds, suggesting that winter habitat quality can affect migrant survival and breeding success, thus supporting winter habitat limitation for the redstart. Discussion of differences in habitat quality for wintering migrants has focused on the role of food abundance (Holmes et al. 1989, Greenberg 1992, Wunderle and Latta 2000), but predators (see Sherry and Holmes 1996) and parasites (Latta 2000) have also been discussed as possibly limiting some winter populations of birds.

Site fidelity, measured in terms of overwinter site persistence or annual return rate, may provide an indication of the adequacy of resources within a site to a wintering bird. A site-persistent individual may be able to better dominate resources, be more familiar with fluctuations in resources, and have a greater ability to evade predators (Gauthreaux 1982, Shields 1984, Dobson and Jones 1986). Fidelity to an overwintering site by migratory birds has been documented both within winters (Holmes et al. 1989, Wunderle and Latta 2000) and between years (Faaborg and Arendt 1984, Wunderle 1995). Various studies have attempted to correlate rates of site fidelity with fitness measures such as pectoral-muscle mass scores, body mass, (Holmes et al. 1989, Wunderle 1995, Sherry and Holmes 1996), and adjusted body mass (Marra 1998, Wunderle and Latta 2000); individuals with higher fitness indices are expected to show higher site fidelity.

However, few studies have examined the ecology and site fidelity of a species across a range of optimal and suboptimal winter habitats (Wunderle 1995). Most studies of site fidelity of win-

tering migratory birds have focused on birds in presumably near-optimal habitats (Holmes et al. 1989, Wunderle and Latta 2000) in which habitats are assumed to be relatively homogeneous across space and time. Yet, we know from breeding-ground studies that bird abundance and species richness (James 1971, Holmes and Robinson 1981, Freemark and Merriam 1986), as well as life history characteristics (Andrewartha and Birch 1954, Dhondt et al. 1992, Both 1998) may shift in response to habitat heterogeneity and the microhabitats that heterogeneity produces. Similarly, although it has been suggested that habitat suitability may vary seasonally (Parrish and Sherry 1994), in most studies environmental or climatic conditions are assumed to be relatively constant throughout the wintering period and only a single annual measure of site fidelity is made (Greenberg 1992, Mabey and Morton 1992, Wallace 1998).

The Prairie Warbler (*Dendroica discolor*) is a Neotropical migrant moderately specialized in terms of its relative rates of occurrence in different habitats in the Greater Antilles (Wunderle and Waide 1993) where it principally winters (Rappole et al. 1983). In the Dominican Republic, the Prairie Warbler occurs in large numbers in pine forest, desert thorn scrub, and desert washes, where it forages by gleaning small insects from low broadleaf trees and shrubs, as well as from needles of taller pine trees. The Prairie Warbler is site faithful and defends distinct territories in these sites. Although Prairie Warblers are apparently not territorial in Puerto Rican overgrown pastures (Staicer 1992, Baltz 2000), territoriality in these Dominican sites was indicated by repeatability of observation of marked individuals in localized areas, response of birds to playback tapes, and surges in chipping activity and other aggressive interactions (SCL, pers. obs.) between adjacent individuals as described by Holmes et al. (1989) for other territorial migrants. This species roosts communally at low elevations, moving from the desert habitats to communal roosts in dense mangroves; there is no evidence of such communal roosting in pine forest (Latta, unpubl. data).

Here we present data on site fidelity of the Prairie Warbler from several habitats in the Dominican Republic. Our objective is to provide habitat-specific demographic data and fitness indices, including sex and age-class ratios, body condition, the prevalence of floaters and seden-

tary birds, overwinter site persistence, and annual return rates of Prairie Warblers in each habitat. We then use these data to help assess geographic variation in the winter ecology of the Prairie Warbler. We are especially interested in the effects of highly seasonal habitats on fitness indices and site persistence, and the effects of habitat heterogeneity on site fidelity.

STUDY SITES AND METHODS

Three study sites of 10–15 ha each were established in each of three habitats: low-elevation thorn scrub forest, dry desert wash (each 20–50 m elevation), and high elevation pine forest (1100–1475 m elevation) near Cabo Rojo and the Sierra de Bahoruco, Pedernales Province, Dominican Republic (18°0′N, 71°38′W). Desert wash sites were slightly smaller than the other sites due to their linear nature. All sites are characterized by having two dry seasons annually (Dec–Mar and July–Aug) with the July–Aug dry season less severe; the dry season in pine forest is less pronounced than at lower elevations.

Desert thorn scrub sites. Low-elevation desert thorn scrub is characteristic of dogtooth limestone substrate (Howard and Briggs 1953, Fisher-Meerow and Judd 1989) with very little exposed soil between the rocks. Vegetation consists of widely scattered, partially deciduous broadleaf trees and shrubs, and various cacti. Common tree species include *Capparis cynophallophora, C. ferruginea, Guaiacum officinale, Haitiella ekmanii, Metopium brownei, Phyllostylon brasiliensei,* and *Plumeria obtusa.* Common shrubs include *Croton origanifolius, C. discolor,* and *Lippia alba* (Fisher-Meerow and Judd 1989).

A foliage height profile (Fig. 1a) constructed from data from these sites (Latta and Brown 1999) shows a low, open canopy with an understory dominated by broadleaf shrubs. Few forbs are present on the rocky floor, with sparse cacti and succulents occasionally extending into the canopy. Canopy cover is spare and averages 22% (SD = 28.4) with greatest cover in the 2–4 m height categories and a maximum height of only 6 m. Mean and median broadleaf tree heights are 1.4 m (SD = 1.0 m) and 1.2 m respectively.

Desert wash sites. Dry washes are very widely scattered, linear habitats approximately 50 m in width surrounded by desert thorn scrub habitat. Dry washes tend to have more exposed soil
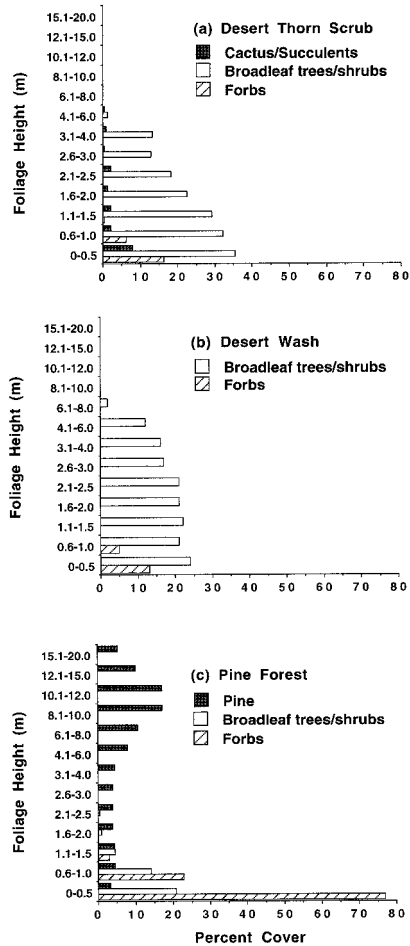

FIGURE 1. Vegetation profiles of (a) desert thorn scrub, (b) desert wash habitat, and (c) pine forest in the Sierra de Bahoruco, Pedernales Province, Dominican Republic. Profiles are derived from twelve 11.3-m-radius circular plots (0.04 ha) in each habitat. Percent cover represents the mean percentage of vegetation touches on a raised pole in a given foliage height category.

than desert thorn scrub sites. Vegetation is dominated by buttonwood trees (*Conocarpus erectus*) which are not deciduous and are not found in the thorn scrub. The foliage height profile (Fig. 1b) shows a moderately dense but uniform cover from 0–6 m in height that is dominated by broadleaf trees. Few forbs are present. Canopy cover averages 46% (SD = 40.8) with a maximum height of 8 m. Mean and median broadleaf tree heights are 4.4 m (SD = 0.8 m) and 4.0 m respectively. Desert wash sites in this study were directly adjacent to desert thorn

scrub sites. Individual birds with >50% of re-sightings in the desert wash (as opposed to adjacent desert thorn scrub) were considered residents of the wash for analyses.

Pine sites. Pine forests in the Sierra de Bahoruco are dominated by Hispaniolan Pine (*Pinus occidentalis*); the only other common tree is the palm *Coccothrinax scoparia.* A well-developed shrub layer is present, and common broadleaf species include *Cestrum brevifolium, Chamaecrista glandulosa, Coreopsis buchii, Hypericum hypericoides, Lyonia truncata, L. microcarpa, Myrica picardae,* and *Senecio picardae.* The ground is covered by a thick layer of grasses (Fisher-Meerow and Judd 1989).

A foliage height profile (Fig. 1c) constructed from data from these sites (Latta and Sondreal 1999) shows a fairly open canopy, a sparse intermediate layer of pine, and a dense, mixed broadleaf and pine understory. Canopy cover averages 51% (SD = 26.4) with greatest cover in the 6–15 m height categories and a maximum pine height of 23 m. Mean and median pine heights are 17.7 m (SD = 4.9 m) and 19.0 m, respectively. The intermediate layer also consists solely of pine. Broadleaf trees and shrubs form a dense ground cover and understory, with broadleaf trees extending to 2.5 m in height. Young pine are also present in the understory.

Temperature and rainfall. Maximum and minimum temperatures and accumulated rainfall during the tenure of this study were recorded weekly from one desert and one pine site.

Sampling birds. We studied Prairie Warblers from 1 October–1 April 1996–1997 and 1997–1998, and from 8 January–15 February 1999. Birds in pine and desert thorn scrub were sampled with mist nets (12 m × 3 m × 30 mm mesh) set in three parallel rows of 11–16 nets each; nets in the desert wash were placed in a single line of 24 nets over approximately 350 m. Birds were sampled three times annually, in early winter (November), midwinter (January), and late winter (March) 1996–1998, and again in January 1999; birds were not sampled in the desert wash in November 1996. All mist-netted birds were identified to species, age (HY = hatching year/second year, immature birds in their first winter; ASY = after hatching year/after second year, adult birds), and sex by plumage characteristics (Pyle et al. 1987), and banded with both a numbered metal band and color bands for identification in the field. We mea-

sured wing chord (unflattened), tarsus and bill length, and weighed birds to the nearest 0.1 g on a 30-g Pesola scale. All migrants were scored for pectoral-muscle mass using a scale of 0–3 (0 = muscle concave and sternum prominent to 3 = muscle convex and sternum not detectable; Holmes et al. 1989, Gosler 1991, Wunderle 1995). All pectoral-muscle scores were made by SCL to decrease observer bias. Pectoral-muscle scores were used to evaluate body condition because a large proportion of birds in the desert habitats were infected with *Knemidokoptes jamaicensis* mites and their body mass, or adjusted body mass (Marra 1998), might have been skewed by the profusion of tissue growth on the legs and feet associated with the mite infestation (Latta 2000, Latta and O'Connor 2001). Pectoral muscle volume is a reliable indicator of condition because it is less prone to the rapid temporal fluctuations in volume that furcular fat deposits undergo, and its assessment is highly repeatable (Gosler 1991).

Following each banding session, color-banded birds were relocated through extensive resighting efforts. A mean of 57.2 ± 5.1 (SE) person-hours were spent relocating color-banded birds at each site each banding session. Resighting effort varied somewhat between sites, but continued until all previously identified site-faithful birds were relocated, or no more newly resighted banded birds were identified after >10 person-hours of searching a site. Locations of resighted birds were plotted on maps using natural features and a 50 × 25 m flagged grid system to plot locations.

Wanderers. We contrast the percentage of wanderers and sedentary birds between habitats (see Rappole et al. 1989, Wunderle and Latta 2000). Wanderers were individually color-banded birds which were never seen >24 hr after banding. Sedentary individuals were observed at least once >24 hr after banding. The percentage of wanderers in a habitat was determined from mist-net samples pooled across banding sessions for each winter. No distinction was made between wanderers in the thorn scrub and desert wash habitats because a wandering individual could not be assigned to one or the other of these adjacent habitats.

Site fidelity. We describe both within-year (overwinter site persistence) and between-year (annual return rate) site fidelity. The former is defined as those birds banded in November and

subsequently recaptured or resighted in January or March of the same field season. We quantify overwinter site persistence during the early winter (November–January) and the late winter (January–March), as well as for the entire November–March winter period. Annual return rate is defined as the percentage of within-year site-persistent birds (from a previous field season) which were captured or resighted in a subsequent field season.

Insect sampling. Insects were sampled monthly with five yellow sticky traps placed for 48 hr at breast height along single transects in pine forest and desert thorn scrub habitats. Although sticky traps sample only volant insects, we chose this method to sample insects because careful inspection of branches and foliage, as well as tree-shaking methods to sample non-volant insects, usually turned up very few individuals (SCL, unpubl. data). All insects of 0.1–5.0 mm length were counted; the few larger insects were excluded because most wintering migrants use primarily small arthropods when in tropical habitats (Greenberg 1995, Lefebvre and Poulin 1996, Poulin and Lefebvre 1996), and no Prairie Warblers were observed to consume any large insects despite hundreds of feeding observations (SCL, pers. obs.). Counts were summarized by early winter (October–November), midwinter (December–January), and late winter (February–March) for analyses.

Differences in insect abundance between desert thorn scrub habitat and desert wash habitat were tested once in late winter (February 1999) by the placement of ten sticky traps in each site for 48 hr. All insects 0.1–5.0 mm in size were counted and recorded.

STATISTICAL ANALYSES

The software package SYSTAT Version 5.2.1 (Wilkinson 1992) was used for statistical analyses. Data presented are means ± SE unless otherwise stated. Data were tested for normality using normal probability plots and tests of skewness and kurtosis. A 2×2 test of independence with a χ^2 statistic was used to test for independence in the frequencies of age and sex of birds within and between habitats, the age and sex of floaters, the proportion of floaters within and between habitats, the proportion of site-persistent birds between years, and the annual return rate of birds by habitat, age class, and sex. A Mann-Whitney *U*-test was used to examine differences

in insect abundance between desert thorn scrub and desert wash habitats. Regression was used to examine the relationship between insect counts, habitat, year, and month of sample, and between insect abundance and rainfall.

Mean pectoral-muscle scores were calculated to show differences among birds in the three habitats. We used a *t*-test to compare pectoral-muscle scores in the early-winter sampling period between years. Scores from midwinter and late-winter samples were not used to study annual effects because these birds were differentially affected by an ectoparasite (Latta 2000, Latta and O'Connor 2001). We used ANOVA on ranked data (Conover and Iman 1981) to examine the effects of habitat, month of sample, sex, and age on all pectoral-muscle scores. With sex removed as a significant factor in scores of body condition, we then used ANOVA on ranked data to examine the interaction between habitat, winter time-period, and age in terms of pectoral-muscle score.

We used a logistic regression to test for interactions between habitat, sex, and age of Prairie Warblers in terms of the proportion of wandering birds (Trexler and Travis 1993). When three-way interactions were not present we then tested for conditional interactions and main effects. Logistic regression also was used to test for interactions between habitat, sex, and age in terms of site persistence in three time periods (November–January, January–March, and November–March), and in terms of the proportion of birds returning the following year.

RESULTS

Rainfall and temperature. Monthly rainfall totals were much lower in the desert than in the pine. Mean monthly rainfall in the desert for the December–March dry period was 7.5 mm and 19.1 mm in 1996–1997 and 1997–1998, respectively. In the pine forest, mean monthly rainfall for the same periods was 41.4 mm and 54.2 mm.

Desert and pine habitats also were distinguished by temperature differences. Bimonthly mean maximum temperatures from both habitats were similar (36.1°C in desert; 37.1°C in pine), but the habitats had dramatically different low temperatures. Bimonthly mean low temperatures were 17.9°C in the desert, but only 9.1°C in the pine forest.

Sex ratios. Sex ratios were not statistically different between thorn scrub and desert wash

TABLE 1. Gender and age-class frequencies (%) of winter resident Prairie Warblers in early winter (November), midwinter (January) and late winter (March) in combined desert habitats and pine forest in southwestern Dominican Republic. ASY = after second year (adult); HY = hatching year/second year (immature).

	n	Male	Female	ASY	HY
Desert (pooled sites)					
Early winter	91	45.0	55.0	58.3*	41.7*
Midwinter	91	49.4	50.6	57.1*	42.9*
Late winter	62	43.5	56.5	59.7*	40.3*
Pine forest					
Early winter	56	69.6*	30.4*	73.2*	26.8*
Midwinter	61	54.1	45.9	72.1*	27.9*
Late winter	59	50.8	49.2	62.7*	37.3*

* Chi-square test, $P < 0.01$.

habitats in early winter, midwinter, or late winter (all $\chi^2_1 < 0.9$, all $P > 0.3$), so all thorn scrub and desert wash birds were combined for further analyses. We then found a significant difference in sex ratios of resident Prairie Warblers between the pine forest and combined desert sites during the early winter ($\chi^2_1 = 8.4$, $P < 0.01$), but no significant difference in sex ratios during the midwinter ($\chi^2_1 = 0.3$, $P = 0.57$) or late-winter ($\chi^2_1 = 0.6$, $P = 0.42$) periods (Table 1).

Within habitats, sex ratios were skewed in the early winter only in the pine forest ($\chi^2_1 = 17.3$, $P < 0.01$), where males predominated (Table 1). In the desert habitat females outnumbered males, but not significantly so ($\chi^2_1 = 1.8$, $P = 0.18$). By midwinter there was a marked decline in these skewed sex ratios, with no significant difference in the number of males and females in the desert or the pine forest (both $\chi^2_1 < 0.8$, $P > 0.3$). This pattern persisted in late winter in the pine forest ($\chi^2_1 < 0.1$, $P = 0.85$). In the desert the sex ratio was again biased towards females in late winter, although not significantly ($\chi^2_1 = 2.1$, $P = 0.15$).

Age classes. Age-class frequencies were not statistically different between desert thorn scrub and desert wash habitats in early winter, midwinter, or late winter (all $\chi^2_1 \leq 1.7$, $P \geq 0.19$), so all thorn scrub and desert wash birds were combined for further analyses. We then examined segregation by age class between pine and desert habitats (Table 1). We found nearly significant preponderances of ASY birds in the pine compared to the desert habitat in early winter ($\chi^2_1 = 3.4$, $P = 0.07$) and midwinter ($\chi^2_1 = 3.5$,

$P = 0.06$), but there was no significant difference in age classes between habitats in the late-winter period ($\chi^2_1 = 0.1$, $P = 0.73$). Within a habitat, ASY birds predominated in all habitats and all time periods, and these differences were always significant (Table 1, all $\chi^2_1 \geq 3.7$, all $P \leq 0.05$).

Wanderers. There was no significant difference in the frequency of wanderers between years in either pine ($\chi^2_1 < 0.1$, $P = 0.96$) or desert ($\chi^2_1 = 0.8$, $P = 0.37$) habitats, so data were pooled across years. We then found no evidence of any interactions between habitat, sex, and age among wandering birds (all $\chi^2_1 \leq 3.1$, all $P \geq 0.08$), so we tested for main effects. Significantly more wanderers were captured in the desert (43% of all captures; $n = 426$) than in the pine (8%, $n = 191$; $\chi^2_1 = 73.8$, $P < 0.01$). More wanderers were female (58% of all wanderers; $n = 197$) than male (42%; $\chi^2_1 = 10.4$, $P = 0.01$), but we found no significant difference in age of wanderers ($\chi^2_1 = 0.82$, $P = 0.36$).

Overwinter site persistence. Pooling all sex and age classes, we found no significant difference in site persistence between years in pooled desert habitats or in pine habitats in early winter, late winter, or the entire winter (all $\chi^2_1 \leq 2.0$, all $P \geq 0.15$). Site persistence data were then pooled across years for further analyses.

Pooled overwinter site persistence values were generally high for Prairie Warblers in November–January (82%), January–March (69%), and all winter (55%). For the entire November–March overwinter period, site persistence was generally higher in the pine forest (65%) than the desert (48%), but this pattern is confounded by significant variation within the desert habitat (Table 2). Site persistence in the desert wash (67%) was comparable to site persistence in the pine, but site persistence in the desert scrub (42%) was significantly lower ($\chi^2_1 = 4.1$, $P = 0.04$) than in the desert wash. Site persistence varied little between males (53%) and females (58%), and between HY birds (49%) and ASY birds (58%) across habitats.

Using logistic regression, a significant three way interaction occurred between habitat, sex, and age for site persistence between November and March ($\chi^2_2 = 6.3$, $P = 0.04$), suggesting that differences in site persistence exist among all ages, sexes, and habitats. Females were significantly more site persistent in pine and in desert scrub (both $\chi^2_1 = 10.1$, $P < 0.01$) than were

TABLE 2.   Site persistence frequencies (n) of winter-resident Prairie Warblers in early winter (November–January), late winter (January–March) and all winter (November–March) in desert thorn scrub, desert wash, and pine forest habitats in southwestern Dominican Republic. ASY = after second year (adult); HY = hatching year/second year (immature).

	Male		Female		
	ASY	HY	ASY	HY	All
Desert thorn scrub					
Nov–Jan	83.3 (18)	92.3 (13)	85.0 (20)	73.3 (15)	83.3 (66)
Jan–Mar	52.9 (17)	50.0 (20)	66.7 (21)	41.7 (12)	54.3 (70)
Nov–Mar	38.9 (18)	46.2 (13)	55.0 (20)	26.7 (15)	42.4 (66)
Desert wash					
Nov–Jan	85.7 (7)	33.3 (3)	80.0 (10)	75.0 (4)	75.0 (24)
Jan–Mar	100.0 (6)	50.0 (2)	75.0 (8)	100.0 (4)	85.0 (20)
Nov–Mar	85.7 (7)	33.0 (3)	60.0 (10)	75.0 (4)	66.7 (24)
Pine forest					
Nov–Jan	76.9 (26)	78.6 (14)	100.0 (15)	100.0 (2)	84.2 (57)
Jan–Mar	70.0 (20)	84.6 (13)	82.6 (23)	100.0 (4)	80.0 (60)
Nov–Mar	53.8 (26)	64.3 (14)	80.0 (15)	100.0 (2)	64.9 (57)

males. In the desert wash habitat we found no significant difference in site persistence between the sexes ($\chi^2_1 = 1.1$, $P = 0.30$), but ASY birds were significantly more site persistent than HY birds ($\chi^2_1 = 21.6$, $P < 0.01$).

These differences in site persistence over the entire November–March winter period were not seen in November–January (Table 2). We found no significant interactions or main effects for site persistence in this period (all $\chi^2_{\leq 2} \leq 2.5$, all P
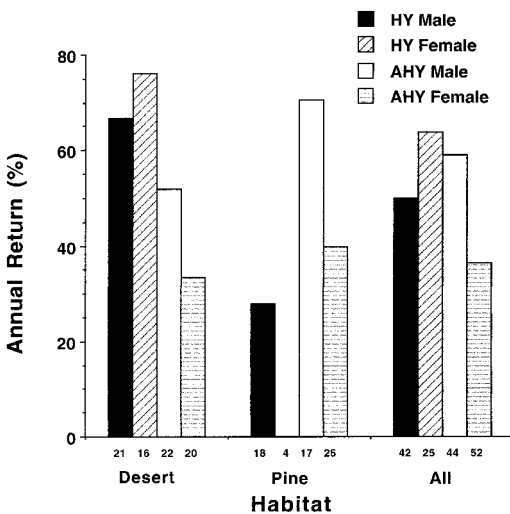

FIGURE 2.   Rates of annual return (n) for all sex and age classes of Prairie Warblers to desert habitats (combined) and pine forest in southwestern Dominican Republic, 1996–1999. Annual return rates are pooled across years.
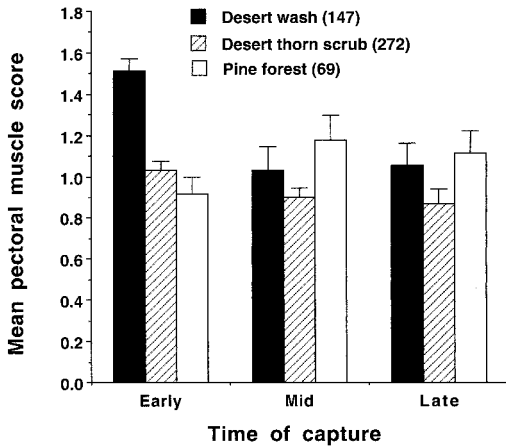
≥ 0.28). In January–March we found a significant main effect for habitat on site persistence ($\chi^2_2 = 11.4$, $P < 0.01$), but no other main effects or interactions (all $\chi^2_{\leq 2} \leq 3.7$, all $P \geq 0.15$). These data suggest that while there was relatively high site persistence in the desert wash (85%) and pine habitats (80%) during January–March, site persistence was significantly lower in the desert scrub (54%).

Annual return. Because birds were not sampled uniformly in the desert wash in 1996–1997, annual return rates to desert wash and desert thorn scrub habitats are considered together. Return rates are combined across years to increase sample sizes. Overall, the annual return rate for Prairie Warblers was 50% ($n = 163$; Fig. 2). Males tended to return at a higher frequency than females (55% vs. 45%), HY birds returned at a higher rate than ASY birds (55% vs. 47%), and annual return was higher in the desert habitats than in the pine forest (56% vs. 42%). However, these differences were nonsignificant (all $\chi^2_1 \leq 2.5$, all $P \geq 0.11$). In logistic regression, there was a statistically significant interaction between habitat and age ($\chi^2_1 = 9.9$, $P < 0.01$), but no other interaction terms were significant (all $\chi^2_1 \leq 1.1$, all $P \geq 0.30$).

Body condition. There was no significant difference between years in the pectoral-muscle scores of birds captured in early winter ($t_{109} = -1.5$, $P = 0.15$), so scores from all years were combined for further analyses. With all pectoral-muscle scores considered together, we found a

FIGURE 3. Mean pectoral-muscle-mass score (*n*) of Prairie Warblers in early (November), middle (January), and late (March) winter, in southwestern Dominican Republic. Bars represent means and standard errors of all birds captured in desert wash, desert thorn scrub, and pine forest.

significant three-way interaction between habitat, winter sampling period, and age of the bird ($F_{12,469} = 2.9$, $P < 0.01$; Fig. 3). Sex was not significant ($F_{1,469} = 0.3$, $P = 0.57$) and so was not considered as a factor in separate analyses for each habitat (Fig. 3). In the desert wash, pectoral-muscle scores varied significantly by winter sampling period ($F_{2,140} = 10.8$, $P < 0.01$), with scores decreasing through the winter, especially in the late-winter period. In the desert thorn scrub, there was a significant interaction between winter sampling period and age of the bird ($F_{2,265} = 4.8$, $P < 0.01$), with ASY birds having higher pectoral-muscle scores than HY birds, and mean scores decreasing through the winter. In contrast to the desert sites, within the pine forest there was no significant effect of winter sampling period ($F_{2,62} = 1.1$, $P = 0.35$), age ($F_{1,62} < 0.1$, $P = 0.92$), or sex ($F_{1,62} = 0.2$, $P = 0.65$) on pectoral-muscle scores, indicating little variation in body condition.

Insects. The abundance of flying insects varied between habitats, months, and years. Insect counts tended to be higher in the desert than in the pine forest ($F_{1,107} = 3.4$, $P = 0.07$) and were higher in 1997–1998 than in 1996–1997 ($F_{1,107} = 3.9$, $P < 0.05$). Analyzed within habitats, counts of insects in the desert were significantly lower in the dry year of 1996–1997 than in 1997–1998 ($F_{1,52} = 4.5$, $P = 0.04$) and counts declined significantly as the winter progressed

($F_{1,52} = 11.3$, $P < 0.01$). Counts of insects in the pine forest also showed a statistically significant decline through the winter months ($F_{1,53} = 14.0$, $P < 0.01$), but there was no significant difference in insect abundance between years ($F_{1,53} = 0.1$, $P = 0.73$). Analyses of insect counts in desert thorn scrub and desert wash habitats showed a statistically significant greater abundance of insects in the desert wash than in the thorn scrub habitat ($U = 14.0$, $P < 0.01$). Mean monthly insect counts were found to be significantly related to monthly rainfall totals in both the desert ($F_{1,8} = 6.2$, $P = 0.04$) and the pine forest ($F_{1,9} = 7.4$, $P = 0.02$).

DISCUSSION

Using demographics, site fidelity as a measure of the adequacy of resources within a habitat, and direct measures of variation in resource availability and physical condition of the birds, we assess geographic variation in the winter ecology of Prairie Warblers.

Demographics. Demographic data of site-persistent birds point to a hierarchy of habitat optimality. Theoretical work (Fretwell 1972) and experimental studies (Morton et al. 1987, Marra et al. 1993, Stutchbury 1994) have suggested that adult birds and males are generally dominant over juvenile birds and females, and fieldwork has found sexual habitat segregation of a number of species of birds on their nonbreeding grounds (e.g., Holmes et al. 1989, Lopez-Ornat and Greenberg 1990, Wunderle 1995). Thus, adult males are expected in optimal habitat; juvenile females are expected in suboptimal habitats and should be represented disproportionately among wanderers. In this study, adult birds predominated in all habitats and all time periods, but the proportion of adults in pine forest was nearly significantly greater than that in desert habitats in early winter (Table 1). Similarly, males tended to be more abundant in the pine forest than in the pooled desert habitats, especially in early winter (Table 1). These sex ratios are similar to those obtained from the Cuban satellite island of Cayo Coco (Wallace 1998) and from Cuba (Wallace et al. 1996), where a significant male bias in Prairie Warblers was found on each island. The ratio of age classes, however, did not vary significantly on Cayo Coco. Results from the present study contrast with data from Puerto Rico, where Baltz (2000) reported a significant skew toward HY birds and a non-

significant bias toward female Prairie Warblers in scrub and wooded pastures in the winter of 1996–1997.

Two possible explanations are available to explain these intra- and inter-island contrasts. First, these data suggest that pine forest is perceived as the preferred habitat of those birds studied on Hispaniola. If we assume that early-winter settlement patterns are the result of behavioral dominance where adults and males exclude subordinate birds from the more suitable habitat, these data suggest that Prairie Warblers must have a more favorable assessment of pine habitat than desert habitat in the early winter on Hispaniola.

More intriguingly, inter-island differences in demographic structure may reflect a level of segregation of birds between islands, with younger birds and other subdominants perhaps forced to migrate to more distant islands. Thus, older birds and males may be disproportionately represented on Cuba and Hispaniola, and females and HY birds on Puerto Rico and other islands more distant to North American breeding grounds. This idea is supported by theoretical considerations (Fretwell 1972, 1986) and evidence of all migrant warbler populations in southwest Puerto Rico being highly skewed toward females (Faaborg and Arendt 1984), but too few data are available to adequately test the possibility for any species. Although latitudinal gradients in the distribution of sex and age classes have been reported for a variety of birds (Ketterson and Nolan 1976, Greenberg 1986), among Neotropical migratory landbirds a pattern of geographic separation has been observed only for adult male Summer Tanagers (*Piranga rubra*; Pearson 1980) and the Yellow-rumped Warbler (*D. coronata*; Hunt and Flaspohler 1998).

Site fidelity. As the broadest measure of habitat suitability, overall rates of overwinter site persistence recorded here (Table 2) appear to be moderately high in pine forest and desert wash habitats (65% and 67%, respectively), but fairly low in desert thorn scrub (42%). Similar data from other wintering sites are unavailable, as the only other studies of the wintering ecology of this species concluded that Prairie Warblers in Puerto Rican scrub and wooded pastures were nonterritorial and wandered over large home ranges (Staicer 1992, Baltz 2000). However, overall site persistence of other parulid warblers wintering in native forests and shade coffee

plantations range from 52–80% for the American Redstart (Holmes et al. 1989, Sherry and Holmes 1996, Wunderle and Latta 2000), 42–76% for the Black-throated Blue Warbler (Holmes et al. 1989, Wunderle 1995, Wunderle and Latta 2000), and 61–77% for the Black-and-white Warbler (*Mniotilta varia*; Wunderle and Latta 2000).

Differences between habitats in site persistence were the result of changes in site persistence in the late-winter dry months. We found no significant difference in site persistence among birds from different habitats in the November–January period, but there was a significant difference in the January–March period, where site persistence of both male and female Prairie Warblers was lower in the desert thorn scrub than it was in either the desert wash or the pine forest.

When this pattern is viewed alongside our data on shifts in sex and age-class ratios, we see a relatively high turnover in birds of both sexes and all age classes in desert thorn scrub in late winter (Table 2). Sex and age-class ratios in the desert wash were relatively stable through the winter, but in pine forest there was a slight shift toward more equality (i.e., more females and more HY birds were present late in the season). A shift in age classes and sex ratios of this sort in the pine forest could result from the immigration of new birds to pine habitat, but few new birds were recorded in pine forest in middle or late winter (SCL, unpubl. data). Rather, the observed shift results from a low site persistence by male and ASY birds, which accounts for the observed change in sex ratios. While relatively low site persistence by ASY birds and males is not predicted by the Ideal Despotic Distribution model, we speculate that these birds may leave wintering grounds earlier than younger birds and females in order to seek high-energy food sources and earlier returns to breeding grounds. ASY male birds tend to arrive later on wintering territories in some habitats (Wunderle 1995, SCL, pers. obs.), and may leave sooner for the northbound migration (Marra 1998).

Beyond leaving territories in preparation for migratory events, low overwinter site persistence may also reflect emigration from a site or mortality. Emigration is difficult to measure, especially in these sites, which were nested in vast expanses of similar habitat, but we assumed that movement of birds to similar habitat outside our

study sites rarely occurred. We did record movements of individual Prairie Warblers between desert sites (a distance <1.6 km), but this occurred only twice, and extensive searching in areas outside of the study sites seldom turned up color-banded birds.

Direct causes of mortality are also difficult to measure. Various avian predators were regularly present in some of our study sites, including the American Kestrel (*Falco sparverius*), Sharp-shinned Hawk (*Accipiter striatus*), Barn Owl (*Tyto alba*), Ashy-faced Owl (*Tyto glaucops*), and Stygian Owl (*Asio stygius*). While no depredations were observed directly, we did recover the bands of a Common Yellowthroat (*Geothlypis trichas*) in an owl pellet (probably of a *Tyto* owl). Mortality may also have been possible as the result of infestation by the ectoparasitic mite *Knemidokoptes jamaicensis,* which heavily infested Prairie Warblers in the desert habitats (Latta 2000, Latta and O'Connor 2001). However, while some individuals may have died as the result of mite infestations during the winter months, the mites did not significantly affect population-level overwinter site persistence rates (Latta 2000).

Mean annual return rates were moderately high (56% in desert, 42% in pine), and compare favorably to the 48% and 49% annual return rates reported by Staicer (1992) and Baltz (2000) for Prairie Warblers in scrub and wooded pastures in Puerto Rico. These rates also fall into the range of annual return rates reported for other parulids in native habitats by Holmes and Sherry (1992), who concluded that a return rate of 50% for small passerines was not unusual. The significant interaction that we found between habitat and age in terms of annual return rate supports the assertion that segregation through behavioral dominance occurs in the Prairie Warbler. Adult birds, especially adult males, returned at a high rate to pine habitat, whereas young birds returned at a higher rate to the dry desert habitats.

Annual return rates reflect survival on the wintering grounds, as well as survival on the breeding grounds and two long migrations. An unknown proportion of birds from each habitat may have returned to another habitat or a more distant site in similar habitat (Holmes and Sherry 1992, Wunderle and Latta 2000), but such site shifts were never recorded in this study. Annual return rates may also be affected by physiolog-ical stress resulting from residence in suboptimal habitats, which may increase the susceptibility of the bird to starvation as well as predation or disease (Esch 1977, Forrester et al. 1978). Although infestation of Prairie Warblers by the parasitic mite did not have a significant impact on overwinter site persistence, no infected individuals ever returned to the desert sites the following year, suggesting that the infestation is lethal (Latta 2000) and that stressed birds were probably incapable of completing the spring migration. Although levels of mite infestation of Prairie Warblers were not high enough to have a statistically significant impact on annual return rates for the population, they did depress return rates of the Palm Warbler (*D. palmarum*) to a level that was significantly lower than that expected in a parasite-free environment (Latta 2000).

Wanderers. The presence of predominately females among wandering birds also supports our finding of sex and age-class segregation through behavioral dominance among Prairie Warblers. Our observation that >40% of net captures in desert habitats were wanderers is consistent with studies of other parulids in the West Indies. For example, Wunderle and Latta (2000) found 41% of Black-throated Blue Warblers wandering in shade coffee plantations, while Wunderle (1995) reported up to 57% of Black-throated Blue Warblers were wanderers in second-growth lower montane forest in Puerto Rico. Wallace (1998) found that wandering warblers of three species made up 38–61% of net captures in three Cuban habitats. The high incidence of wandering in the desert in this study is consistent with the expectation that the incidence of wandering will be highest in the lowest quality habitats (Fretwell 1972).

Our finding of <10% wanderers in pine forest is more surprising. Only Wunderle (1995) and Wunderle and Latta (2000) had comparable rates for any species; Wunderle reported 11–20% wandering among Black-throated Blue Warblers in Puerto Rican subtropical wet forest, while Wunderle and Latta (2000) reported wandering rates of 12% for Black-and-white Warblers and 21% for American Redstarts in shade coffee plantations in the Dominican Republic. Rappole et al. (1989) and Wunderle and Latta (2000) suggested that a low incidence of wanderers may reflect a relatively low mortality rate among sedentary birds. Alternatively, the distribution of

habitat, particularly in this system where the dense broadleaf understory preferred by Prairie Warblers is patchily distributed within the pine forest (SCL, pers. obs.), may discourage wanderers from seeking territories in these widely dispersed patches. Wandering across larger expanses of continuous habitat, such as low-elevation desert thorn scrub, may be more profitable even though the habitat is suboptimal.

Physiological condition. We sought to relate these demographic and site-fidelity data to fitness indices and resource availability. One might expect, for example, that variation in habitat quality will be reflected not only in variation in site persistence, but also variation in body condition. Indeed, we found that pectoral-muscle scores did not decline in the pine forest where adult males predominated and overwinter site persistence was high. However, pectoral-muscle scores declined significantly in both the desert thorn scrub and the desert wash, with the lowest scores recorded in the desert thorn scrub where females predominated and site persistence was markedly low. These data clearly indicate a physiological effect of habitat on Prairie Warblers which may in turn be reflected in measures of overwinter site persistence and annual return rates. A negative physiological effect of overwinter residence in dry scrub habitats has also been shown for American Redstarts in Jamaica (Marra and Holberton 1998), where birds lost body mass. Their poor physical condition did not result in lower overwinter survival, as we found in this study, but it did delay time of departure for spring migration. Unfortunately, we do not have data from these sites to measure the effect of depressed physical condition on departure times.

Resources. Prairie Warblers are gleaning insectivores, mostly taking very small insects from leaf surfaces. The observed significant decline in insect abundance throughout the winter in desert and pine forest habitats is similar to that shown in other studies in the seasonal tropics where arthropod numbers decrease during the dry season (Janzen 1973, Wolda 1978, Strong and Sherry 2000). Of the two winters we studied, insect numbers were also shown to be lower in the drier winter than in the moister winter in desert habitat, but not in the pine forest, suggesting that pine habitats may be less impacted by dry seasons and thus be more stable. Parrish and Sherry (1994) also showed that the degree

of seasonal resource constancy may differ between habitats and that this is related to moisture levels.

The observed dry-season declines in insect abundance may be related to rainfall patterns through rainfall's effects on broadleaf trees' ability to retain their leaves (Murphy and Lugo 1986). Differences in vegetational response to the dry season correspond to changes in insect abundance. Loss of foliage from deciduous trees in the desert thorn scrub is greater than leaf loss in the higher-elevation pine forest where the dry season is less severe, and leaf loss is greater in the desert scrub than it is in the desert wash, where the buttonwood trees retain their leaves. Although we did not quantify leaf loss at these sites, patterns of temperature, rainfall, and evapotranspiration that affect dry season events are described by Fisher-Meerow and Judd (1989). Parrish and Sherry (1994) documented similar changes in vegetation structure and insect abundance from dry scrub habitat in Jamaica.

The documented reduction in insect abundance may not be responsible for the decline in body condition in desert birds, however, because pine habitat also saw lowered insect abundance in late winter but did not show a consistent decline in pectoral-muscle scores. Other differences between habitats which may account for changes in body condition include quality of prey items (Poulin and Lefebvre 1996), differences in prey characteristics and handling time (Sherry and McDade 1982), reduced activity by desert birds during the midday heat, resulting in less foraging time (SCL, pers. obs.), energetic costs associated with daily movements to nighttime roosts in desert habitats (SCL, pers. obs.), and abundance of ectoparasites (Latta 2000, Latta and O'Connor 2001). These possibilities merit further research attention.

Habitat hierarchies. Results from this study suggest that there are several possible trade-offs that Prairie Warblers may face when selecting overwintering sites. Pine habitat, with its preponderance of ASY and male birds and generally high site persistence, may be the optimal habitat among the range of habitats studied. Desert habitat may provide the better overwinter site only if an individual can establish a territory which includes part of the dry desert wash, where the abundance of non-deciduous trees may provide a more reliable source of insects

through the dry season. The heterogeneity of habitat in the desert, and the restricted amount of desert wash habitat, may promote intense competition for desert wash territories, especially since the consequences of being forced into the dry scrub habitat appear to be rather severe.

This response to habitat heterogeneity, even at the small scale represented by narrow desert washes, is not surprising, as migrants have been found to be common in some very small habitat patches elsewhere (Greenberg 1992, Wunderle 1999), and some species have shown site fidelity to small shade-coffee plantations in an agricultural matrix even when the plantations were smaller than the mean winter home-range size (Wunderle and Latta 2000). Site fidelity might be even higher when these habitat patches are placed in a matrix of alternative habitat types which are more desirable than an agricultural field (as in this study). Competition for optimal desert wash sites in a matrix of suboptimal desert scrub sites, or for patches of broadleaf shrubs in a pine forest, may also explain the territoriality that we find in southwestern Dominican Republic, but which appears to be absent from scrub and wooded pasture sites in Puerto Rico (Staicer 1992, Baltz 2000).

Future habitat-specific demographic studies of wintering migrants should consider habitat heterogeneity, the juxtaposition of habitats on the landscape, and the impact of this heterogeneity on demographics and site fidelity. Contiguous habitats can differ dramatically in microclimate, soil types, and vegetative cover, which in turn affect leaf loss and insect abundance (Wolda 1978, Parrish and Sherry 1994, this study). Studies should also measure seasonal changes (or stability) of habitats to understand the effects of highly seasonal habitats on avian fitness indices and site fidelity, as habitat suitability may vary seasonally as a result of the dramatic effect the lack of water can have on vegetation (Parrish and Sherry 1994, this study). In addition, it should be remembered that the effects of habitat seasonality in the overwinter period may not be seen until late in the winter period.

ACKNOWLEDGMENTS

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