The Condor 106:915–921

BODY CONDITION AND PARASITE LOAD PREDICT TERRITORY OWNERSHIP IN THE GALÁPAGOS HAWK

NOAH KERNESS WHITEMAN[1] AND PATRICIA G. PARKER
Department of Biology and International Center for Tropical Ecology, 223 Research Building, University of Missouri-St. Louis, 8001 Natural Bridge Road, St. Louis, MO 63121

Abstract. We tested for associations between body condition, territory ownership, and permanent parasite load of Galápagos Hawks (*Buteo galapagoensis*) on Isla Marchena, Galápagos. Two louse species were collected from most of the 26 hawks sampled: the amblyceran *Colpocephalum turbinatum* and the ischnoceran *Degeeriella regalis*. Nonterritorial hawks were in significantly poorer body condition than territorial hawks. Body condition was negatively correlated with the abundance of *C. turbinatum*. Nonterritorial hawks had significantly higher mean abundances, mean intensities, and median intensities of both louse species than territorial hawks. The amblyceran's mean abundance and intensity were significantly higher than the ischnoceran's. Abundances of the two lice were positively related when the population size of *C. turbinatum* was <100 individuals, and negatively related when >100 individuals. Parasite load and body condition both predicted territory ownership well.

Key words: *body condition, ectoparasite, Falconiformes, Galápagos, Phthiraptera, territoriality.*

La Condición Corporal y la Carga Parasitaria Predicen la Posesión de Territorios en *Buteo galapagoensis*

Resumen. Probamos la relación entre la condición corporal, la posesión de territorios y la carga parasitaria permanente en el Gavilán de Galápagos (*Buteo galapagoensis*) en la Isla Marchena, Galápagos. En la mayoría de los 26 gavilanes muestreados se colectaron dos especies de piojo: el ambliceránido *Colpocephalum turbinatum* y el ischnoceránido *Degeeriella regalis*. Los gavilanes no territoriales se encontraron en condiciones corporales significativamente peores que los gavilanes territoriales. Encontramos una correlación negativa significativa entre la condición corporal y la abundancia de *C. turbinatum*. Los gavilanes no territoriales tuvieron significativamente mayor abundancia, intensidad media e intensidad mediana de las dos especies de piojo que los gavilanes territoriales. La abundancia promedio y la intensidad de los ambliceránidos fueron significativamente mayores que las de los ischnoceránidos. Las abundancias de las dos especies de piojo estuvieron positivamente correlacionadas cuando el tamaño poblacional de *C. turbinatum* fue <100 individuos y negativamente correlacionadas cuándo fue >100 individuos. Tanto la carga parasitaria como la condición corporal predijeron bien la posesión de territorios.

Nonterritorial birds occur within wild populations of many bird species (Brown 1969, Krebs 1971, McCrary et al. 1992, Blanco 1997, Newton 1998), including the Galápagos Hawk (*Buteo galapagoensis*; Faaborg et al. 1980, Faaborg 1986). Generally, nonterritorial birds are in poorer body condition (Fretwell 1969, Hogstad 1987) and suffer from higher parasite loads than territorial birds (Jenkins et al. 1963). However, the relationships among these variables are not well understood (Jenkins et al. 1963, Halvorsen 1986, Potti and Merino 1995, Harper 1999, Darolova et al. 2001, Calvete et al. 2003). Moreover, reports linking these factors are scarce. In this study, we examined the interrelationships between host territoriality, body condition, and parasite load.

The Galápagos Hawk is endemic to nine islands within the Galápagos archipelago, Ecuador (de Vries 1975). This species has been of particular interest to biologists due to its unusual mating system, cooperative polyandry (Faaborg et al. 1995). Polyandrous groups are composed of two to five males and one female on Marchena, our study island (Bollmer et al. 2003). These individuals form permanent all-purpose territories, which both sexes defend throughout the year (de Vries 1975). Territorial birds rarely leave the occupied territory (de Vries 1975, Faaborg and Bednarz 1990, Donaghy Cannon 2001). Individuals do not attain group membership while they have immature plumage (de Vries 1975).

Nonterritorial hawks live in areas of poorer habitat quality and do not breed (de Vries 1975, Faaborg et al. 1980, Faaborg 1986, Donaghy Cannon 2001). Nonterritorial hawks also suffer higher mortality than territorial hawks (Faaborg et al. 1980, Faaborg 1986, Faaborg and Bednarz 1990). Given this information, it is reasonable to predict that nonterritorial birds will be in poorer physical condition and suffer higher parasite loads than territorial birds.

Lice (Phthiraptera) comprise the largest number of ectoparasitic insect species (Marshall 1981). The chewing/biting lice (paraphyletic Mallophaga) are grouped into two monophyletic lineages: the Ambly-

Manuscript received 23 January 2004; accepted 15 July 2004.
[1] E-mail: nkwf38@studentmail.umsl.edu

cera and the Ischnocera (Marshall 1981, Cruickshank et al. 2001, Johnson and Whiting 2002). Amblycerans consume most epidermal tissues and blood, are generally less host specific, less restricted to a particular region of the host's body, and are more vagile than feather-feeding ischnocerans (Ash 1960, Marshall 1981). Data from other studies indicate that when these suborders co-occur on hosts, amblycerans are more abundant than ischnocerans (Nelson and Murray 1971, Lindell et al. 2002). Thus, it is reasonable to predict (1) that amblycerans should be more abundant than ischnocerans on an individual host and (2) that high numbers of amblycerans should reduce ischnoceran population sizes (assuming either competition or amblyceran predation on ischnocerans, Nelson 1971).

Two louse species were previously collected from the Galápagos Hawk (de Vries 1975): the amblyceran *Colpocephalum turbinatum* Denny, and the ischnoceran *Degeeriella regalis* (Giebel). Forty-seven host species within the Falconiformes and the domestic pigeon (*Columba livia*) are known hosts of *C. turbinatum* (Price and Beer 1963, Price et al. 2003). The known hosts of *D. regalis* are typically limited to the Galápagos Hawk and the Swainson's Hawk (*B. swainsoni*) in the New World (Clay 1958). Both louse species are probably restricted to Galápagos Hawks in the Galápagos, as they have never been reported from any other host there. Given this limited louse fauna, and the differences in their evolutionary and life histories, the opportunity exists to examine the degree to which these two dissimilar species coexist and vary with host territorial status. Terminology with regard to parasite load follows Bush et al. (1997).

METHODS

The Galápagos archipelago is approximately 1000 km west of mainland Ecuador, South America. We studied the hawk population of Isla Marchena (00°18′N, 90°31′W; 130 km^2 in area, rising to 343 m elevation; Black 1973), which is situated in the northern portion of the archipelago (Thornton 1971).

Territorial Galápagos Hawks were characterized by at least two of the following criteria: (1) they defended territories against foreign hawks; (2) they gave a distinct warning call when humans or foreign hawks crossed the territorial bounds (de Vries 1975); (3) when nesting, they defended the nest when we approached; or (4) they performed aerial displays (with soaring-circling-spiral flight, de Vries 1975). All nonterritorial adults were captured on an area of southeastern coastline not defended by territorial adults and were not observed in any territorial group thereafter, nor were any territorial birds ever seen within this area.

Hawks were captured using a pole and noose from 4–15 June 2001. Mature adults were identified by uniform dark-brown plumage. Juveniles and immatures had distinct light-brown mottled plumage and were analyzed collectively as ''immatures'' (de Vries 1975). To calm each bird after capture, we placed a loose cloth hood over the head during handling. To avoid cross-contamination, the hood was visually inspected and thoroughly cleaned between handlings. All birds were banded with aluminum alphanumeric colored bands or numeric aluminum bands. Mass was measured with a Pesola scale (to the nearest 5 g) and wing chord was measured to the nearest mm (unflattened length from the tip of the longest primary feather to the wrist).

To quantify ectoparasite loads, birds were sampled via dust ruffling (Walther and Clayton 1997) with pyrethroid insecticide (derived from the chrysanthemum, and nontoxic to birds; Zema® Z3 Flea and Tick Powder for Dogs, St. John Laboratories, Harbor City, California) composed of 0.10% pyrethrins and 1.00% of the synergist piperonyl butoxide. A small amount ($\sim$2 g) of insecticide was evenly applied to each bird's plumage. This was followed by four to six 30-sec bouts of feather ruffling to dislodge the parasites. Ruffling ended when the last bout yielded $<$5% of the total number of lice collected during all previous bouts combined (Whiteman and Parker 2004, Whiteman et al. 2004). Our louse removal efficiencies were congruent with other studies attempting to quantify such loads (Clayton et al. 1992). Each bird was held over a clean plastic tray during ruffling to collect dislodged ectoparasites (stored in 95% ethanol). Ectoparasites were examined in the laboratory using a stereomicroscope and identified to species.

STATISTICAL ANALYSES

In order to calculate the overall body condition of territorial and nonterritorial Galápagos Hawks, a linear regression of body mass against wing length was performed in SPSS (1997). The residuals of this analysis were used as the index of body condition (Brown 1996). To determine if data from adult and immature nonterritorial birds could be combined to increase statistical power we first tested for differences in body condition between them (independent samples *t*-tests in SPSS 1997). The average body condition of nonterritorial birds was then compared to that of the territorial birds using independent samples *t*-tests. To test for a general relationship between host body condition and louse abundance, louse abundance data were first transformed (ln[louse abundance +1]) for each species due to the high variance in louse abundance. A bivariate two-tailed Pearson's correlation was then performed for host condition vs. louse abundance, for each parasite species.

Rózsa et al. (2000) cautioned that misleading results are easily obtained when using nonparametric statistical tests to compare parasite populations. Thus, where possible, we used the Quantitative Parasitology 2.0 program, which employs distribution-free tests (Rózsa et al. 2000, Reiczigel and Rózsa 2001). Using bootstrapped *t*-tests, mean abundances (a metric that includes uninfested birds) and intensities (a metric that includes only infested birds) were compared within a parasite species, between territorial and nonterritorial hawks, and between parasite species (Rózsa et al. 2000). Prevalences (the percentage of birds infected out of the total number sampled) were also compared between these hawks using Fisher's exact tests (Rózsa et al. 2000). Median intensities were compared using Mood's test of medians (Rózsa et al. 2000). To determine if data from adult and immature nonterritorial hawks could be combined to increase statistical power, we first tested for differences between these groups.

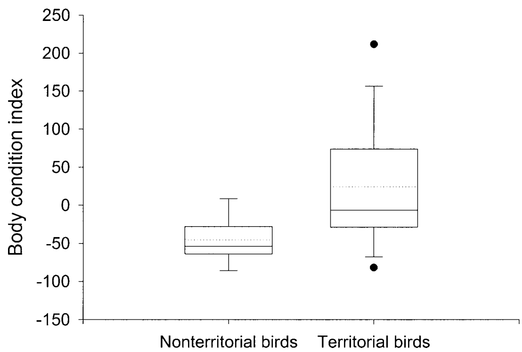

FIGURE 1. Nonterritorial Galápagos Hawks ($n = 9$) were in significantly poorer physical condition than territorial hawks ($n = 17$). Box and whisker plots show means (dotted lines), medians (solid lines) and 5th and 95th percentiles. Body condition was indexed as the residuals of a regression of body mass on wing chord.

We expected the amblyceran to negatively influence the population size of the ischnoceran, if the two are competitive or if the former depredates the latter. Thus, we performed a linear regression analysis in SAS (SAS Institute 1997) to test their degree of coexistence. In the model, dummy variables separated territorial from nonterritorial hawks. Abundance of *D. regalis* was the dependent variable, and the abundance of *C. turbinatum* and the product of this value and the dummy variable were the independent variables. The relationship between territorial hawk group size (which varies on many islands in the Galápagos) and louse abundance is treated elsewhere (Whiteman and Parker 2004).

RESULTS

We captured and sampled 26 Galápagos Hawks, over one-third of the total estimated host population on Marchena. Of the 26 hawks, 21 were adults (17 territorial, four nonterritorial) and five were nonterritorial immatures.

Average body condition did not differ between adult nonterritorial and immature nonterritorial birds ($t_7 = 0.8$, $P = 0.43$). Thus, condition data for the two groups were pooled. Nonterritorial birds were in significantly poorer body condition than territorial hawks (equal variances not assumed, $t_{23} = 2.9$, $P < 0.01$; Fig. 1).

We collected 3186 lice from 25 infested Galápagos Hawks. Of these, 2872 were *C. turbinatum* and 314 were *D. regalis*. Most *D. regalis* specimens were collected from wing and tail feathers, whereas *C. turbinatum* were collected from all body regions. Host body condition and louse abundance were significantly negatively related for *C. turbinatum* ($r = -0.43$, $P = 0.03$, but not for *D. regalis* ($r = -0.33$, $P > 0.05$; Fig. 2).

There were no significant differences between adult nonterritorial ($n = 4$) and immature nonterritorial hawks ($n = 5$) for any of the parasite load metrics (*C. turbinatum*: all $t \leq 0.8$, all $P > 0.4$; *D. regalis*: all $t \leq 0$, all $P > 0.4$). Thus, parasite data were pooled for adult and immature nonterritorial hawks. Mean abundances (Table 1) and mean and median intensities (Fig. 3) of both louse species were significantly higher for

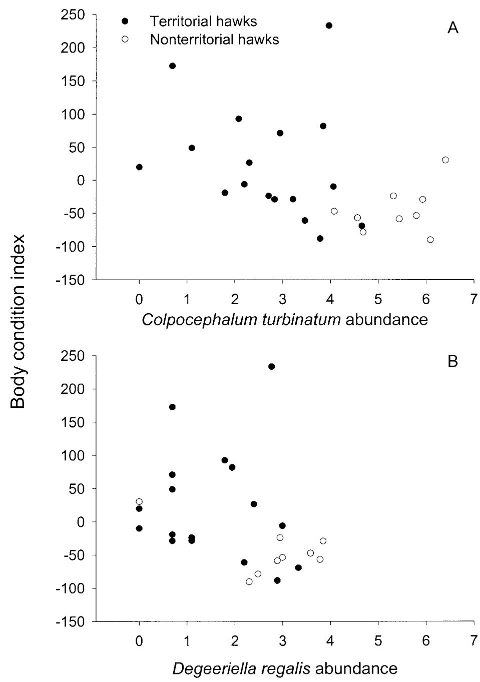

FIGURE 2. Scatterplots of body condition vs. abundance of two louse species (ln transformed) for territorial and nonterritorial Galápagos Hawks ($n = 26$). (A) *Colpocephalum turbinatum* ($r = -0.43$, $P = 0.03$); (B) *Degeeriella regalis* ($r = -0.33$, $P > 0.05$).

nonterritorial hawks compared to territorial hawks; thus, parasite load was indicative of hawk territorial status.

Mean abundance (Table 1) and mean intensity of *C. turbinatum* were significantly higher than that of *D. regalis* for both groupings of hawks (nonterritorial hawks: mean intensities: $t_9 = 4.1$, $P < 0.01$; territorial hawks: mean intensities: $t_{17} = 2.7$, $P = 0.03$). Median intensities of *C. turbinatum* were higher than *D. regalis* for nonterritorial (Mood's test of medians, $P < 0.01$) but not territorial hawks ($P > 0.05$).

In the regression of *D. regalis* abundance on *C. turbinatum* abundance, the intercepts and slopes for territorial and nonterritorial hawks differed significantly and SAS (SAS Institute 1997) separated the two data sets (intercepts: $t_1 = -4.5$, $P < 0.001$; slopes: $t_1 = 2.5$, $P = 0.02$; Fig. 4). The regression equation for territorial hawks was $y = 0.187x + 2.006$ and for nonterritorial hawks was $y = -0.043x + 33.747$. The slope for territorial hawks was significantly positive ($r = 0.41$, $t_1 = 3.2$, $P < 0.01$) and for nonterritorial hawks was significantly negative ($r = 0.25$, $t_1 = -2.3$, $P = 0.04$; Fig. 4).

DISCUSSION

We found a strong relationship between louse load, host body condition, and territorial status in a population of the Galápagos Hawk. Nonterritorial birds were in significantly poorer body condition and had

TABLE 1. Prevalences and mean abundances of the lice *Colpocephalum turbinatum* (Amblycera) and *Degeeriella regalis* (Ischnocera) for nonterritorial ($n = 9$) and territorial ($n = 17$) Galápagos Hawks from Isla Marchena, Galápagos, Ecuador.

	Prevalence (%)[a]			Mean abundance[b]	
	Nonterritorial	Territorial	*P*	Nonterritorial	Territorial
C. turbinatum	100	94	1.0	270.6 (162.3-385.2)	25.7 (13.7-38.4)
D. regalis	89	88	1.0	22.0 (12.1-31.6)	6.8 (3.2-10.5)

[a] All prevalence comparisons were significant with a Fisher's exact test. Prevalence is the percentage of individuals infested with lice out of the total number of hawks sampled.

[b] Values in parentheses are 95% bootstrap confidence limits around the mean abundance (2000 replications). All abundance comparisons were significant (all $t \geq 2.7$, all $P \leq 0.03$).

higher loads of both louse species than did territorial hawks. Some studies of other taxa have found similar results (Jenkins et al. 1963), although others have not (Blanco et al. 2001, Darolova et al. 2001).

We also found a negative relationship between host body condition and the abundance of *C. turbinatum*. Thus, the abundance of the amblyceran louse, *C. turbinatum*, had a stronger correlation with body condition than the ischnoceran. Do these lice directly reduce host body condition? This seems possible, given that they feed on blood and vector endoparasites, and are at least in part transmitted by physical contact involving individuals other than parents and their offspring (Whiteman and Parker 2004), each of which may correlate with increased virulence (Seegar et al. 1976, DeVaney et al. 1980, Clayton and Tompkins 1994). Ischnoceran lice, however, can influence host fitness as well, usually by damaging feathers, which compromises thermoregulatory ability, and reduces survivorship and male mating success (Booth et al. 1993, Clayton et al. 1999). In contrast to our findings, Calvete et al. (2003) found that the relationship between body condition and the abundances of both amblyceran and ischnoceran lice (each louse species was analyzed separately) were significantly inversely related; thus generalizations on the effects of these two suborders are not yet possible.

Alternatively, parasite populations may respond to changes in host behavior that independently affect host body condition. For example, preening rate is perhaps the most important regulator of ectoparasite load (Clayton 1991). However, preening consumes time and energy (Giorgi et al. 2001). It is reasonable to assume that resource-stressed hosts (nonterritorial) preen less than non-resource-stressed hosts (territorial). Thus, preening rate and body condition may be linked, which

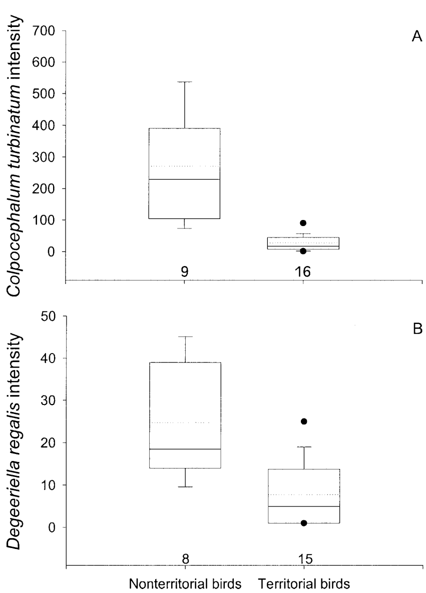

FIGURE 3. Infestation intensity by two louse species on territorial and nonterritorial Galápagos Hawks. Box and whisker plots show mean (dotted lines), median (solid lines) and 5th and 95th percentiles for (A) *Colpocephalum turbinatum*; (B) *Degeeriella regalis*. Intensity is a measure of parasite abundance calculated from infested hawks only. Numbers below plots are numbers of hawks sampled. Note difference in *y*-axis scales.

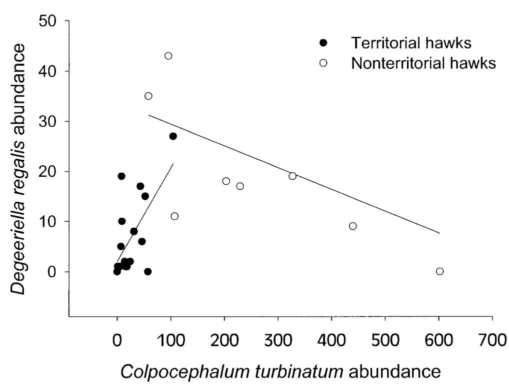

FIGURE 4. Scatterplot of total abundances of the lice *Colpocephalum turbinatum* vs. *Degeeriella regalis* for territorial ($n = 17$) and nonterritorial ($n = 9$) Galápagos Hawks. Slopes of both regression lines were significantly different from zero.

would release constraints on parasite population growth rates, resulting in higher parasite loads in nonterritorial hosts, which are also in poorer body condition. Generally, hosts with better nourishment are more resistant to parasites (Nelson et al. 1975, Marshall 1981, Nelson 1984, cf. Kartman 1949), which may be directly linked with immunocompetence (Christe et al. 1998). The relationship may also be more complicated than any of these scenarios. The association between condition and parasite load may instead generate a feedback loop (poor condition leading to increased parasitism leading to poorer condition).

We found that the mean abundance and median and mean intensity of the amblyceran, *C. turbinatum*, were significantly higher than in the ischnoceran, *D. regalis*, within nonterritorial and territorial hawks. The abundance of *D. regalis* appeared to be negatively affected by abundances of *C. turbinatum* in excess of 100 individuals. For territorial hawks, the relationship between the abundances of the two louse species was positive and linear, whereas the abundances of the two louse species for nonterritorial hawks was negative and linear. Possible mechanisms to explain this pattern include interspecific predation or competition (Gotelli 1998). There is evidence to suggest that *C. turbinatum* is predaceous on lice (Nelson 1971). When its abundances are relatively high, it may begin feeding on other lice. Alternatively, competition may begin when the abundance of *C. turbinatum* is above a threshold and individuals begin to invade microhabitats typically occupied only by *D. regalis* (Nelson 1972). Clayton (1991) found that *Columbicola columbae* lice were more resistant to host preening than *Campanulotes bidentatus*, suggesting that preening regulated the latter's abundance. Hopkins (1949) also demonstrated that louse coexistence was mediated by grooming behavior in guinea pigs (*Cavia porcellus*). We speculate that once a Galápagos Hawk becomes territorial, the abundances of the two louse species equilibrate and become positively related instead of being negatively related as occurs when *C. turbinatum* abundances become large. Future research should focus on decoupling the degree to which parasite load drives host territoriality and the degree to which territorial status drives parasite load (and parasite coexistence).

All collection and sampling procedures were approved by the University of Missouri-Saint Louis Animal Care and Use Committee and the Galápagos National Park Service, Ecuador. This research was funded by a grant from the Field Research for Conservation Program of the Saint Louis Zoo (F.R.C. #01–9), and funds from the E. Des Lee Collaborative Vision in Zoological Studies from the University of Missouri-St. Louis. We gratefully acknowledge the Servicio Parqué Nacional de Galápagos and the Charles Darwin Foundation. Jenny Bollmer and Pedro Castillo were steadfast field companions during the 2001 season. Ivan Jiménez and Jenny Bollmer graciously aided in the statistical analyses. The Parker lab group and two anonymous reviewers provided helpful comments on a previous version of this manuscript.

LITERATURE CITED

ASH, J. S. 1960. A study of the Mallophaga of birds with particular reference to their ecology. Ibis 102:93–110.

BLACK, J. 1973. Galápagos, archipélago del Ecuador. Imprenta Europa, Quito.

BLANCO, G. 1997. Role of refuse as food for migrant, floater and breeding Black Kites (*Milvus migrans*). Journal of Raptor Research 31:71–76.

BLANCO, G., J. L. TELLA, AND J. POTTI. 2001. Feather mites on birds: costs of parasitism or conditional outcomes? Journal of Avian Biology 32:271–274.

BOLLMER, J. L., T. SANCHEZ, M. DONAGHY CANNON, D. SANCHEZ, B. CANNON, J. C. BEDNARZ, T. DE VRIES, S. STRUVE, AND P. G. PARKER. 2003. Variation in morphology and mating system among island populations of Galápagos Hawks. Condor 105: 428–438.

BOOTH, D. T., D. H. CLAYTON, AND B. A. BLOCK. 1993. Experimental demonstration of the energetic cost of parasitism in free-ranging hosts. Proceedings of the Royal Society of London Series B 253:125–129.

BROWN, J. L. 1969. Territorial behavior and population regulation in birds. Wilson Bulletin 81:293–329.

BROWN, M. E. 1996. Assessing body condition in birds. Current Ornithology 13:67–135.

BUSH, A. O., K. D. LAFFERTY, J. M. LOTZ, AND A. W. SHOSTAK. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. Journal of Parasitology 83:575–583.

CALVETE, C., R. ESTRADA, J. LUCIENTES, AND A. ESTRADA. 2003. Ectoparasite ticks and chewing lice of Red-legged Partridge, *Alectoris rufa*, in Spain. Medical and Veterinary Entomology 17:33–37.

CHRISTE, P., A. P. MØLLER, AND F. DE LOPE. 1998. Immunocompetence and nestling survival in the House Martin: the tasty chick hypothesis. Oikos 83:175–179.

CLAY, T. 1958. Revisions of Mallophaga genera. *Degeeriella* from the Falconiformes. Bulletin of the British Museum of Natural History, Entomology 7:121–207.

CLAYTON, D. H. 1991. Coevolution of avian grooming and ectoparasite avoidance, p. 258–298. *In* J. E. Loy and M. Zuk [EDS.], Bird-parasite interactions: ecology, evolution and behaviour. Oxford University Press, Oxford, UK.

CLAYTON, D. H., R. D. GREGORY, AND R. D. PRICE. 1992. Comparative ecology of Neotropical bird lice (Insecta: Phthiraptera). Journal of Animal Ecology 61:781–795.

CLAYTON, D. H., P. L. M. LEE, D. M. TOMPKINS, AND E. D. BRODIE III. 1999. Reciprocal natural selection on host-parasite phenotypes. American Naturalist 154:261–270.

CLAYTON, D. H., AND D. M. TOMPKINS. 1994. Ectoparasite virulence is linked to mode of transmission. Proceedings of the Royal Society of London Series B 256:211–217.

CRUICKSHANK, R. H., K. P. JOHNSON, V. S. SMITH, R. J. ADAMS, D. H. CLAYTON, AND R. D. PAGE. 2001. Phylogenetic analysis of partial sequences of elongation factor 1∝ identifies major groups of lice

(Insecta: Phthiraptera). Molecular Phylogenetics and Evolution 19:202–215.

DAROLOVA, A., H. HERBER, J. KRISTOFLIK, AND C. HOI. 2001. Horizontal and vertical ectoparasite transmission of three species of Malophaga, and individual variation in European Bee-Eaters (*Merops apiaster*). Journal of Parasitology 87:256–262.

DE VRIES, T. 1975. The breeding biology of the Galápagos Hawk, *Buteo galapagoensis*. Le Gerfaut 65: 29–57.

DEVANEY, J. A., J. H. QUISENBERRY, B. H. DORAN, AND J. W. BRADLEY. 1980. Dispersal of the northern fowl mite, *Ornithonyssus sylviarum* (Canestrini and Fanzago), and the chicken body louse, *Menacanthus stramineus* (Nitzsch), among some thirty strains of egg-type hens in a caged laying house. Poultry Science 59:1745–1749.

DONAGHY CANNON, M. M. 2001. Breeding ecology of cooperatively polyandrous Galápagos Hawks (*Buteo galapagoensis*) on Santiago Island, Galápagos. M.Sc. thesis, Arkansas State University, Jonesboro, AR.

FAABORG, J. 1986. Reproductive success and survivorship of the Galápagos Hawk (*Buteo galapagoensis*): potential costs and benefits of cooperative polyandry. Ibis 128:337–347.

FAABORG, J., AND J. C. BEDNARZ. 1990. Galápagos and Harris' Hawks: divergent causes of sociality in two raptors, p. 359–383. *In* P. B. Stacey and W. D. Koenig [EDS.], Cooperative breeding in birds: long term studies of ecology and behaviour. Cambridge University Press, Cambridge, UK.

FAABORG, J., T. DE VRIES, C. B. PATTERSON, AND C. R. GRIFFIN. 1980. Preliminary observations on the occurrence and evolution of polyandry in the Galápagos Hawk (*Buteo galapagoensis*). Auk 97: 581–590.

FAABORG, J., P. G. PARKER, L. DELAY, T. DE VRIES, J. C. BEDNARZ, S. MARIA PAZ, J. NARANJO, AND T. WAITE. 1995. Confirmation of cooperative polyandry in the Galápagos Hawk (*Buteo galapagoensis*). Behavioral Ecology and Sociobiology 36:83–90.

FRETWELL, S. 1969. Dominance behavior and winter habitat distribution in juncos (*Junco hyemalis*). Bird-Banding 40:1–25.

GIORGI, M. S., R. ARLETTAZ, P. CHRISTE, AND P. VOGEL. 2001. The energetic grooming costs imposed by a parasitic mite (*Spinturnix myoti*) upon its bat host (*Myotis myotis*). Proceedings of the Royal Society London Series B 268:2071–2075.

GOTELLI, N. J. 1998. A primer of ecology. 2nd ed. Sinauer Associates, Sunderland, MA.

HALVORSEN, O. 1986. On the relationship between social status of host and risk of parasitic infection. Oikos 47:71–74.

HARPER, D. G. C. 1999. Feather mites, pectoral muscle condition, wing length and plumage coloration of passerines. Animal Behavior 58:553–562.

HOGSTAD, O. 1987. Social rank in winter flocks of Willow Tits *Parus montanus*. Ibis 129:1–9

HOPKINS, G. H. E. 1949. The host-associations of the lice of mammals. Proceedings of the Zoological Society of London 119:387–604.

JENKINS, D., A. WATSON, AND G. R. MILLER. 1963. Population studies on Red Grouse *Lagopus lagopus scoticus* (Lath.) in north-east Scotland. Journal of Animal Ecology 32:317–376.

JOHNSON, K. P., AND M. F. WHITING. 2002. Multiple genes and the monophyly of Ischnocera (Insecta: Phthiraptera). Molecular Phylogenetics and Evolution 22:101–110.

KARTMAN, L. 1949. Preliminary observations on the relation of nutrition to pediculosis of rats and chickens. Journal of Parasitology 35:367–374.

KREBS, J. R. 1971. Territory and breeding density in the Great Tit, *Parus major* L. Ecology 52:2–22.

LINDELL, C. A., T. A. GAVIN, R. D. PRICE, AND A. L. SANDERS. 2002. Chewing louse distributions on two Neotropical thrush species. Comparative Parasitology 69:212–217.

MARSHALL, A. G. 1981. The ecology of ectoparasitic insects. Academic Press, London.

MCCRARY, M. D., P. H. BLOOM, AND M. J. GIBSON. 1992. Observations on the behavior of surplus adults in a Red-Shouldered Hawk population. Journal of Raptor Research 26:10–12.

NELSON, B. C. 1971. Successful rearing of *Colpocephalum turbinatum* (Phthiraptera). Nature 232:255.

NELSON, B. C. 1972. A revision of the New World species of *Ricinus* (Mallophaga) occurring on Passeriformes (Aves). University of California Publications in Entomology 68:1–175.

NELSON, B. C., AND M. D. MURRAY. 1971. The distribution of Mallophaga on the domestic pigeon (*Columba livia*). International Journal for Parasitology 1:21–29.

NELSON, W. A. 1984. Effects of nutrition of animals on their ectoparasites. Journal of Medical Entomology 21:621–635.

NELSON, W. A., J. E. KEIRANS, J. F. BELL, AND C. M. CLIFFORD. 1975. Host-ectoparasite relationships. Journal of Medical Entomology 12:143–166.

NEWTON, I. 1998. Population limitation in birds. Academic Press, San Diego, CA.

POTTI, J., AND S. MERINO. 1995. Louse loads of Pied Flycatchers: effects of host's sex, age, condition and relatedness. Journal of Avian Biology 26: 203–208.

PRICE, R. D., AND J. R. BEER. 1963. Species of *Colpocephalum* (Mallophaga: Menoponidae) parasitic upon the Falconiformes. Canadian Entomologist 95:731–763.

PRICE, R. D., R. A. HELLENTHAL, R. L. PALMA, K. P. JOHNSON, AND D. H. CLAYTON. 2003. The chewing lice: world checklist and biological overview. Illinois Natural History Survey Special Publication 24, Champaign, IL.

REICZIGEL, J., AND L. RÓZSA. 2001. Quantitative Parasitology 2.0. J. Reiczigel and L. Rózsa, Budapest.

RÓZSA, L., J. REICZIGEL, AND G. MAJOROS. 2000. Quantifying parasites in samples of hosts. Journal of Parasitology 86:228–232.

SAS INSTITUTE. 1997. SAS/STAT software: changes and enhancements through release 6.12. SAS Institute Inc., Cary, NC.

SEEGAR, W. S., E. L. SCHILLER, W. J. L. SLADEN, AND M. TRPIS. 1976. A mallophagan, *Trinoton anse-*

rinum, as a cyclodevelopmental vector for a heartworm parasite of waterfowl. Science 194:739–741.

SPSS. 1997. SPSS v. 10. SPSS Inc., Chicago.

THORNTON, I. 1971. Darwin's islands: a natural history of the Galápagos. Natural History Press, Garden City, NJ.

WALTHER, B. A., AND D. H. CLAYTON. 1997. Dust-ruffling: a simple method for quantifying ectoparasite loads of live birds. Journal of Field Ornithology 68:509–518.

WHITEMAN, N. K., AND P. G. PARKER. 2004. Effects of host sociality on ectoparasite population biology. Journal of Parasitology, in press.

WHITEMAN, N. K., D. SANTIAGO ALARCON, K. P. JOHNSON, AND P. G. PARKER. 2004. Differences in straggling rates between two genera of dove lice (Insecta: Phthiraptera) reinforce population genetic and cophylogenetic patterns. International Journal for Parasitology, in press.

The Condor 106:921–925

PHYSIOLOGICAL RESPONSES TO TEMPERATURE BY WHIP-POOR-WILLS: MORE EVIDENCE FOR THE EVOLUTION OF LOW METABOLIC RATES IN CAPRIMULGIFORMES

JEFFREY E. LANE[1,4], DAVID L. SWANSON[2], R. MARK BRIGHAM[1] AND ANDREW E. MCKECHNIE[3]
[1]*Department of Biology, University of Regina, Regina, SK S4S 0A2, Canada*
[2]*Department of Biology, University of South Dakota, Vermillion, SD 57069-2390*
[3]*School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag 3, Wits 2050, South Africa*

Abstract. We measured the metabolic responses of nine Whip-poor-wills (*Caprimulgus vociferus*), captured in southeast South Dakota, to incremental changes in ambient temperature within the range of 0–40°C. Similar to other members of the Caprimulgiformes, Whip-poor-wills exhibited a basal metabolic rate that was lower than predicted by allometry. We compared basal metabolic rates of six caprimulgiform species (our data plus published values for five other species) with those of 82 other avian species using both conventional and phylogenetically independent ANCOVAs. The low basal metabolic rate of Caprimulgiformes was not explained by phylogenetic position. A low basal metabolic rate, together with the widespread ability of birds in this order to use daily torpor, seemingly has enabled members of this group to occupy their unique ecological niche (crepuscular insectivory).

Key words: basal metabolic rate, Caprimulgiformes, Caprimulgus vociferus, *phylogenetically independent ANCOVA, Whip-poor-will.*

Respuestas Fisiológicas de *Caprimulgus vociferus* a la Temperatura: Más Evidencia a Favor de la Evolución de una Baja Tasa Metabólica en Caprimúlgidos

Resumen. Medimos las respuestas metabólicas a aumentos de la temperatura ambiental en un rango de 0–40°C en nueve individuos de *Caprimulgus vociferus* capturados en Dakota del Sur. De manera similar a otros Caprimúlgidos, *C. vociferus* presentó una tasa metabólica basal menor a la predicha por parámetros alométricos. Comparamos las tasas metabólicas basales de seis especies de caprimúlgidos (nuestros datos más datos publicados para otras cinco especies) con aquellas de otras 82 especies de aves utilizando análisis de co-varianza (ANCOVA) convencionales y filogenéticamente independientes. La baja tasa metabólica basal de los caprimúlgidos no fue explicada por su posición filogenética. La baja tasa metabólica basal, junto a la capacidad generalizada de las aves de este orden de usar torpor diario, aparentemente han permitido a los miembros de este grupo a ocupar un nicho ecológico único (insectivoría crepuscular).

The Caprimulgiformes occupy an ecological niche that is rare among birds. Members of this order are active during crepuscular and nocturnal periods, and most forage for aerial insects (Holyoak 2001). Reliance on insectivory increases the likelihood that an animal will face occasional energy deficits because the abundance of insects is positively correlated with ambient temperature (Csada and Brigham 1994). Consequently,

Manuscript received 24 November 2003; accepted 2 July 2004.

[4] Present address: Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada. E-mail: jelane@ualberta.ca