

## EFFECTS OF SCALEY-LEG MITE INFESTATIONS ON BODY CONDITION AND SITE FIDELITY OF MIGRATORY WARBLERS IN THE DOMINICAN REPUBLIC

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**ABSTRACT.**—Rates of infestation by the scaley leg mite (*Knemidokoptes jamaicensis*) were examined on two overwintering Nearctic–Neotropical migrants, Palm Warbler (*Dendroica palmarum*) and Prairie Warbler (*D. discolor*), in low-elevation desert thorn scrub and high-elevation pine forest in the Dominican Republic. Ectoparasites were common on birds in the dry thorn scrub where birds roosted communally, but were never found on birds in the moister pine forest where communal roosting was not detected. Prevalence of ectoparasites varied between years and generally increased in prevalence within winters, with mean rates of infestation reaching as high as 25% among Palm Warblers in late-winter. Parasitized Palm Warblers showed significant decreases in mean pectoral muscle mass scores indicating a negative effect on body condition and physiological stress. Infestation had a significant effect on overwinter site persistence and annual return rates; no infected individuals ever returned the following year. Results of a path analysis indicated that mite infestation was more important than general physiological condition (as represented by pectoral muscle score) in determining annual return. Data suggest that environmental variables and host behavior may affect parasite infestation rates, and further attention should be given to the potential contribution of parasite infestation to winter limitation of avian populations. Received 31 July 2002, accepted 5 February 2003.

**RESUMEN.**—Investigué en los meses de invierno los índices de infestación por el ácaro *Knemidokoptes jamaicensis* a dos especies de aves migratorias, *Dendroica palmarum* y *D. discolor*, en los matorrales del desierto de elevación baja y en el bosque de pino de elevación alta en la República Dominicana. Los ectoparásitos eran comunes en las aves en los matorrales del desierto donde las aves se posan comunalmente, pero nunca se encontraban en las aves en el bosque de pino, donde el hábitat es más húmedo y donde las aves no se posan comunalmente. El predominio de los ectoparásitos varió entre años, y generalmente aumentó en frecuencia dentro los inviernos, con los índices de infestación ascendiendo a 25% entre *D. palmarum* hacia fines de invierno. La masa de los músculos pectorales bajó significativamente en los individuos de *D. palmarum* con parásitos, indicando un impacto negativo en la condición del ave y estrés fisiológico. Encontré un efecto significativo de la infestación en la fidelidad al lugar y la tasa anual de retorno; ningún individuo infectado retornó el año siguiente. Los análisis indican que la infestación por los parásitos era más importante que la condición fisiológica (representada por la condición de la masa de los músculos pectorales) determinando la tasa anual de retorno. Los datos sugieren que los índices de infestación podrían ser afectados por variables ambientales y el comportamiento del hospedador, y que debemos dar más atención a la función potencial de infestaciones de parásitos en el período invernal a la limitación de poblaciones de aves.

A FUNDAMENTAL ISSUE in ecology and conservation is the mechanism of population limitation. Population limitation refers to the determination of abundance and has been defined as the sum of density-dependent and density-independent factors causing a population to increase or decline (Sherry and Holmes 1995). Populations of breeding birds are most often thought to be

naturally regulated by food supply (Lack 1968, Williams 1966, Martin 1987), predation (Lack 1954, Skutch 1985, Martin 1995), or nest-site availability (von Haartman 1956, Brawn and Balda 1988). However, a growing literature addresses the role of parasites and disease in the limitation of some breeding populations (e.g. Loya and Zuk 1991, Clayton and Moore 1997). Host populations with parasites may be expected to have a lower equilibrium or lower population growth rate than those without parasites (Toft 1991, Anderson and May 1979, May and Anderson 1979). Parasites have been

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shown to drive population cycles (e.g. Hudson et al. 1998) and affect host dispersal and local recruitment patterns (Heeb et al. 1999). They may additionally affect the nutritional status of hosts (Hudson and Dobson 1991, Chapman and George 1991), expression of secondary sexual characteristics and mate choice (Hamilton and Zuk 1982), and reproductive success (Arendt 1985, Brown and Brown 1986, Hudson 1986, Richner et al. 1993). However, the greatest consequence of parasites may be to increase the susceptibility of the host to other mortality factors such as predation, other diseases, or starvation (Esch 1977, Forrester et al. 1978), which may vary between habitats and with host behavior. Few studies have documented the influence of differing environmental conditions and host behavior in different habitats on levels of parasite infection or mortality.

Events on the wintering or nonbreeding grounds of migratory birds also may affect population size (Rappole and McDonald 1994; Sherry and Holmes 1995, 1996; Latta and Baltz 1997; Newton 1998). Rappole and McDonald (1994) and Sherry and Holmes (1995, 1996) summarized arguments for winter limitation of Neotropical migratory species through age and sex-specific survival characteristics and site faithfulness across an array of habitats, suggesting that differences in habitat quality, usually based on food supplies, limit populations. Marra et al. (1998) 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 the hypothesis of winter habitat limitation for the American Redstart (*Setophaga ruticilla*). However, less often cited as a population regulatory mechanism, and absent from discussions of winter limitation of populations of migratory birds, is the influence of parasites on host populations.

*Knemidokoptes jamaicensis* (Turk 1950) is an ectoparasitic mite of passeriform birds, living and reproducing by burrowing into the cornified epithelium beneath the skin of the legs and feet or occasionally other unfeathered parts of the body (Kirmse 1966). The tissue of infected birds responds to the presence of mites by growing warty lesions and ribbon-like proliferations of the skin, as well as through overgrowth of the toenails, sometimes affecting the birds' ability

to perch in advanced stages of the infestation (Kirmse 1966; S. C. Latta pers. obs.). That pathological condition is referred to as "scaley-leg". *Knemidokoptes* spends its entire life cycle on its host; and although direct physical contact may not be required to transmit the parasite from one host to another (Poulson 1964, Kirmse 1966), close contact likely promotes transmission (Wichmann and Vincent 1958).

Here, data are presented on (1) the rate of infestation by *Knemidokoptes jamaicensis* on two Nearctic–Neotropical migrants, Palm Warbler (*Dendroica palmarum*) and Prairie Warbler (*D. discolor*), in two contrasting habitats; (2) temporal differences in rates of infestations and body condition; and (3) indices of survival. Possible effects of environmental variables and host behavior on parasite infestation rates and survival are then examined.

#### STUDY SITE AND METHODS

Study sites of 12–15 ha each were established in low-elevation desert thorn scrub (20–50 m elevation) and high-elevation pine forest (1,100–1,475 m elevation) near Cabo Rojo and the Sierra de Bahoruco, Pedernales Province, Dominican Republic (18°0'N, 71°38'W). Two study sites were established in desert thorn scrub in October 1996 and a third site was added in October 1997. Three study sites were established in pine forest in October 1996. All sites were along a north–south transect of <30 km. Mean temperature in January is 25.0°C in desert thorn scrub and 15°C in pine forest. Mean rainfall is <500 mm per year in the desert and 1,700 mm per year in pine forest. (Fisher-Meerow and Judd 1989). There are two pronounced dry seasons annually (December–March and July–August). December to March is normally exceedingly dry in the desert especially.

*Desert thorn scrub sites.*—Low-elevation desert thorn scrub, found on a characteristic dogtooth limestone substrate, has been studied by Fisher-Meerow and Judd (1989). Vegetation consists of widely scattered broadleaf trees that are partially deciduous, small broadleaf shrubs, and various cacti. Common broadleaf tree species include *Capparis cynophallophora*, *C. ferruginea*, *Guaiacum officinale*, *Haitiella ekmanii*, *Metopium brownei*, *Phyllostylon brasiliensei*, and *Plumeria obtusa*. Common shrubs include *Croton organifolius*, *C. discolor*, and *Lippia alba*.

A foliage height profile (Latta and Brown 1999) shows a low, open canopy with an understory dominated by broadleaf shrubs. Few forbs are present on the rocky floor, and although cacti and succulents are also sparse, they do occasionally extend into the canopy. Canopy cover is sparse and averages 22.0% (SD =

28.4) with 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.

*Pine sites.*—Pine forest is 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*, *Chamaescrista glandulosa*, *Coreopsis buchii*, *Hypericum hypericoides*, *Lyonia truncata*, *L. microcarpa*, *Myrica picardae*, and *Senecio picardae*, as well as the succulent *Agave antillana* (Fisher-Meerow and Judd 1989). The ground is covered by a thick layer of grasses.

A foliage height profile (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 51.1% (SD = 26.4) with 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, and broadleaf trees extend to 2.5 m in height.

*Sampling birds.*—Palm and Prairie warblers were found in large numbers in both pine forest and desert thorn scrub habitats. The Palm Warbler is a site-faithful species that occupies large home ranges and forages in loose but cohesive flocks mostly on the ground and low vegetation for small insects. The Prairie Warbler is also site faithful, but more territorial, occupying and defending distinct territories in those sites (Latta and Faaborg 2001). Importantly, both Palm and the Prairie warblers apparently roost communally at low elevations, moving from the desert habitats to roosts in a narrow strip (~10 m) of dense mangroves bordering the sea. Although individual birds were not observed at night, evidence for communal roosting includes large unidirectional movements of both species towards mangroves in late-afternoon and away from mangroves in early morning. In addition, mist nets placed along those mangroves captured warblers banded and resighted at study sites 0.5–1 km away. There is no evidence of such communal roosting by either species in pine forest.

I studied winter resident birds from 1 October to 1 April 1996–1997 and 1997–1998, and from 8 January to 15 February 1999. Birds were sampled with mist nets (12 m × 3 m × 30 mm mesh) set in three parallel rows of 11–16 nets each three times annually, in November, January, and March 1996–1998. Birds were not sampled in January 1999 except to determine annual return rates. All mist-netted Prairie Warblers were identified to age (immature = HY/SY [hatching year/second year]; adult = AHY/ASY [after hatching year/after second year]), and sex by plumage characteristics (Pyle et al. 1987). Palm Warblers could not be reliably identified to age or sex. All birds were inspected for evidence of *Knemidokoptes* infestations. Classic evidence for *Knemidokoptes* includes wart-like skin proliferations <1 mm in diameter to

large confluent lesions that take on a ribbon-like appearance (Kirmse 1966). Samples of mites collected from skin scrapings of those lesions were identified as *K. jamaicensis* (Latta and O'Connor 2001). All birds were banded with both a numbered metal band and color bands for identification in the field. Following each banding session, color-banded birds were relocated through extensive resighting efforts. A mean of 59.7 ± 5.3 (SE) person-hours were spent relocating color-banded birds at each pine site each banding session; a mean of 54.2 ± 5.0 (SE) person-hours were spent relocating color-banded birds at each desert site each banding session. Resighting effort varied somewhat among sites but continued until all previously identified site-faithful birds were relocated, or no more banded birds not already resighted during that banding session were identified.

Birds 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; Gosler 1991). All pectoral muscle mass scores were made by S.C.L. to reduce observer bias. Pectoral muscle mass scores were used to evaluate body condition because body mass, or adjusted body mass (Johnson et al. 1985, Ringleman and Szymczak 1985, Dufour and Weatherhead 1998), which may be expected to decline in parasitized birds if foraging ability was negatively affected, might be masked by the profusion of tissue growth on the legs and feet associated with *Knemidokoptes* infestation. In severe infestations, legs may be 5× their normal diameter (Kirmse 1966; S. C. Latta pers. obs.). Pectoral muscle volume has been used in numerous studies as a reliable indicator of bird condition (Holmes et al. 1989, Gosler 1991, Wunderle 1995, Latta and Faaborg 2001) because it is less prone to the rapid fluctuations in volume that furcular fat deposits undergo, and its assessment is highly repeatable (Gosler 1991, Harper 1999); whereas the shape of the pectoral muscle is highly correlated with actual lean dry muscle mass in small birds (Selman and Houston 1996) and changes consistently with body mass changes (Lindstrom et al. 2000). Although some change in muscle mass might be expected on a daily basis because of, for example, dehydration or feeding schedules, that technique can not be expected to estimate those small changes. The technique is, however, likely to be accurate as applied here in comparing large groups of birds or for determining changes over longer periods.

I describe both within-year (overwinter site persistence) and between-year (annual return rate) site fidelity. Overwinter site persistence is most generally defined as those birds banded in November and subsequently recaptured or resighted in March of the same field season. I also quantify site persistence for only the late-winter period (January–March) in assessing effects of the parasitic mites which often were not seen in the early winter. As the broadest measure

of habitat suitability, overwinter site persistence reflects emigration from a site and mortality within a season. Emigration is difficult to measure, especially in those sites, which were nested in vast expanses of similar habitat, but movement of birds to similar habitat outside my study sites is assumed to occur infrequently. I did record movement of individual birds between desert sites (a distance <1.6 km), but that occurred very few times (Latta and Faaborg 2001), and extensive searching in areas outside of the study site seldom turned up color-banded birds. Thus, low rates of overwinter site persistence are assumed to be highly correlated with within-season mortality rates. Annual return rate is defined as any of the within-year site-persistent birds (from a previous field season) that were captured or resighted in a subsequent field season. Annual return rate reflects 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 distant site in similar habitat, but such site shifts have never been recorded here or in similar studies (Holmes et al. 1989, Wunderle and Latta 2000, Latta and Faaborg 2001). Thus, low annual return rates are assumed to be highly correlated with mortality rates.

*Statistical analyses.*—The software packages SYSTAT version 5.2 (Wilkinson 1992) and SAS (SAS Institute 1990) were used to perform various statistical tests described by Sokal and Rohlf (1995). Data were tested for normality using normal probability plots and tests of skewness and kurtosis. Regression was used to examine the relationship between infestation rates and sampling period, year, and rainfall. A  $2 \times 2$  test of independence with a chi-square statistic was used to test for independence in the age and sex of mite-infested birds, and site persistence and annual return rates of parasitized and nonparasitized birds. A row  $\times$  column test of independence with a G-statistic was used to test for independence in annual return rate among birds with different late-winter pectoral muscle scores.

Mean pectoral muscle mass scores were calculated to test for differences in body condition between parasitized and nonparasitized birds (i.e. bird "condition") residing in desert and pine habitats. I used analysis of variance (ANOVA; PROC GLM; SAS Institute 1990), to examine differences in ranked pectoral muscle mass scores (Conover and Iman 1981) among parasitized and nonparasitized birds in two habitats (pine forest and desert) and three sampling periods (November, January, March). Because two class variables were completely missing (i.e. there were no parasitized birds in the pine habitat, and there were no parasitized birds in the November sampling period) logistic regression could not be used, and two separate analyses were done. A  $3 \times 2$  factorial ANOVA was used to examine effects of month and habitat on

pectoral muscle mass scores of nonparasitized birds. A  $2 \times 3$  factorial ANOVA was used to examine effects of month and condition (pine birds, parasitized desert birds, nonparasitized desert birds) on pectoral muscle mass scores. Mean differences using ranked data were determined using Fisher's least-significant difference.

Potential for pseudoreplication of my data existed because individual birds could potentially be repeatedly scored as recaptures within sampling periods, among sampling periods, or among years. However, pseudoreplication was addressed in three ways. First, recaptures within sampling periods were excluded from the data set. Second, percentage of birds recaptured among sampling periods within a year (November and January, January and March, November and March) was low (for either species: 7.8–10.7% for any pair of sampling periods) so a repeated measures ANOVA could not be used. Instead, for each factorial ANOVA I reduced the denominator degrees of freedom by the number of replications that occurred in the sampling periods. That resulted in very little if any effect on *P*-value so only the results of the original factorial ANOVAs are reported here. Third, pooling of pectoral muscle scores between years to achieve larger sample sizes was justified because there was no significant difference between years in pectoral muscle scores of site-persistent nonparasitized birds captured in early-winter (Palm Warbler:  $t = 1.270$ ,  $df = 124$ ,  $P = 0.21$ ; Prairie Warbler:  $t = 1.466$ ,  $df = 109$ ,  $P = 0.15$ ). In addition, pooling of pectoral muscle scores between years did not severely violate assumptions of independence because only 3.2% of Palm Warblers and 1.7% of Prairie Warblers were scored in both years.

Path analysis (Sokal and Rohlf 1995) was used to estimate relative importance of mite infestation and general physiological condition in determining annual return. Path analysis has been employed in a variety of ecological contexts (Palomares et al. 1998, Bart and Earnst 1999, McCarty and Winkler 1999) and uses multiple regression to interpret causal relationships among sets of correlated variables in an independently generated *a priori* hypothesis and then infers relative strengths of different interaction pathways among variables. Problems associated with the use of path analysis in ecological studies include collinearity of data, small sample sizes, and use of categorical variables (Petraitis et al. 1996). Collinearity was not a problem with the data set here (all Pearson's correlations <0.26, S. C. Latta unpubl. data). Sample sizes here were large and exceeded the recommended minimum of 5–20 samples per path in the model. However, use of categorical data in the path analysis dictates that caution be used in interpreting results. Estimations of path coefficients are not affected by non-normal data (Bollen 1989) so the order and magnitude of the estimates of the path coefficients are probably quite accurate, but the *P*-values associated

with the significance tests of path coefficients are only approximate. Thus, path analysis at least allows the evaluation of the influence of potential causal factors in this analysis.

Path analysis using PROC CALIS (SAS Institute 1990) was performed to evaluate two *a priori* models, with presence of mites (presence-absence) and pectoral muscle score (0–3) as predictor variables and annual return (returned-did not return) as the criterion variable. In model 1, return rate is affected directly by body condition (pectoral muscle size) that also affects annual return indirectly through mite infestation. Here it is hypothesized that weakened individuals will be less likely to return but will also be more susceptible to mite infestations. In model 2, mites affect annual return directly by decreasing survival, and indirectly by affecting body condition that in turn affects survival. The strength of the interaction pathways are represented by the path coefficients that are the standardized regression coefficients or beta weights. Significance testing of individual path coefficients is accomplished by comparing *t*-values, but the categorical nature of my data set limits the value of the path diagram to assessing the relative importance of the predictor variables to the criterion variables in the models. For that reason, *t*-values are not presented and the focus is placed on the relative contribution of direct and indirect effects of mites and body condition in determining annual return.

## RESULTS

*Rates of infestation.*—Rates of infestation of Palm and Prairie warblers by mites varied by habitat, avian host species, and year. Relatively large numbers of birds in the desert were infected by the parasite, but no individual of either species was ever found infected with the parasite in the pine forest (Table 1). Across

the three desert study sites, rates of infestation of the Palm Warbler varied from 0 to 9.1% in 1996–1997, and from 3.5 to 41.7% in 1997–1998. Infestation rates of Palm Warblers generally increased from early winter thru midwinter to late-winter, but the effect of season on infestation rates was not quite significant ( $F = 3.146$ ,  $df = 2$  and  $11$ ,  $P = 0.08$ ). Infestation rates did, however, vary significantly between years ( $F = 8.391$ ,  $df = 1$  and  $11$ ,  $P = 0.01$ ). Rates of mite infestation of the Prairie Warbler in the desert were lower than those of the Palm Warbler and varied from 0 to 7.4% in 1996–1997 and from 0 to 16.7% in 1997–1998. Rates of infestation of the Prairie Warbler also generally increased from early winter thru midwinter to late-winter, but the increase also was not statistically significant ( $F = 1.438$ ,  $df = 2$  and  $11$ ,  $P = 0.28$ ). There was also no significant difference in infestation rates of Prairie Warblers between years ( $F = 3.011$ ,  $df = 1$  and  $11$ ,  $P = 0.11$ ), though rates were generally higher in 1997–1998. Overall, rates of infestations of Palm Warblers were significantly higher than those of Prairie Warblers ( $F = 4.866$ ,  $df = 1$  and  $26$ ,  $P = 0.04$ ). Proportion of birds infested with mites (47% of infected birds were male, 33% of infected birds were juvenile) did not vary significantly from the population of late-winter resident Prairie Warblers (44% of birds were male, 40% of birds were juvenile) in terms of sex ( $\chi^2 = 0.181$ ,  $df = 1$ ,  $P = 0.67$ ) or age class ( $\chi^2 = 1.058$ ,  $df = 1$ ,  $P = 0.30$ ). A similar analysis for the Palm Warbler was not possible because most individuals cannot be reliably aged or sexed.

How the rate of infestation by mites of Palm

TABLE 1. Percentage of Palm and Prairie warblers infected (*n*) with *Knemidokoptes* mites in three desert thorn scrub study sites in November, January, and March 1996–1998.

Site	1996–1997			1997–1998		
	November	January	March	November	January	March
<b>Palm Warbler</b>						
D1	0.0 (77)	6.5 (92)	6.0 (50)	8.8 (57)	16.3 (43)	41.7 (36)
D2	0.0 (33)	0.0 (31)	9.1 (22)	15.8 (19)	6.3 (32)	11.4 (35)
D3	–	–	–	3.5 (29)	16.7 (30)	21.2 (33)
Mean	0.0 (110)	4.9 (123)	6.9 (72)	8.6 (105)	13.3 (105)	25.0 (104)
<b>Prairie Warbler</b>						
D1	0.0 (41)	2.6 (38)	7.4 (27)	8.8 (34)	0.0 (12)	5.6 (18)
D2	0.0 (20)	5.0 (20)	0.0 (20)	0.0 (4)	13.3 (15)	14.3 (14)
D3	–	–	–	2.3 (88)	16.7 (12)	4.0 (25)
Mean	0.0 (61)	3.5 (58)	4.3 (47)	4.0 (126)	10.3 (39)	7.0 (57)



and Prairie warblers varied with local rainfall was examined because infestation rates appeared to increase as the dry season progressed. Midwinter (January) and late-winter (March) infestation rates were compared with the amount of dry season (December–March) rainfall that had accumulated prior to each mist-netting session. A negative association between rates of infestation and rainfall was found for the Palm Warbler, and that was marginally significant ( $F = 4.616$ ,  $df = 1$  and  $8$ ,  $P = 0.06$ ). The relationship was not significant for the Prairie Warbler ( $F = 0.007$ ,  $df = 1$  and  $8$ ,  $P = 0.94$ ).

**Body condition.**—Among Palm Warblers (Fig. 1), pectoral muscle scores of nonparasitized birds declined significantly across winter sampling periods ( $F = 14.28$ ,  $df = 2$  and  $694$ ,  $P < 0.001$ ). A highly significant interaction between winter sampling period and habitat of nonparasitized birds ( $F = 7.11$ ,  $df = 2$  and  $694$ ,  $P < 0.001$ ) was found because pectoral muscle scores among pine forest birds remained relatively constant across the winter whereas scores for nonparasitized birds in the desert declined from November to March. Looking only at late-winter months (January, March), pectoral muscle scores of parasitized desert birds, nonparasitized desert birds, and nonparasitized pine birds were significantly different ( $F = 9.42$ ,  $df = 2$  and  $541$ ,  $P < 0.001$ ) and declined significantly with sampling period

( $F = 24.19$ ,  $df = 1$  and  $541$ ,  $P < 0.001$ ). I found a marginally significant interaction between sampling period and bird condition ( $F = 2.88$ ,  $df = 2$  and  $541$ ,  $P = 0.06$ ) because pectoral muscle scores for parasitized desert birds decreased more than those of nonparasitized desert birds, whereas scores of pine forest birds remained stable.

Patterns of differences in pectoral muscle scores among Prairie Warblers are similar to those seen in the Palm Warbler. In some comparisons, however, the sample sizes of parasitized birds are small and the differences are not statistically significant. Among Prairie Warblers (Fig. 2), pectoral muscle scores of nonparasitized birds declined significantly across winter sampling periods ( $F = 13.97$ ,  $df = 2$  and  $468$ ,  $P < 0.001$ ). A highly significant interaction between winter sampling period and habitat of nonparasitized birds ( $F = 6.55$ ,  $df = 2$  and  $468$ ,  $P < 0.01$ ) was found because pectoral muscle mass scores among pine forest birds remained relatively constant across the winter whereas pectoral muscle scores for nonparasitized birds in the desert declined from November to March. Looking only at late-winter (January, March) months, pectoral muscle scores of parasitized desert birds, nonparasitized desert birds, and nonparasitized pine birds were marginally significantly different ( $F = 2.36$ ,  $df = 2$  and  $250$ ,

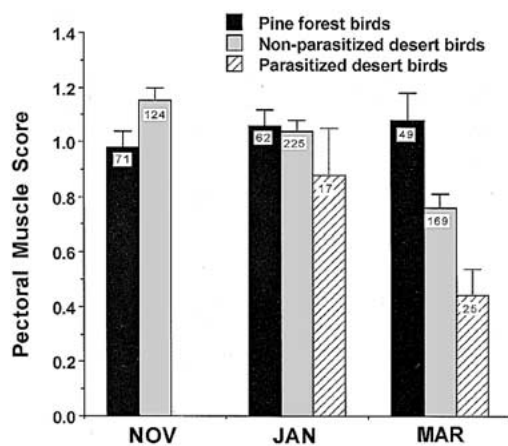


FIG. 1. Mean pectoral muscle scores (SE) of parasitized and nonparasitized Palm Warblers in two habitats (pine forest, desert thorn scrub) and three sampling periods (November, January, March). Birds were scored for pectoral muscle mass using a scale of 0–3 (0 = muscle concave and sternum prominent to 3 = muscle convex and sternum not detectable).

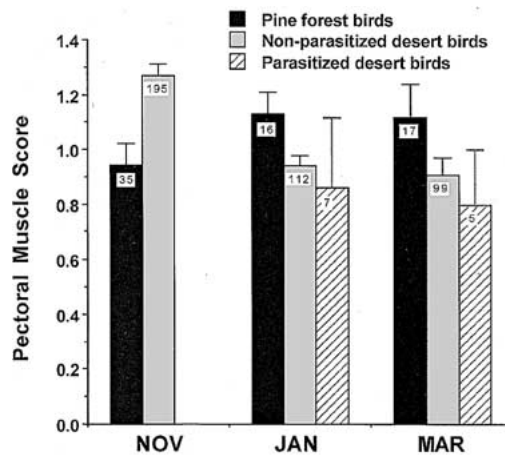


FIG. 2. Mean pectoral muscle scores (SE) of parasitized and nonparasitized Prairie Warblers in two habitats (pine forest, desert thorn scrub) and three sampling periods (November, January, March). Birds were scored for pectoral muscle mass using a scale of 0–3 (0 = muscle concave and sternum prominent to 3 = muscle convex and sternum not detectable).

$P = 0.10$ ) but did not decline significantly from January to March ( $F = 0.17$ ,  $df = 1$  and  $250$ ,  $P = 0.68$ ). Interaction between winter sampling period and bird condition was not significant ( $F = 0.01$ ,  $df = 2$  and  $250$ ,  $P = 0.99$ ), but pectoral muscle scores for parasitized desert birds generally decreased more than those of nonparasitized desert birds, whereas scores of pine forest birds remained stable.

*Overwinter site persistence.*—Among Palm Warblers, site persistence for the entire November–March overwinter period ranged from 50.0 to 65.7% across habitats and years. There was no statistically significant difference in site persistence between habitats in 1996–1997 (55.2% in desert, 61.5% in pine;  $\chi^2 = 0.739$ ,  $df = 1$ ,  $P = 0.39$ ); but in 1997–1998 site persistence was higher in the desert than in the pine (65.7% in desert, 50.0% in pine;  $\chi^2 = 5.280$ ,  $df = 1$ ,  $P = 0.02$ ). There was no significant difference in site persistence of Palm Warblers within habitats across years (for desert:  $\chi^2 = 0.536$ ,  $df = 1$ ,  $P = 0.46$ ; for pine:  $\chi^2 = 2.455$ ,  $df = 1$ ,  $P = 0.12$ ).

Among Prairie Warblers, site persistence for the entire November–March overwinter period ranged from 39.0 to 72.0%. Site persistence was significantly higher in pine forest than desert sites in 1996–1997 (39.0% in desert, 59.4% in pine;  $\chi^2 = 8.058$ ,  $df = 1$ ,  $P < 0.01$ ) and again in 1997–1998 (56.0% in desert, 72.0% in pine;  $\chi^2 = 5.591$ ,  $df = 1$ ,  $P = 0.02$ ); site persistence was higher in 1997–1998 than in 1996–1997 in both desert ( $\chi^2 = 5.823$ ,  $df = 1$ ,  $P = 0.02$ ) and pine forest ( $\chi^2 = 3.756$ ,  $df = 1$ ,  $P = 0.05$ ).

Quantification of the effects of parasitism on site persistence was difficult because infestations frequently showed up only in late-winter months. By limiting my analysis to site persistence during the January–March period, sample sizes were sufficiently large to assess effects of mite infestation only for Palm Warblers in 1997–1998. There was a significant difference in site persistence of parasitized individuals (70% site persistent) and nonparasitized individuals (92% site persistent) in the late-winter period ( $\chi^2 = 16.562$ ,  $df = 1$ ,  $P < 0.001$ ).

*Annual return rate.*—Annual return rates of all Palm Warblers were similar between habitats but varied between years. In 1997, there was no significant difference between habitats in terms of rate of return (62.7% in desert, 61.3% in pine;  $\chi^2 = 0.085$ ,  $df = 1$ ,  $P = 0.77$ ). In 1998, return rates were significantly lower than in 1997 in both

desert (26.5%;  $\chi^2 = 26.813$ ,  $df = 1$ ,  $P < 0.001$ ) and pine (34.3%;  $\chi^2 = 14.802$ ,  $df = 1$ ,  $P < 0.001$ ) sites, but again there was no significant difference between habitats ( $\chi^2 = 1.158$ ,  $df = 1$ ,  $P = 0.28$ ).

Among all Prairie Warblers, rates of return were significantly higher in the desert than in pine in both 1997 (68.0% in desert, 38.1% in pine;  $\chi^2 = 18.352$ ,  $df = 1$ ,  $P < 0.001$ ) and 1998 (40.0% in desert, 25.0% in pine;  $\chi^2 = 5.163$ ,  $df = 1$ ,  $P = 0.02$ ), and proportion of birds returning was significantly higher in 1997 than 1998 in both desert ( $\chi^2 = 16.001$ ,  $df = 1$ ,  $P < 0.001$ ) and pine ( $\chi^2 = 3.937$ ,  $df = 1$ ,  $P = 0.05$ ) sites.

Effects of parasitism on annual return rates was dramatic because no individual identified as having any level of *Knemidokoptes* infestation ever returned the following year, indicating that the infestation is probably lethal. For Palm Warblers, there was a significant difference in annual return rate of parasitized and nonparasitized individuals in both 1997 when 64.4% of nonparasitized birds returned ( $\chi^2 = 120.060$ ,  $df = 1$ ,  $P < 0.001$ ), and again in 1998 when 34.0% of nonparasitized Palm Warblers returned ( $\chi^2 = 54.147$ ,  $df = 1$ ,  $P < 0.001$ ). For Prairie Warblers, there was also a significant difference in annual return rate of parasitized and nonparasitized individuals in 1997 when 69.8% of nonparasitized birds returned ( $\chi^2 = 135.410$ ,  $df = 1$ ,  $P < 0.001$ ), and again in 1998 when 42.9% of nonparasitized Prairie Warblers returned ( $\chi^2 = 70.150$ ,  $df = 1$ ,  $P < 0.001$ ).

Results of path analyses (Figs. 3, 4; Table 2) suggest that mite infestation was more important than general body condition (as represented by pectoral muscle mass score) in determining annual return. Among Palm Warblers (Fig. 3) and Prairie Warblers (Fig. 4) and pattern of relationships between predictor variables and the criterion variable was the same in all models. Mites showed a strong negative effect on annual return, and in three of the four models that relationship was highly significant. Similarly, in all models muscle scores had a positive effect on annual return. The relationship between mite infestation and muscle score was also consistent among models, with mite presence having a negative effect on muscle size. Path analyses for the Palm Warbler especially emphasize importance of mites in decreasing annual return rates. In either model, effects of mites are much greater than effects of muscle score on annual return (Table 3). Model 2, in which mites show both direct and

TABLE 2. Direct effects (percentage of total effects), indirect effects (percentage of total effects), and total effects for models displayed in Figures 5 and 6.

Variables	Effects on annual return		
	Direct	Indirect	Total
<b>Palm Warbler</b>			
Model 1			
Muscle score	0.10 (67%)	0.05 (33%)	0.15
Mites	-0.28	-	-0.28
Model 2			
Mite presence	-0.28 (93%)	-0.02 (7%)	-0.30
Muscle score	0.10	-	0.10
<b>Prairie Warbler</b>			
Model 1			
Muscle score	0.05 (83%)	0.01 (17%)	0.06
Mites	-0.08	-	-0.08
Model 2			
Mite presence	-0.08 (89%)	-0.01 (11%)	-0.09
Muscle score	0.05	-	0.05

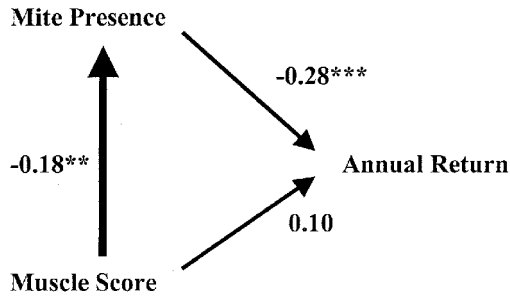
indirect effects on annual return, is particularly strong. Although data from the Prairie Warbler are less convincing, in both models the pattern seen in that species is the same as that seen in the Palm Warbler, with mite presence having a greater effect on annual return than muscle score has on annual return, even when indirect effects are considered (Table 2).

DISCUSSION

Prairie Warblers, and especially Palm Warblers, showed high but variable levels of infestation by the scaly leg mite (*Knemidokoptes jamaicensis*) in desert thorn scrub habitat. Those are some of the highest infestation rates recorded for that parasitic mite (Latta and O'Connor 2001). Neither male or female, nor hatching year or after-hatching year birds, appeared to be disproportionately affected by the parasite, because the group of mite-infested birds was representative of the general population. Individual birds were clearly affected negatively by mite infestations as evidenced by significantly reduced muscle mass scores, lowered site persistence, and the failure of any infested birds to return following annual migration. Results of a path analysis support the hypothesis that mite infestation was more important than pectoral muscle size in determining annual return.

The data presented here suggest the possibility of both environmental and host behavioral factors affecting rates of parasite infestation

**Model 1**



**Model 2**

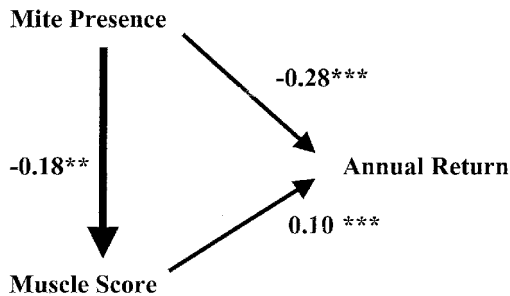


FIG. 3. Path diagrams showing the effects of *Knemidokoptes* mites and pectoral muscle scores on annual return rates of Palm Warblers ( $n = 177$ ) evaluated in late-winter. Values indicated are the standardized partial coefficients or "path coefficients" and represent the relative strength of the path in the model. Statistical significance of individual path coefficients is indicated by asterisks but because of the categorical nature of the data used in the path analyses,  $P$ -values are only approximate. No asterisk indicates  $P > 0.05$ , \* indicates  $0.05 > P \geq 0.01$ , \*\* indicates  $0.01 > P \geq 0.001$ , \*\*\* indicates  $P < 0.001$ .

by *Knemidokoptes jamaicensis*. High infestation rates may be related to environmental factors in two nonexclusive ways. First, the increasingly dry and difficult environment may exert physiological stress on potential avian hosts (Esch et al. 1975). That may play a role in either promoting transmission of the parasite to a weakened or immuno-compromised individual (Deerenberg et al. 1997, Saino et al. 1997), or in the external manifestation of parasites previously contracted elsewhere (Weatherhead and Bennett 1991). Birds in suboptimal habitats



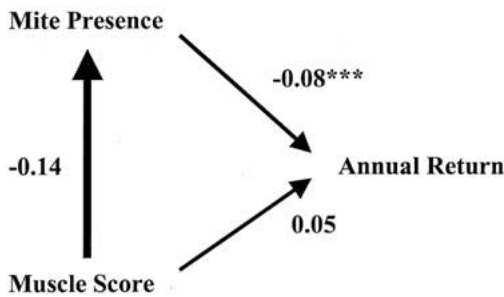
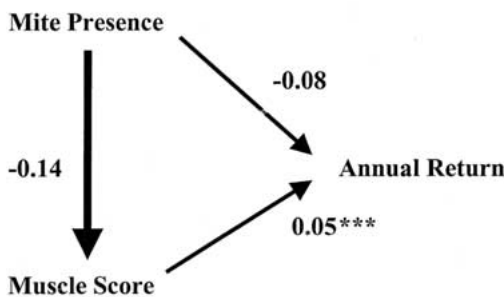
**Model 1****Model 2**

FIG. 4. Path diagrams showing the effects of *Knemidokoptes* mites and pectoral muscle scores on annual return rates of Prairie Warblers ( $n = 104$ ) evaluated in late winter. Values indicated are the standardized partial coefficients or "path coefficients" and represent the relative strength of the path in the model. Statistical significance of individual path coefficients is indicated by asterisks but because of the categorical nature of the data used in the path analyses,  $P$ -values are only approximate. No asterisk indicates  $P > 0.05$ , \* indicates  $0.05 > P \geq 0.01$ , \*\* indicates  $0.01 > P \geq 0.001$ , \*\*\* indicates  $P < 0.001$ .

may spend more time and energy in foraging or territory defense, and an increase in those energetically costly activities may suppress immune function (Deerenberg et al. 1997, Saino et al. 1997). Hudson (1986) and Hudson and Dobson (1991) showed a relationship between low nutritional status of the host and increased parasite infection rates. That drier winter habitats may be suboptimal for at least some species of migratory warblers has been shown by Marra and Holberton (1998) who measured increased levels of corticosterone in birds in dry scrub.

That is supported by results presented here that show significant seasonal decreases in pectoral muscle mass scores in desert birds even among birds not affected by mites. Thus, if the desert thorn scrub is suboptimal habitat for those bird species (see below), they may be expected to experience a higher parasite load because of the effects of increased physiological stress.

The second way in which environmental factors may affect infestation rates is through the habitat requirements of the parasite itself. The contrast between the high rate of mite infestation in the desert thorn scrub, especially in late winter, and absence of mites in the pine forest, suggests that perhaps desert habitat is conducive to mite survival and reproduction, because a parasite may require a well-defined environment or microclimate (Van Riper 1991) and would likely react on a seasonal basis to variations in weather (Taylor and Muller 1974). My observation of a generally positive association between an increasingly dry environment and a high incidence of mites among Palm Warblers might support the hypothesis that mites favor dry habitat, the drier late-winter months, and dry years for reproduction, survival, and growth, but the relationship was not quite statistically significant. Few other data are available on the ecology and distribution of *Knemidokoptes jamaicensis* mites across habitats, and the sparse reports of the occurrence of mites on various hosts in North America make little or no mention of habitats in which hosts were found (Kirmse 1966, Fain and Elsen 1967, Pence 1970). Clearly, further work needs to be done on the habitat requirements of that parasite.

Beyond environmental factors, host behavior may also affect parasite infestation rates (Møller et al. 1990, Loye and Zuk 1991, Fischer et al. 1997). My finding that mite infestations were high in desert habitats where birds roost communally, but nonexistent in pine forest where the same species of birds do not roost communally, might suggest a behavioral component to infestation rates and a mode of transmission. Where canopy height and canopy closure are low, Palm Warblers and Prairie Warblers may be forced to seek communal nighttime roosts which increases the opportunity for parasite transmission between hosts. Similar roosts have been described from the Puerto Rican dry zone and attributed to the need for nighttime protection from adverse weather (Baltz 2000). Such

roosts, or other social behaviors, have been implicated in the transmission or increased incidence of disease in many studies (Alexander 1974, Brown and Brown 1986, Fischer et al. 1997). The possible transmission of mites between hosts at communal roost sites may explain the pattern of increasing levels of infestation through the nonbreeding season and also suggests that birds are contracting the parasite at the wintering site rather than bringing the mites with them from breeding areas.

Host behavior may also explain the difference in infestation rates experienced by the two focal species. Although both birds are gleaning insectivores, Palm Warblers tend to feed more frequently on the ground and lower in the vegetation than do Prairie Warblers (S. C. Latta unpubl. data). Because small shrubs and forbs are affected by dry season events and lose their leaves more quickly than larger trees (S. C. Latta pers. obs.), Palm Warblers may be adversely affected before Prairie Warblers by dry season events. Palm Warblers would thus be expected to be more stressed physiologically and more susceptible to parasite infestation. In addition, ground-feeding Palm Warblers may experience more physical irritations to the legs and feet, especially in desert thorn scrub on a characteristic dogtooth-limestone substrate (Howard and Briggs 1953), and that may promote the appearance of *Knemidokoptes* mite lesions. In an experimental study, Kirmse (1966) found that the disease was increased in severity by mechanical irritation of diseased legs and speculated that natural injuries result in more rapid development of lesions.

The question of how environmental and behavioral factors affect infestation rates hinges in part on identifying relatively optimal and suboptimal habitats for the hosts. Although the prevalence of mite lesions and parasite infestation rates of those migrant species, combined with negative changes in body condition (at least for the Palm Warbler), is consistent with desert thorn scrub being suboptimal habitat among those studied, site-fidelity data are more equivocal. Overwinter site persistence was lower in desert than pine sites for the Prairie Warbler, as would be expected if desert were suboptimal habitat; but among Palm Warblers, overwinter site persistence was lower in desert than in pine in only one of two years. Although annual return rate reflects events throughout the annual cycle

and so may be a less reliable measure of winter habitat quality, I nevertheless found no difference between habitats in annual return rate of Palm Warblers, whereas annual return rate was actually higher in desert than in pine in both years for the Prairie Warbler, despite the negative effect of mite infestations on return rates in desert habitat. Those inconsistencies may be in part the result of habitat heterogeneity in the desert and the presence of higher quality microhabitats within a generally low-quality desert thorn scrub matrix. Previous work has shown that overwinter site persistence of the Prairie Warbler may vary among those microhabitats (Latta and Faaborg 2001), and that may be true of Palm Warblers too. A similar dynamic may also influence annual return rates of both Palm Warblers and Prairie Warblers.

Although it is equivocal whether desert thorn scrub is suboptimal habitat, several lines of evidence support the idea that previously healthy birds contracted mites at the desert site, and that subordinate birds and birds in already poor body condition did not settle disproportionately in that habitat as might be predicted by ideal-despotic distribution models (Fretwell 1972). First, birds in the desert habitat had significantly higher pectoral muscle scores than birds in the pine forest in early winter (Figs. 1 and 2), which suggests that already weakened individuals did not predominate in the desert habitat. Second, as previously mentioned, the group of mite-infested Prairie Warblers was representative of the general population in terms of sex and age class, which suggests that subordinate individuals did not settle in the desert habitat. Third, many permanent resident species were also found to have infestations of *Knemidokoptes jamaicensis* (Latta and O'Connor 2001), which suggests that winter residents were less likely to have brought the parasite with them to that habitat. While that suggests that birds contracted the parasite in the desert, it remains unresolved as to whether birds that settle in dry habitats are more likely to become infested with parasitic mites because of the physiological stress of the increasingly dry environment, or whether parasitic mites have such narrow habitat requirements that birds become infested regardless of their physiological condition.

The role of habitat-specific parasites or disease is particularly important in territorial birds where models of winter population limitation in mi-

grants (Fretwell 1972, Morse 1980, Rodenhouse et al. 1977) based on ideal-despotic distributions (Fretwell 1972) predict that habitat of optimal suitability for a species will fill with birds before habitat of lower suitability, and that settlement of subsequent individuals will be constrained by territorial behavior. Fitness variation results because fitness (in terms of survival) is expected to decline with increased density of birds and from optimal to suboptimal habitats. Until now, discussions of differences in habitat quality for wintering migrants have focused on the role of food abundance and predators (Sherry and Holmes 1995, 1996) and their possible roles in limiting winter populations. However, the potential cost of increased parasite loads resulting from environmental and host behavioral differences between habitats of varying quality ought now be further considered as well. In that case, infestation by parasites is not thought to lead directly to death, but the presence of mites and the compromised physiological condition of the infected individual probably increases susceptibility of the bird to other mortality factors. A long migration in an obviously weakened condition is likely fatal to those physiologically stressed birds. The fact that among wintering Palm Warblers up to 25% of the population may experience mite infestations, and that all of those birds fail to return the following year, emphasizes the potential importance of that parasite. Even though that parasite does not necessarily limit the host population, the incidence of parasites can still influence the host's ability to compete, slow the population growth rate (Anderson and May 1979), and have an important effect on the population. Because the incidence and effects of parasites on nonbreeding birds remains woefully understudied and extremely few attempts have been made to assess parasite loads of migrants on the wintering grounds (Garvin and Marra 1991, Davidar and Morton 1993, Tarof et al. 1997), the generality of such a model is difficult to assess. However, further studies to investigate the patterns and consequences of parasite infestation among nonbreeding bird populations, especially in suboptimal habitats, are warranted.

#### ACKNOWLEDGMENTS

Fine field assistance was provided by C. Brown, B. Cabrera, F. deLacour, H. Gamper, B. Gibbons, J.

Hammond, M. Heredia, D. Mejía, V. Mejía, R. Moore, B. Ryder, M. Sondreal, J. Tietz, E. Vásquez, H. Walker, and K. Wallace. The manuscript benefited from comments by T. Grubb, Jr., C. Howell, J. Faaborg, R. Ricklefs, M. Ryan, A. Scheuerlein, F. Thompson, and anonymous reviewers. M. Ellersieck provided statistical advice. Funding or equipment was provided by the University of Missouri Research Board, National Fish and Wildlife Foundation, Wildlife Conservation Society, Association of Avian Veterinarians, and U.S. Department of Agriculture Forest Service, North-Central Forest Experiment Station. S.C.L. was supported by a Science to Achieve Results (STAR) Graduate Fellowship from the U.S. Environmental Protection Agency. Permission to work in the Sierra de Bahoruco was provided by the Dirección Nacional de Parques and the Departamento de Vida Silvestre, Santo Domingo, Dominican Republic.

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Associate Editor: T. Grubb