



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

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SHORT COMMUNICATIONS

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MIGRATORY CONNECTIVITY IN BICKNELL'S THRUSH: LOCATING MISSING POPULATIONS WITH HYDROGEN ISOTOPES

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Abstract. The measurement of the abundance of naturally occurring deuterium (δD) in feathers grown in North America can provide geographical information on location where the feather was grown. Previously, we used this technique to link populations of Bicknell's Thrush (*Catharus bicknelli*) breeding in northeastern North America (to 46°N) with wintering grounds in the Dominican Republic. That study indicated the presence of a subpopulation of wintering birds with more depleted feather δD values than those measured on their known breeding grounds. This suggested either a more northerly or a higher altitude breeding source population than previously measured. We located two populations of Bicknell's Thrush in Quebec, Canada, at Mine Madeleine (49°N) and at Mont Gosford (45°N). The Mine Madeleine birds had feather δD values overlapping those of the unidentified subpopulation found wintering in the Dominican Republic. At Mont Gosford, hatch-year birds were more depleted in their feather δD values than after-second-year birds suggesting their more northerly origins and capture during the early fall migration period. Our study demonstrates how the stable-isotope approach can be used to document connectivity between breeding and wintering populations of migratory birds.

Key words: *Catharus bicknelli*, deuterium, migratory connectivity, stable isotopes.

**Conectividad Migratoria en *Catharus bicknelli*:
Localización de Poblaciones Perdidas con
Isótopos de Hidrógeno**

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Resumen. La medición de la abundancia de deuterio en estado natural (δD) en las plumas formadas en América del Norte puede brindar información geográfica sobre la localización en donde se formó la pluma. Anteriormente usamos esta técnica para relacionar las poblaciones de *Catharus bicknelli* que se reproducen en el noreste de América del Norte (hasta 46°N) con las áreas de invernada en República Dominicana. Ese estudio indicó la presencia de una subpoblación de aves invernantes con valores de δD en las plumas por debajo de los valores medidos de los sitios conocidos de cría. Esto sugirió la presencia de una población reproductiva proveedora de individuos localizada más al norte o a mayor elevación que las registradas anteriormente. Localizamos dos poblaciones de *C. bicknelli* en Québec, Canadá, una en Mine Madeleine (49°N) y otra en Mont Gosford (45°N). Las aves de Mine Madeleine tuvieron valores de δD en las plumas que se superpusieron con aquellos de la subpoblación no identificada encontrada invernando en República Dominicana. En Mont Gosford, las aves del primer año de edad presentaron valores más bajos de δD en las plumas que aquellos encontrados en aves del segundo año de edad o mayores, sugiriendo un origen más boreal y que fueron capturadas durante el inicio del período de migración otoñal. Nuestro estudio demuestra como el método de isótopos estables puede ser usado para documentar conectividad entre poblaciones reproductivas e invernales de aves migratorias.

Events occurring during one period of the annual cycle of a migratory bird can affect events during a subsequent period, a phenomenon termed the seasonal interaction hypothesis (Webster et al. 2002). Thus, to fully understand the demographics of migratory species and to devise effective conservation approaches, it is necessary to delineate connections between breeding, stopover, and wintering sites. For the vast majority

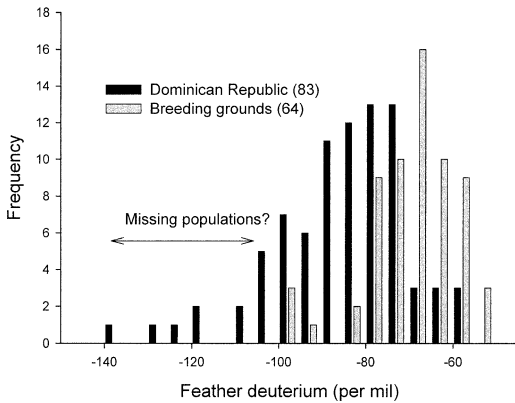


FIGURE 1. Distribution of feather deuterium isotope values (δD_f) for Bicknell's Thrush tail feathers sampled by Hobson et al. (2001) on breeding grounds and on the Dominican Republic wintering grounds. "Missing populations" refers to birds with more negative δD_f values that are not accounted for in the distribution of δD_f values of breeding individuals. Numbers in parentheses are the number of birds sampled.

of migratory birds breeding in North America this task was all but impossible using conventional approaches such as banding (Hobson 2002). However, the advent of stable-isotope tracking techniques has provided a powerful means of making connections between regions and habitats used by migratory birds (Marra et al. 1998, Hobson and Wassenaar 2001, Kelly et al. 2002, Rubenstein et al. 2002) and other migratory organisms in North America (Wassenaar and Hobson 1998, Hobson et al. 1999). This approach is based on the fact that deuterium isotope ratios in feathers (δD_f) and other tissues reflect those in their diet and these, in turn, are closely correlated with mean deuterium abundance in growing-season precipitation (δD_p), which show distinct latitudinal patterns in North America (Hobson and Wassenaar 1997).

Previously, we investigated connectivity between breeding and wintering sites of Bicknell's Thrush (*Cat-harus bicknelli*) using measurements of deuterium in their feathers obtained on both the breeding and wintering grounds in the Dominican Republic (Hobson et al. 2001). That investigation revealed that several wintering individuals originated from sites with more negative deuterium isotope values than those measured for the majority of their known breeding range in New England and southeastern Quebec (Rimmer et al. 2001; Fig. 1). Hobson et al. (2001) speculated that there were two likely explanations for this. Birds with more negative deuterium isotope values in feathers could have originated from sites farther north than those sampled on the breeding grounds, or they could have originated from higher altitude sites since deuterium values in rainfall also become depleted with altitude (Hobson et al. 2003). A combination of both factors may have been involved. Since several high-altitude sites where Bicknell's Thrushes were known to breed were sampled by Hobson et al. (2001), a more parsimonious explanation appeared that there were in

fact unidentified or untested breeding populations of Bicknell's Thrush wintering in the Dominican Republic. The species has a fragmented breeding range and its relative abundance across the northern portion of this range is generally poorly known (Rimmer et al. 2001). This prompted us to look for the "missing" populations of Bicknell's Thrush in the southeastern boreal region of Quebec which represents the northernmost portion of the known breeding range of the species (Rimmer et al. 2001). Previous field seasons of searching several hundred square kilometers of potential habitat in this region using point counts and song playback located Bicknell's Thrushes at Mont Gosford and Mine Madeleine in sites dominated by balsam fir (*Abies balsamea*). Our objectives then were to collect feathers from individuals in these two new populations and compare them with values previously obtained from breeding locations in New England and wintering locations in the Dominican Republic.

METHODS

After-hatch-year (AHY) Bicknell's Thrushes were captured on their breeding grounds during June and July 1999–2001 at two sites in southern Quebec: Mine Madeleine, Réserve faunique des Chic-Chocs (49°16'N, 66°06'W) and Mont Gosford, Eastern Townships (45°18'N, 70°52'W; Fig. 2). Hatch-year birds (HY) were captured during July and August 2001 at Mont Gosford. Both sites were located at high elevation (700–900 m) in the southern boreal mixedwood forest. Individuals were captured with mist nets either by targeting specific individuals with playbacks or through regular passive mist netting on sites. Once captured, birds were aged (as hatch year, second year [SY], or after second year [ASY]) and sexed according to criteria outlined in Pyle (1997). A tail feather (penultimate rectrix of the right side) was removed and stored in a labeled envelope.

STABLE-ISOTOPE ANALYSES

Feathers were cleaned with a 2:1 chloroform:methanol solvent to remove surface contaminants. Cleaned feather vanes were then subsampled for deuterium isotope analysis. Values reported here are equivalent to nonexchangeable feather hydrogen (Wassenaar and Hobson 2000). Elsewhere we describe how we use keratin standards as a means of correcting for the effect of hydrogen isotopic exchange with ambient vapor so that the values reported here are equivalent to nonexchangeable feather hydrogen (Wassenaar and Hobson 2003). Briefly, the process involves the simultaneous measurement of unknowns with several replicates of three different keratin standards whose nonexchangeable δD values are known and which span the range of expected feather values. Algorithms generated from each run that relate δD values of unknowns to their expected nonexchangeable values are then used on a run-by-run basis. Stable-hydrogen isotope measurements on feathers and keratin standards were performed on H_2 derived from high-temperature flash pyrolysis of feathers and continuous-flow isotope-ratio mass spectrometry (CF-IRMS). A Eurovector 3000TM (Milan, Italy) high temperature elemental analyzer with autosampler was used to automatically pyrolyze feather samples to a single pulse of H_2 gas. The re-

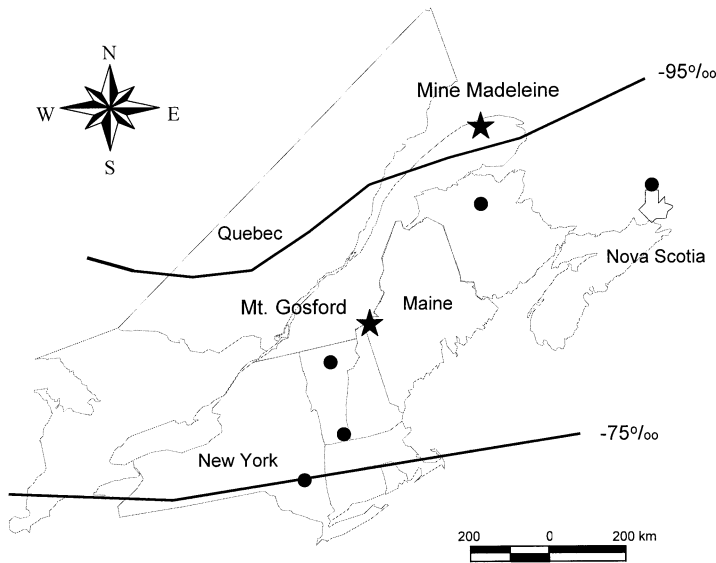


FIGURE 2. Location of study sites examined in this study (stars) and in Hobson et al. (2001; solid circles). The two contours correspond to expected values of δD_f as derived from interpolations of the kriged contours of Wassenaar and Hobson (2001).

solved H_2 sample pulse was then introduced to the isotope-ratio mass spectrometer (Micromass Isoprime[®] with electrostatic analyzer, Manchester, UK) via an open split capillary. All δD results are expressed in the typical delta notation, in units of per mil (‰), and normalized on the Vienna Mean Ocean Water–Standard Light Antarctic Precipitation (VSMOW–SLAP) standard scale. Repeated analyses of hydrogen isotope intercomparison material IAEA-CH-7 (–100‰), routinely included as a check, yielded an external repeatability of better than $\pm 1.5\%$.

RESULTS

Bicknell's Thrush feathers from the Mine Madeleine site showed more negative distributions of δD_f compared with those from breeding sites analyzed by Hob-

son et al. (2001). This new Quebec site included several individuals with δD_f values in the range of –100 to –121‰ (Table 1, Fig. 3) corresponding, in part, to the “missing” populations we identified from the distribution of birds wintering in the Dominican Republic. Among Quebec feathers stratified by age and site, distributions differed significantly ($F_{3,107} = 24.0$, $P < 0.001$). Differences were driven by the Mont Gosford ASY group (Fig. 3a) that was significantly more enriched in deuterium than the other three groups, Mont Gosford SY and Mine Madeleine ASY and SY (Turkey's post hoc, $P < 0.001$) which did not differ ($P > 0.05$; Fig. 3).

Using interpolation of the kriged contours presented in Wassenaar and Hobson (2001), we estimated that birds growing feathers at the northern site, Mine Mad-

TABLE 1. Results of deuterium analyses of feathers of Bicknell's Thrush from Hobson et al. (2001) and this study. Breeding grounds from Hobson et al. (2001) included six sites: New Brunswick; Cape Breton, Nova Scotia; Mt. Megantic, Quebec; N. Green Mountains, Vermont; S. Green Mountains, Vermont; and Catskills, New York.

Location	Age	<i>n</i>	Median δD_f (‰)	Range (‰)
Hobson et al. (2001)				
Dominican Republic	AHY	83	–93.8	–135.1 to –73.9
Breeding grounds	AHY	64	–82.2	–105.3 to –47.1
This study				
Mont Gosford, Quebec	ASY	24	– 87.1	–99.0 to –78.3
	HY	16	–103.5	–115.0 to –90
Mine Madeleine, Quebec	ASY	46	–104.8	–114.8 to –51.6
	SY	25	–103.3	–120.7 to –89.9

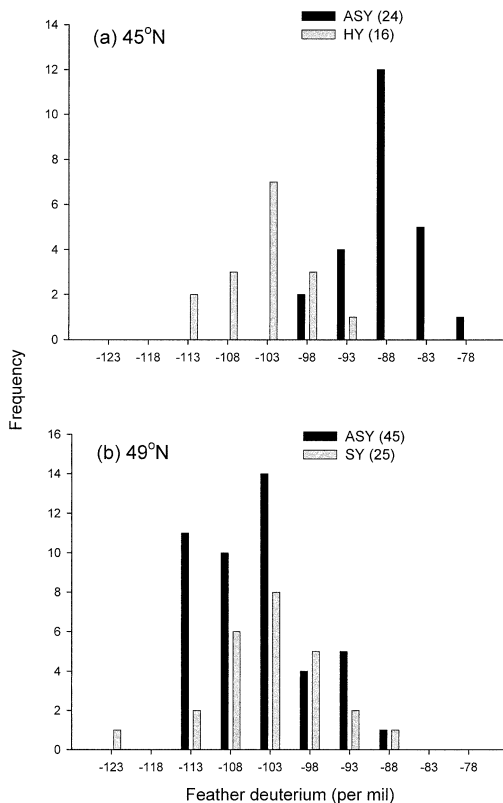


FIGURE 3. Distribution of feather deuterium isotope values (δD_f) for (a) after-second-year (ASY) and hatch-year (HY) Bicknell's Thrush tail feathers collected at Mont Gosford, Quebec, Canada, and for (b) after-second-year and second-year (SY) Bicknell's Thrush tail feathers collected at Mine Madeleine, Quebec, Canada. Numbers in parentheses are the number of birds sampled.

eleine, should have average δD_f values of -98% , whereas those grown at Mont Gosford, should have average δD_f values of -89% . Our results showed that SY and ASY birds captured at Mine Madeleine had average δD_f values close to those expected (Table 1). Similarly, ASY birds captured at Mont Gosford had average δD_f values close to those expected (Table 1). The more depleted values for HY birds at Mont Gosford suggested they originated from a more northern population that was statistically indistinguishable from those measured at Mine Madeleine.

DISCUSSION

The Bicknell's Thrush feathers we analyzed provided support for the hypothesis that some individuals wintering in the Dominican Republic came from more northern breeding sites than the ones Hobson et al. (2001) sampled. This demonstrates how stable isotope measurements of individuals on the wintering grounds can provide insight into wintering-population structure and so guide forensic research into locating "missing"

populations or provide crucial information on the relative importance of various areas of production (e.g., Hobson et al. 1999). This is particularly useful for species like Bicknell's Thrush that occur in relatively small, discrete breeding clusters throughout their limited breeding range in eastern North America (Ouellet 1993).

An interesting result of our isotopic investigations was the isotopic difference between ASY and HY birds captured at the more southern site of Mont Gosford, Quebec. The more depleted than expected δD_f values of the HY birds for that location suggests that they originated farther north and were sampled during early migration or natal dispersal, possibly from the Mine Madeleine population. This was consistent with the fact that these birds were captured during passive mist netting, whereas the ASY birds were captured on territories using call playback. Alternatively, a less likely possibility is that there may be an intrinsic isotopic difference between HY and AHY birds from the same location (e.g., Meehan et al. 2003).

We noted that although there was a close agreement between our expected mean δD_f values at both Quebec sites and those of AHY birds captured at these sites, our measured values tended to be slightly more negative than those from the kriged relationship depicted in Wassenaar and Hobson (2001). This may be due to the fact that the growing-season average relationship of Wassenaar and Hobson (2001) did not take into account altitudinal effects. It has been well established that δD values in precipitation show depletion with altitude (Poage and Chamberlain 2003, Hobson et al. 2003) and it will be useful to compare our results to expected values derived from an altitude-corrected dataset of mean growing season average δD_f . On the other hand, our measured AHY δD_f values were remarkably close to expected given the numerous sources of variation we might expect (Hobson 2004).

Our study demonstrates the power of the stable-isotope approach for making connections between breeding and wintering populations. In our case, we used this technique as more of a forensic tool than has previously been demonstrated. That is, our wintering-ground δD_f values indicated the presence of a breeding population not accounted for from previous knowledge of the breeding distribution of the species and this led us to look for the "missing" populations. We suggest that such a forensic approach will prove useful in other studies, especially where it may be relatively easy to capture birds where they are more concentrated on their wintering grounds. Our study also proved useful for inferring sources of HY birds that had clearly dispersed or migrated from their natal origins (Hobson et al. 2004). However, we caution that such forensic approaches are open to error, especially when not all of the caveats or assumptions of the stable-isotope approach are understood (Rubenstein and Hobson 2004). In our case, it is still possible that the altitude effect on feather δD_f values is a source of variance. Nonetheless, our approach led directly to the discovery of previously unknown populations of Bicknell's Thrush.

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CAN MIGRANTS DO IT FASTER? ACCELERATED MOLT OF BAIRD'S SPARROWS AND FURTHER INSIGHTS INTO SOUTHWESTERN MOLTING GROUNDS

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Abstract. Using museum specimens, I document the prebasic flight-feather molt and molting grounds of Baird's Sparrow (*Ammodramus bairdii*). Prebasic molt can apparently be carried out to some extent during fall migration. When initiating or completing molt, most Baird's Sparrows appear to be concentrated at the northern edge of their wintering range, and well within the late-summer monsoon zone. This staging may be to make use of the monsoon zone, broadly defined, but also to avoid the heavier monsoon rains found farther south in the wintering range. During prebasic molt, adult female Baird's Sparrows replace their primaries in 27 days, whereas adult males take 46 days; the mean replacement time is 39 days when sexes are combined. This is the fastest rate yet reported for a western U.S. breeding passerine, and I hypothesize that it might be due to being released from energetic constraints imposed by additional extensive migration.

Key words: *Ammodramus bairdii*, molt, molting grounds, monsoon region.

¿Pueden las Aves Migratorias Hacerlo más Rápido? Muda Acelerada en *Ammodramus bairdii* y Consideraciones Adicionales sobre los Sitios de Muda en el Suroeste

Resumen. Utilizando especímenes de museo, documenté la muda prebásica de las plumas de vuelo y sitios de muda de *Ammodramus bairdii*. Aparentemente, la muda prebásica puede ser llevada a cabo, en cierta medida, durante la migración de otoño. Al iniciar o completar la muda, la mayoría de los individuos de *A. bairdii* parecen concentrarse en el borde norte de su rango de distribución invernal y en el interior de la zona del monzón tardío de verano. Este comportamiento puede ser para utilizar la zona del monzón, definida de modo general, pero también para evitar las lluvias monzónicas más fuertes que se observan más al sur en el rango de invernada. Durante la muda prebásica, las hembras adultas de esta especie reemplazan sus primarias en 27 días, mientras que los machos adultos toman 46 días. El tiempo de reemplazo promedio es de 39 días cuando se combinan los sexos. Esta es la tasa más rápida reportada para un ave pasarina que se reproduce en el oeste de EUA, y sugiero

que esto se puede deber a que esta especie se ve liberada de restricciones energéticas impuestas por grandes migraciones adicionales.

Over approximately the last decade, a number of studies have shown the importance of the southwestern U.S.-northwestern Mexico as molting grounds for a number of Western-breeding passerine species (Thompson 1991, Young 1991, Voelker and Rohwer 1998, Butler et al. 2002). These molting grounds are subject to late-summer monsoons (Comrie and Glenn 1998), and there is strong support for the idea that migrants use the late-summer resources (food flushes) that result from summer rain by stopping there during migration to initiate or complete prebasic molt (Young 1991, Voelker and Rohwer 1998, Butler et al. 2002). For most of the species studied, there is no or very little overlap of the molt-migration area and breeding and wintering grounds. In a few cases, species which breed to a large extent in this molt-migration monsoon region but which winter farther south, do not use this area as the migrant stop over species do (Voelker 2000, Voelker and McFarland 2002). Western-breeding species differ substantially in the speed at which they replace flight feathers, and strictly transient species may be able to molt faster than species which breed largely within the molt-migration region (Voelker 2000, Voelker and McFarland 2002).

To further examine the interaction between flight-feather molt rate and the molt-migration zone across Western-breeding species, I examined molt in Baird's Sparrows (*Ammodramus bairdii*). This species breeds in the northern Great Plains from mid-May to mid-August, and winters from mid-October to mid-April almost entirely within the molt-migration, late-season monsoon zone of the southwestern U.S. and northwestern Mexico. Because the molt-migration zone is the end point of Baird's Sparrow fall migration, rather than a stop over area, it is possible that they use the area in a different fashion than migrants or species which breed there.

METHODS

I examined 235 adult Baird's Sparrow specimens from museum collections (see acknowledgments). I used data from museum labels to establish the sex, collection date, and collection locality of each specimen. Data from museum labels or plumage characters (see Pyle 1997) were used to exclude hatch-year birds from the analyses.

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I examined specimens under a $3\times$ magnifying lamp lighted with a 22-W fluorescent bulb, using a small forceps to lift feathers and quantify molt. Baird's Sparrows have nine primaries and nine secondaries on each wing, and 12 rectrices. To score flight-feather molt, I estimated the fraction of the full length (by 0.1 intervals) each developing feather had reached. Missing feathers were scored as 0, "N" was used to designate newly replaced feathers, and "X" was used to designate not yet replaced feathers on actively molting specimens (Voelker and Rohwer 1998). I scored asymmetrical primary feather molt if one or more contiguous feathers were missing on one wing and not the other as long as primary 1 was included in the missing feathers. I did this because primary molt often is not synchronized, and it is common for one wing to start molting slightly before the other wing (Voelker and Rohwer 1998, Voelker 2000).

I estimated the rate and duration of molt using Pimm's (1976) regression method employing date of collection (converted to Julian days) as the dependent variable and the summed score of growing and newly replaced primary feathers as the independent variable. The y-intercept from the regression is converted from Julian days to a calendar date, giving the mean molt initiation date. Mean molt completion date is calculated by replacing the x value from the regression equation with the maximum possible molt score value (here, 18), and solving for a value that is then converted to a calendar date. This method correctly provides a mean estimate of primary molt duration for all individuals, and thus is more appropriate than reversing the axes, which would be appropriate if only a single bird were being followed through time (Pimm 1976, Langston and Rohwer 1996). All specimens that were actively replacing primaries were included in the regression analyses. The duration of primary feather replacement appeared to encompass the replacement duration of all flight-feather tracts (see Results), and therefore only primary feather scores were used in the regression analyses.

I followed Langston and Rohwer (1996) in determining molt series. For a detailed explanation of the rules of feather replacement and the identification of a molt series, consult Yuri and Rohwer (1997). Briefly, based on its stage of growth, and the stage of growth of adjacent feathers, each developing feather can be placed into one of three categories: nodal, terminal, or directional. Nodal feathers are replaced first in a series and are always closer to full length than adjacent feathers. Terminal feathers are replaced last in a series and are always less fully grown than adjacent feathers. The lengths of other developing feathers will indicate whether the direction of feather replacement within a series proceeds proximally to distally, or distally to proximally.

RESULTS

Baird's Sparrows molted flight feathers from August to October (Fig. 1). Of the 35 specimens I examined from this period, 19 (54%) were molting. All flight feathers were replaced during this molt. Primaries were replaced proximally to distally in a single series (Table 1). P1 is always nodal, but was the sole nodal feather

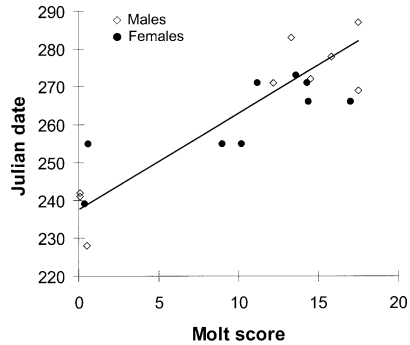


FIGURE 1. Regression of collection date (Julian) on primary molt score, to estimate the time necessary to complete prebasic flight-feather molt in Baird's Sparrows. Unfilled diamonds denote males ($n = 9$), filled circles denote females ($n = 9$). The average molt initiation date was 28 August (Julian date 240) and the average completion date was 6 October (Julian date 279). One molting female was removed from the analysis (see Results).

for just two of the six specimens replacing P1. Data from four specimens indicated that P1–P3 or P1–P4 were nodal (Table 1). P9 was always the sole terminal primary feather (Table 1).

The regression of collection date on primary molt score suggested that primary replacement lasted a mean of 35 days, for males and females combined. When analyzed separately, males ($n = 9$) took 46 days to replace primaries ($r^2 = 0.86$, $P < 0.001$), while females ($n = 10$) surprisingly took just 20 days ($r^2 = 0.33$, $P < 0.08$). However, the duration for females was skewed by a single individual that initiated molt in late September; the average molt completion date was estimated to be 6 October. This specimen (CAL 30087), collected on 2 October in southern Arizona, had each of P1–P4 scored as 0.4, and P5 scored as 0.1, strongly suggesting that it arrived late to the molting area. Removing this specimen from the regression analysis resulted in a duration of 27 days for females ($r^2 = 0.66$, $P = 0.008$), and 39 days when males and females were combined ($r^2 = 0.77$, $P < 0.001$) (Fig. 1).

Secondaries were replaced in two or possibly three series: S1 to S6 and S7 to S9, or S1 to S5, S6, and S7 to S9. The inner series started first, and could be complete or nearly complete by the time that replacement of the outer series began. Both nodal and terminal feathers varied in this series (Table 1). The outer secondary series was replaced distally to proximally, and initiation appeared to commence shortly after the nodal feathers of the primary series were dropped. In most cases S5 appeared to be part of this series; in four cases it was scored as a terminal feather. However in one instance S5 was scored as being part of an S6-included series. This is most likely a function of the fact that S6 appears to constitute its own molt series, and was simply dropped earlier than S5 in that single instance.

S6 appeared to constitute its own molt series. In eight cases where both S6 and S7 were being replaced simultaneously, S6 was scored as less than or equal to

TABLE 1. Patterns of flight feather replacement in 19 molting Baird's Sparrows. Numbers in each column refer to the number of times that each focal feather was being replaced across all molting specimens. Nodal feathers are lost first in a molt series and indicate molt series initiation points, while terminal feathers are replaced last and indicate molt series completion points. Other growing feathers indicate directionality, which is determined by the condition of adjacent feathers, relative to each focal feather.

Molt pattern	Focal feather ^a																								
	S9	S8	S7	S6	S5	S4	S3	S2	S1	P1	P2	P3	P4	P5	P6	P7	P8	P9	R1	R2	R3	R4	R5	R6	
Proximal to distal molt			1	4								1	3	7	8	8	11				1				4
Distal to proximal molt			4	2	1	2	8	10				4	4	1											
Nodal feathers									11	6	4	4	1												
Terminal feathers	2		3	4	4	1												9							

^a S = secondary; P = primary; R = rectrix. Secondaries are numbered distally to proximally; primaries are numbered proximally to distally; rectrices are numbered medially to laterally.

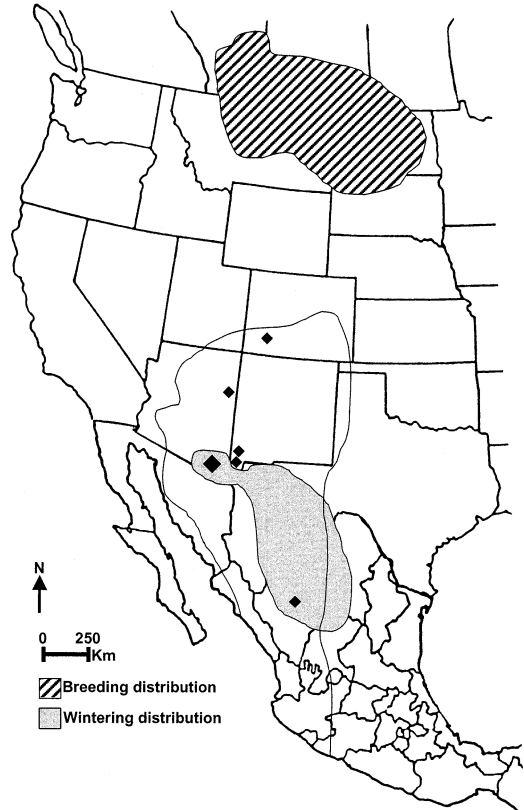


FIGURE 2. Geographic distribution of 19 molting Baird's Sparrow specimens (filled diamonds; the large diamond indicates 14 specimens taken across southeastern Arizona). The cross-hatched area indicates the approximate breeding range. The shaded area indicates the approximate wintering range (Green et al. 2002). The narrow line denotes the approximate limits of the desert monsoon region (Comrie and Glenn 1998).

0.5 in length when S7 was 1.0 or new. Were S6 part of the S7–S9 series, it is unlikely that there would be such a gap in growth lengths. In four of these same cases, S6 was longer than S5, suggesting that S6 had been dropped first. These factors combine then to suggest that S6 is a single-feather molt series.

Rectrix molt appeared to begin at the same time as primary molt, or shortly thereafter, proceeded rapidly, and was completed prior to the conclusion of primary molt. There was directional information on replacement from just five feathers (Table 1) indicating that rectrices tend to be dropped simultaneously, or nearly so, and thus form a single molt series.

Fifteen (eight males, seven females) of 19 molting specimens were collected on the wintering grounds (Fig. 2). However, 14 of these 15 were collected at the extreme northern edge of the wintering range, at or north of the Mexico-Arizona border. The 14 specimens were collected from all three Arizona counties which form part of the wintering range, on 10 separate dates

in seven different years ranging from 1873–1934. Of these molting specimens, eight had primary scores of greater than 4.5 (right wing only), and were therefore about half way or more towards completing molt. All four molting specimens collected north of the wintering range (two males, two females) had primary molt scores of greater than 6.6 (right wing only), and were collected after 25 September, suggesting a late departure from breeding grounds. The location and advanced condition of molt in most specimens suggested that molt can be initiated during migratory flights, or at least in migratory stopover areas. All molting specimens were collected in the late-summer monsoon area delimited by Comrie and Glenn (1998; Fig. 2). Of the remaining specimens collected from August to October ($n = 15$), six were collected on the breeding grounds, five from New Mexico, and four from the northwestern portion of the wintering range in Arizona or Sonora. These latter four specimens (two males, two females) were collected from 12 September to 24 October, and had completed flight feather molt.

DISCUSSION

Contrary to published accounts (Pyle 1997), adult Baird's Sparrows do not appear to perform prebasic flight-feather molt on summer grounds, nor does it appear that this molt is mostly or wholly completed after migration, as has been suggested (Green et al. 2002). Instead, it appears that prebasic flight feather molt is often started in the migratory range. This is not an unlikely assumption, given that fall migration occurs from late August to mid-October (Green et al. 2002) thus overlapping completely the molt timing and duration estimates. Further, molt is possibly completed, or nearly completed, in just a small portion of the wintering range.

In this regard, it seems that Baird's Sparrows may molt during migratory flights. Molting during migratory flights was suggested for western Warbling Vireos (*Vireo gilvus swainsonii*; Voelker and Rohwer 1998), but was not found in a recent study of Western Tanagers (*Piranga ludoviciana*) which specifically investigated that possibility (Butler et al. 2002). I found no evidence that Baird's Sparrows stop during migration to molt, as the four molting specimens collected in the migratory range were collected at roughly the same time as other molting specimens collected on the wintering grounds (and were in similar stages of molt). Based on the fact that most well-documented specimen records for migratory species in Kansas are TV tower kills, Thompson and Ely (1992) suggested that most species possibly fly over Kansas at night. If this is the case for Baird's Sparrows, then migration by single individuals might be rapid and those individuals may not be prone to stopping to complete molt.

There is also evidence that molting Baird's Sparrows are, in effect, staging at the northern tip of their wintering range to complete molt. While this could certainly be an artifact of historical collecting efforts (focused on southern Arizona), there is also a possible biological explanation for the observed pattern. The monsoon region delimited by Comrie and Glenn (1998) covers a broad area, which can be subdivided into four regions, three with roughly equivalent levels

of rainfall that peak during July and August (Comrie and Glenn 1998). Broadly, the extent of these three regions includes the northern halves of Sonora and Chihuahua, Mexico, and all U.S. states shown in Figure 2. To the south of these is the fourth region, which receives over twice the rain as the others (200 mm versus roughly 75 mm of rainfall in July and August; Comrie and Glenn 1998). I hypothesize that if Baird's Sparrows do indeed stage at the northern edge of their wintering grounds as suggested by molting specimens, they do so to (1) make use of the molt migration area, broadly defined, and (2) to avoid the comparatively heavy rainfall found farther south until the climate begins to ameliorate in September. It is possible that heavy rainfall could both affect thermoregulation during molt (light to heavy body molt occurs during flight feather molt; GV, unpubl. data), and decrease available food or foraging time.

Baird's Sparrows are not the only species to show this potential pattern of staging outside the southern monsoon zone. Before moving into this region, some Lazuli Buntings (*Passerina amoena*) use the Arizona-Mexico border zone to molt (Young 1991), and western Painted Buntings (*Passerina ciris ciris*) show a roughly similar pattern in that most molting birds are found either north of, or on the western or eastern fringes of, the southern monsoon zone (Thompson 1991). The same appears to hold true for Western Tanagers (Butler et al. 2002), and perhaps for Bullock's Orioles (*Icterus bullockii*) where most molting specimens were described as being from the southwestern U.S. or northern Mexico (Rohwer and Manning 1990; locations were not mapped). These results, from diverse passerine taxa, suggest that while portions of the monsoon zone may in fact facilitate a rapid molt (Voelker 2000), still other portions may not during certain times. We can therefore predict that in future studies of molt in relation to the monsoon region we should find only birds that have completed or very nearly completed prebasic flight-feather molt in the southern monsoon zone.

Baird's Sparrows complete prebasic flight feather molt in just 39 days, the fastest rate yet documented for a Western-breeding passerine. Baird's Sparrows may achieve this increased rate as compared to molt-migration species because they winter almost exclusively within the southwestern U.S. and northern Mexico. In general, the species mentioned above (buntings, tanager, oriole) must still perform some level of migration after molting. Therefore, while they generally molt faster than species not using the molt-migration region (i.e., Gray Vireo [*Vireo vicinior*], Voelker 2000; Lucy's Warbler [*Vermivora luciae*], Voelker and McFarland 2002), they do not molt as fast as Baird's Sparrows. I speculate that Baird's Sparrows can use available resources to complete their molt, while other species must dedicate a substantial portion of these resources toward completing migration.

Butler et al. (2002) discussed the importance of the Mexican monsoon region as a conservation area. The exact location of monsoon rains varies from year to year (Comrie and Glenn 1998) throughout this vast region, which therefore makes prioritizing areas for conservation difficult. The only clear areas for conser-

vation are montane and riparian habitats (Butler et al. 2002). If there are in fact staging areas this might present more tractable areas for conservation, or could at least allow for the identification of conservation focal points where birds initiate their molt. If we are to fully understand the nature of this important biological-geographical system, we clearly need more studies of Western-breeding passerines to include field-based investigation of both migration through the monsoon region and wintering ecology.

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

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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 es-

pecies de piojo estuvieron positivamente correlacionadas cuando el tamaño poblacional de *C. turbinatum* fue <100 individuos y negativamente correlacionadas cuando 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-

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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 km² 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 non-territorial adults were captured on an area of south-eastern 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 mea-

sured 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 (~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 non-territorial 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 ($\ln[\text{louse abundance} + 1]$) 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.

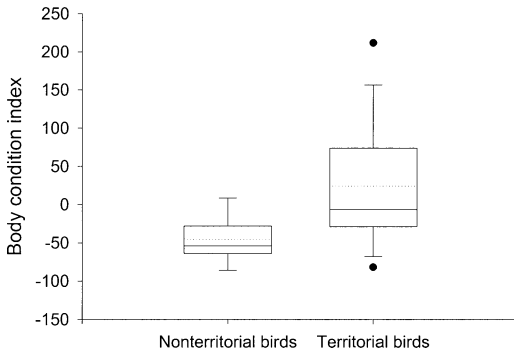


FIGURE 1. Nonterritorial Galapagos Hawks ($n = 9$) were in significantly poorer physical condition than territorial hawks ($n = 17$). Box and whisker plots show means (dotted lines), medians (solid lines) and 5th and 95th percentiles. Body condition was indexed as the residuals of a regression of body 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 Galapagos) and louse abundance is treated elsewhere (Whiteman and Parker 2004).

RESULTS

We captured and sampled 26 Galapagos 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 Galapagos 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

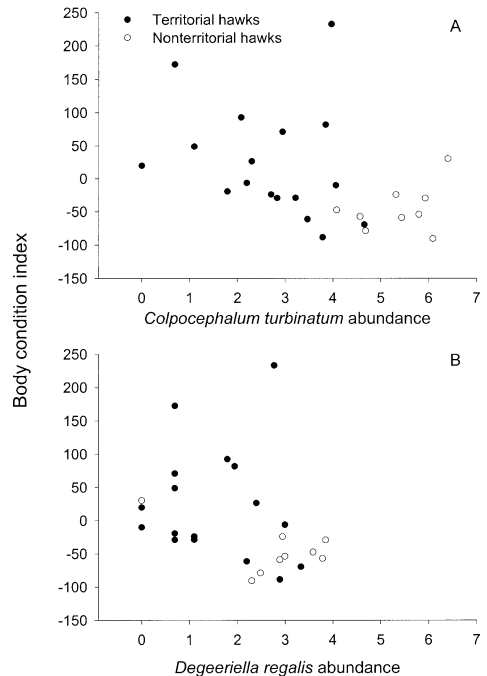


FIGURE 2. Scatterplots of body condition vs. abundance of two louse species (ln transformed) for territorial and nonterritorial Galapagos Hawks ($n = 26$). (A) *Colpocephalum turbinatum* ($r = -0.43$, $P = 0.03$); (B) *Degeeriella regalis* ($r = -0.33$, $P > 0.05$).

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 Galapagos 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	<i>P</i>	Nonterritorial	Territorial
<i>C. turbinatum</i>	100	94	1.0	270.6 (162.3-385.2)	25.7 (13.7-38.4)
<i>D. regalis</i>	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 involv-

ing 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

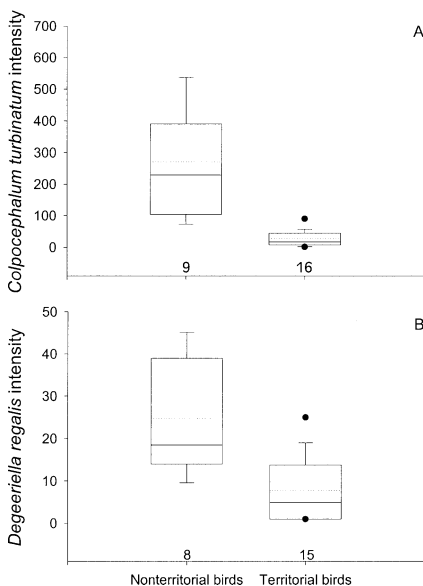


FIGURE 3. Infestation intensity by two louse species on territorial and nonterritorial Galápagos Hawks. Box and whisker plots show mean (dotted lines), median (solid lines) and 5th and 95th percentiles for (A) *Colpocephalum turbinatum*; (B) *Degeeriella regalis*. Intensity is a measure of parasite abundance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

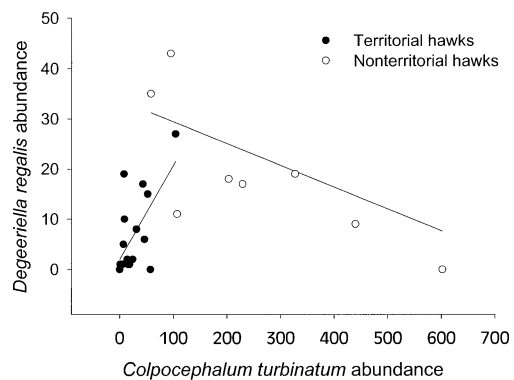


FIGURE 4. Scatterplot of total abundances of the lice *Colpocephalum turbinatum* vs. *Degeeriella regalis* for territorial ($n = 17$) and nonterritorial ($n = 9$) Galápagos Hawks. Slopes of both regression lines were significantly different from zero.

would release constraints on parasite population growth rates, resulting in higher parasite loads in non-territorial 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).

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

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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 Caprimúlpidos

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 Caprimúlpidos, *C. vociferus* presentó una tasa metabólica basal menor a la predicha por parámetros alométricos. Comparamos las tasas metabólicas basales de seis especies de caprimúlpidos (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 caprimúlpidos 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,

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during cold periods, the metabolic energy required to maintain a euthermic body temperature may be greater than the energy that can be acquired through foraging (Dawson and Hudson 1970). A low basal metabolic rate (BMR) is one physiological trait that may aid in enduring energetic shortfalls. A depressed BMR effectively reduces daily energetic maintenance requirements (Tieleman and Williams 2000), and is common in the Caprimulgiformes (Bech and Nicol 1999).

Whip-poor-wills (*Caprimulgus vociferus*) are a North American caprimulgiform that has recently been shown to use torpor to cope with energy shortages (Lane et al. 2004). Whether this species also possesses a low BMR has not been determined. Additionally, the apparent metabolic differences between the Caprimulgiformes and other orders have not yet been examined using phylogenetically independent approaches. In this study, we provide physiological data for Whip-poor-wills (e.g., basal and resting metabolic rates, thermal conductance, and the thermoneutral zone), which have never been reported, and test the hypothesis that the Caprimulgiformes have evolved lower BMRs than other birds. We use both conventional and phylogenetically independent methods to test this hypothesis.

METHODS

Nine male Whip-poor-wills were captured in riparian woodlands of southeast South Dakota, near the town of Vermillion (42°47'N, 97°0'W), between 5 June and 1 July 2000 and between 14 May and 3 August 2001. Following capture, birds were held in cloth bags and transported to the laboratory, where we recorded mass (to the nearest 0.1 g), age (Pyle 1997), and wingspan. Upon visual inspection, metabolic rates were not seen to differ noticeably between adults ($n = 7$) and juveniles ($n = 2$), so the data were pooled.

Birds were provided with water *ad libitum* and held overnight. Food was withheld to ensure that the birds were post absorptive the next day. Birds were divided into four experimental groups and, for each group, metabolic measurements were conducted at three temperatures (with one bird measured at five temperatures). The first group was measured at 30°C, 15°C, and 0°C ($n = 3$), the second at 35°C, 20°C, and 5°C ($n = 2$), the third at 40°C, 25°C, and 10°C ($n = 2$), and the last at 37.5°C, 32.5°C, and 27.5°C ($n = 2$, one of which was also measured at 22.5°C and 10°C).

METABOLIC RESPONSE TO TEMPERATURE MEASUREMENTS

Basal metabolic rate. Basal metabolic rate was determined by indirect calorimetry (as oxygen consumption, $\dot{V}O_2$) using an open-circuit respirometry system. Basal metabolic rate measurements for the birds began during daylight hours (trial start times: 11:34–21:49, the normal rest phase of the circadian cycle for *C. vociferus*). The trial for one bird began at 21:49, so there is the possibility that its metabolic rate was elevated owing to it having begun the active phase of its circadian cycle. Birds were placed in one of two metabolic chambers (3.8-L paint can or 5-L metal cylinder). Both chambers had black interiors to provide emissivities near 1.0. Flow rates of dried (with Drierite; W.A. Hammond Drierite Company, Xenia, Ohio), CO₂-free air (using Ascarite; Fisher Scientific Inc.,

Springfield, New Jersey) were regulated between 290 and 618 mL min⁻¹. The O₂ concentration in the excurrent airflow did not decline below 20.3%. Flow rates were regulated with a precision rotameter (Cole-Parmer Model FM082–03ST; Vernon Hills, Illinois) previously calibrated to $\pm 1\%$ accuracy (Swanson 1990). The fractional concentrations of oxygen (F_cO₂) in the dry excurrent gas stream were analyzed with an Ametek (Paoli, Pennsylvania) S-3A oxygen analyzer and fractional concentrations of CO₂ (F_cCO₂) in the excurrent gas stream with an Ametek CD-3A carbon dioxide analyzer. Both F_cO₂ and F_cCO₂ were recorded every 60 sec, and $\dot{V}O_2$ and CO₂ production values ($\dot{V}CO_2$) were corrected to standard temperature, pressure, and dry conditions to account for atmospheric pressure and temperature differences during the analyses. The $\dot{V}O_2$ values were converted to kJ day⁻¹ for the representation of BMR.

The metabolic chamber was submerged in a circulating bath (Forma Scientific Model 2095; Marietta, Ohio) filled with ethylene glycol and water, which allowed temperature regulation to within 0.5°C. Chamber temperature was measured with a copper-constantan thermocouple attached to a thermocouple thermometer (Cole Parmer Model 8500–40), previously calibrated against a thermometer traceable to the National Institute of Standards and Technology. We defined the thermoneutral zone of Whip-poor-wills as the range of ambient temperatures over which metabolic rate did not vary, and the BMR was taken as the mean minimum metabolic rate within the thermoneutral zone (Schmidt-Nielsen 1997).

Birds were allowed to acclimate to the experimental temperature in the metabolic chamber for a minimum of 1 hr prior to metabolic measurements. We calculated the steady-state $\dot{V}O_2$ following Hill (1972), using the minimum F_cO₂ concentration for a continuous 10-min period in the 1 hr following the equilibration. If the F_cO₂ had not reached a steady low level in the 1 hr after acclimation, we extended our measurement period until it did so. Respiratory exchange ratio was calculated as $\dot{V}CO_2/\dot{V}O_2$.

Resting metabolic rate. Following BMR measurements, the temperature of the circulating bath was decreased by 15°C ($n = 7$) or 5°C ($n = 2$), and maintained at this temperature for a minimum of 1 hr, during which time another metabolic measurement was taken. The same procedure used for BMR calculation was then used to calculate resting metabolic rate (RMR) at each T_a . Subsequently, the temperature of the circulating bath was decreased by a further 15°C or 5°C and $\dot{V}O_2$ was measured again. In this manner, we determined the metabolic rate (*MR*) of Whip-poor-wills at 5°C intervals between 0°C and 20°C, and at 2.5°C intervals between 20°C and 40°C. Upon removal from the metabolic chamber, the core body temperature of five birds was recorded by inserting a 30-gauge copper-constantan thermocouple thermometer (Cole Parmer Model 8500–40) 1 cm into the cloaca. Wet thermal conductance was then calculated, following Schmidt-Nielsen (1997), as $MR (T_b - T_a)^{-1}$.

Upon conclusion of the experiment, we outfitted the birds with U.S. Fish and Wildlife Service numbered

aluminum leg bands and released them at the site of capture.

EVALUATION OF BASAL METABOLIC RATE IN CAPRIMULGIFORMES

We compared the BMR of six caprimulgiform species to that of other birds using both conventional analyses of covariance (ANCOVA) and phylogenetically independent ANCOVA (Garland et al. 1993). All BMR values were converted to kJ day^{-1} , and BMR and body mass data were log transformed. We obtained a phylogeny for the six Caprimulgiformes from Sibley and Ahlquist (1990). No information was available on relationships within the Podargidae, and we included *Podargus ocellatus* along the branch leading to *P. strigoides* with a phylogenetic distance of 5.0 between these two species. We inserted the phylogeny for the six Caprimulgiformes into Tieleman and Williams' (2000) phylogeny (82 species for which BMR data were available). After verifying homogenous slopes of BMR vs. body mass regressions (Zar 1996), phylogenetically independent ANCOVA were performed using the programs PDSINGLE on the raw data, and PDA-NOVA on 1000 sets of tip values generated by PDSIMUL (Garland et al. 1993). The significance of conventional F -statistics was tested against the critical F -values for $\alpha = 0.05$ of the phylogenetically independent null F -distributions. We generated phylogenetically independent null F -distributions using three evolutionary models: (1) gradual Brownian with bounds, with correlation set to default value calculated by PDSIMUL; (2) gradual Brownian with bounds, correlation set to zero; and (3) speciation with bounds, correlation set to zero. For bounds, we used a minimum body mass of 1 g (the body mass of the smallest extant bird species, *Calypte helenae*, is 1.6 g; Calder 1985) and a maximum body mass of 450 000 g (estimated body mass for the extinct *Aepyornis maximus*; Calder 1985). To obtain BMR bounds, we calculated a conventional linear regression of BMR and body mass for the species in Tieleman and Williams' (2000) data set and calculated predicted BMR for *C. helenae* and *A. maximus* of 4.9 kJ day^{-1} and $14\,757 \text{ kJ day}^{-1}$, respectively. The bounds algorithm was set to "replace". No trends were set. We calculated a phylogenetically independent regression of caprimulgiform $\log \text{BMR}$ and $\log M_b$, using the methods described in Garland and Ives (2000).

ADDITIONAL STATISTICAL ANALYSES

We tested for differences in morphological variables between adults and juveniles and in wet thermal conductance below and within the thermoneutral zone using Student's t -test (Zar 1996). The upper and lower critical limits of the thermoneutral zone were determined following the method of Nickerson et al. (1989). Means are presented \pm SD and significance was accepted at $\alpha = 0.05$. All statistical analyses were conducted using Systat (SPSS 1998).

RESULTS

The mean body mass of adult birds ($n = 7$) was significantly greater than that of juveniles ($n = 2$) immediately after capture (body mass = $52.6 \pm 1.5 \text{ g}$ and $46.0 \pm 0.6 \text{ g}$, respectively; $t_7 = 7.7$, $P < 0.001$).

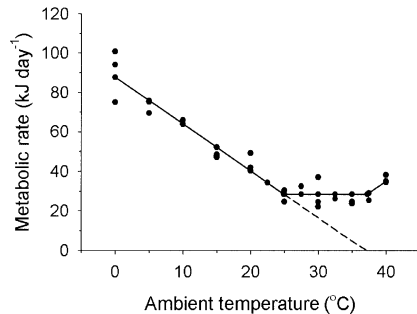


FIGURE 1. Rate of metabolism as a function of ambient temperature in eight Whip-poor-wills. The slope of the line below thermoneutrality extrapolates to a metabolic rate of zero (indicated by the dashed line) at 37.0°C .

The mean rate of body mass loss during the first 24 hr postcapture was $0.27 \pm 0.10 \text{ g hr}^{-1}$. The mean body mass of adults prior to next-day trials was $47.3 \pm 2.0 \text{ g}$, and the mean body mass of juveniles prior to next-day trials was $40.5 \pm 0.3 \text{ g}$.

METABOLIC RESPONSES TO AMBIENT TEMPERATURE

Data for oxygen consumption relative to ambient temperature, used to calculate the thermoneutral zone and BMR, came from eight of the nine birds (Fig. 1). The excluded bird was molting, and thus had a metabolic rate higher than typical below the thermoneutral zone. The lower and upper critical limits of the thermoneutral zone were 24.9°C and 37.2°C , respectively, and BMR was 28.3 kJ day^{-1} . Above and below the thermoneutral zone, metabolic rate increased with temperature. The regression line for values below the lower critical limit extrapolates to zero metabolism at 37.0°C , which is in the range of body temperatures for eutherian Whip-poor-wills (34.4°C to 37.2°C following metabolic trials). Wet thermal conductance at thermoneutrality was $3.06 \pm 0.25 \text{ kJ day}^{-1} \text{ }^\circ\text{C}^{-1}$. This value was not significantly different from the wet thermal conductance below the lower critical limit of the thermoneutral zone ($2.58 \pm 0.41 \text{ kJ day}^{-1} \text{ }^\circ\text{C}^{-1}$; $t_5 = 1.5$, $P > 0.05$). However, above the upper critical limit, wet thermal conductance increased 2.4-fold (conductance above the upper critical limit = $6.82 \text{ kJ day}^{-1} \text{ }^\circ\text{C}^{-1}$). The mean respiratory exchange ratios at each temperature ranged from 0.68 to 0.73, indicating that all birds were postabsorptive and relying on fat as the metabolic substrate (Kleiber 1961).

BASAL METABOLIC RATE OF CAPRIMULGIFORMES

The BMRs of the six caprimulgiform species (Table 1, Fig. 2) were significantly lower than those of other birds when analyzed using both conventional ANCOVA ($F_{1,87} = 35.2$, $P < 0.05$) and, phylogenetically independent ANCOVA using three evolutionary models (gradual Brownian, no correlation: $F_{1,87} = 35.2$, $P = 0.003$; gradual Brownian, correlation: $F_{1,87} = 35.2$, $P = 0.008$; speciation Brownian, no correlation: $F_{1,87} = 35.2$, $P = 0.007$). The phylogenetically independent

TABLE 1. Metabolic parameters for seven species of Caprimulgiformes from the Nearctic and Australasian zoogeographical zones. Basal metabolic rate (BMR) predictions were calculated using Reynolds and Lee's (1996) phylogenetically-corrected least squares regression. Data for *Podargus papuensis* were not included in the phylogenetically independent ANCOVA because both individuals were immature.

Species	Mass (g)	Body temperature (°C)	Whole-animal BMR (kJ day ⁻¹)	Percent of allometric prediction	Mass-specific BMR (kJ g ⁻¹ day ⁻¹)
Tawny Frogmouth <i>Podargus strigoides</i> ^a	341	37.9	104.2	61	0.3
Marbled Frogmouth <i>Podargus ocellatus</i> ^b	145	37.0–38.2	48.9	49	0.3
Papuan Frogmouth <i>Podargus papuensis</i> ^c	315	38.8	92.5	57	0.3
Spotted Nightjar <i>Eurostopodus argus</i> ^d	88	36.2–39.5	35	48	0.4
Common Poorwill <i>Phalaenoptilus nuttallii</i> ^e	35	39.1 ^f	13.3	33	0.4
Common Nighthawk <i>Chordeiles minor</i> ^g	76	38.0	37.9	59	0.5
Whip-poor-will <i>Caprimulgus vociferous</i> ^h	46	34.4–37.2	28.3	59	0.6

^a Bech and Nicol 1999.

^b Lasiewski et al. 1970.

^c McNab and Bonaccorso 1995.

^d Dawson and Fisher 1969.

^e Withers 1977.

^g Lasiewski and Dawson 1964.

^h Present study.

regression (Garland and Ives 2000) of caprimulgiform $\log BMR$ and $\log M_b$ was $\log BMR = -0.162 + 0.881(\log M_b)$.

DISCUSSION

The BMR of Whip-poor-wills was 59% of that predicted by allometry for birds (Reynolds and Lee 1996). This value is qualitatively consistent with BMR values reported for other Caprimulgiformes (Table 1). The low BMR of Caprimulgiformes is not explained by

their phylogenetic affiliations, but evolved in this order following their divergence from other taxa. Our analyses, however, do not indicate whether a low BMR evolved once, early in the evolutionary history of the Caprimulgiformes, or evolved repeatedly within the lineage more recently. Irrespective of when a low BMR evolved, the fact that all the Caprimulgiformes investigated so far exhibit reduced maintenance requirements suggests that this physiological trait is adaptive for this group of birds.

Reduced BMR occurs in Caprimulgiformes from diverse habitats and regions, suggesting that the metabolic traits of these birds are related to a factor other than zoogeographical zone. Variation in endotherm BMR also appears to be related to diet. Mammals and birds that feed on aerial insects, arboreal leaves, and food suspended in the soil tend to have low BMR (McNab 1980, 1988). The impact of feeding on soil invertebrates (e.g., kiwis [Apterygidae]) and arboreal leaves (e.g., sloths [Bradypodidae]) is potentially explained by the low quality of the food source, along with the sedentary nature of the animals that exploit this food source. The BMR response to foraging on aerial insects, on the other hand, may result from the substantial weather-induced variation in abundance of this prey item over short temporal scales (Hickey and Fenton 1996). Thus, environmental stochasticity can prominently influence the energy budget of aerial insectivores. Not surprisingly, Chiroptera and Caprimulgiformes, which exploit the nocturnal/crepuscular aerial insectivore niche, consistently show low basal metabolic rates (McNab 1980, 1988). In addition, both

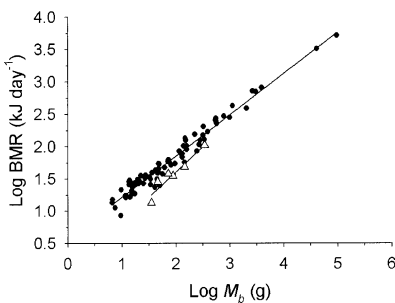


FIGURE 2. Log body mass (M_b) and log basal metabolic rate (BMR) for 82 bird species used by Tieleman and Williams (2000; filled circles) and six Caprimulgiformes (unfilled triangles). Conventional least-squares linear regressions are $\log BMR = 0.046 + 0.780\log M_b$ for Caprimulgiformes and $\log BMR = 0.575 + 0.638\log M_b$ for other birds.

Chiroptera and Caprimulgiformes use daily torpor to conserve energy (Wang 1989).

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ESTIMATING SURVIVAL PROBABILITIES OF UNMARKED DEPENDENT YOUNG
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Abstract. We present a capture–recapture modeling approach to the estimation of survival probability of dependent chicks when only the attending adult bird is marked. The model requires that the bird's nest is found prior to hatching and that the number of eggs that hatch are counted. Subsequent data are sightings of the marked adult and a count of chicks with the adult. The model allows for imperfect detection of chicks, but the number of chicks can never exceed the number of eggs in the nest (i.e., adults cannot adopt chicks). We use data from radio-tagged adult Mountain Plovers (*Charadrius montanus*) and their unmarked chicks as an example. We present the model in terms of precocial bird species, but the method extends to many other taxa.

Key words: capture–recapture, Cormack–Jolly–Seber model, Mountain Plover, open population models, survival estimation.

Estimación de las Probabilidades de Supervivencia de Crías Dependientes no Marcadas cuando la Detección es Imperfecta

Resumen. Presentamos un enfoque de captura y recaptura para modelar la estimación de la probabilidad de supervivencia de polluelos dependientes cuando sólo el adulto que atiende a los polluelos esta marcado. El modelo requiere que el nido sea encontrado antes de la eclosión y que se cuenten el número de huevos que eclosionan. Los datos subsiguientes necesarios son los avistamientos del adulto marcado y el conteo de los polluelos que se encuentran con el adulto. El modelo permite la detección imperfecta de los polluelos, pero el número de polluelos nunca puede exceder el número de huevos en el nido (i.e., los adultos no pueden adoptar polluelos). Como ejemplo, utilizamos datos de adultos marcados con radio transmisores de

Charadrius montanus y de sus polluelos no marcados. Presentamos el modelo en términos de especies de aves precociales, pero el método también se extiende a muchas otras especies.

Survival probability of juvenile animals can be important for understanding the population dynamics of a species. Past methods of estimating survival of dependent young have assumed an accurate count of the number of chicks remaining in the brood (Flint et al. 1995, Manly and Schmutz 2001). For some species this may be a reasonable assumption, but for other species the number of chicks cannot be reliably counted after the chicks leave the nest. Imperfect counts may occur for a variety of reasons, but most often because the chicks hide when humans are present. Therefore, the counts of chicks detected are less than or equal to the total number of chicks remaining alive in the brood.

If chicks are uniquely marked, a Cormack–Jolly–Seber (CJS) model could be used to estimate survival of the chicks (Cormack 1964, Jolly 1965, Seber 1965), but young birds often cannot be uniquely marked. For example, radio transmitters may be too large, the leg structure of the young birds may not be developed enough for banding, marking may decrease survival of the chicks, or there may not be enough unique color band combinations to band both adults and young. Therefore, an estimation method which does not require uniquely marked individuals and allows for imperfect detection would be useful.

We present a likelihood-based extension to the CJS model which estimates survival of dependent young when only the adult is marked and some young may not have been counted. In theory the method may be used for broods of any number of chicks. In practice it is most useful for species that have fewer than five chicks per brood and do not show brood mixing. This method relaxes the assumption made by Flint et al. (1995) and Manly and Schmutz (2001) that all of the young must be counted at every sampling occasion, but it does not allow brood mixing as their methods do. In addition, the Manly and Schmutz (2001) estimator models heterogeneity in survival probabilities

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directly, while our estimator allows a form of individual heterogeneity in survival to be modeled. Our method is designed for species with uniparental care. Cases of biparental care would require both adults to be uniquely marked and sampled nearly simultaneously.

We present data from radio-tagged adult Mountain Plovers (*Charadrius montanus*) and their broods from eastern Colorado as an example of the method and types of models which may be constructed. Mountain Plovers are endemic to the Great Plains region of North America. Females lay up to 3 eggs each in two or more nests in disturbed native prairie or agricultural landscapes of the western Great Plains, and in shrub semideserts to the immediate west. Mountain Plover chicks are precocial, leaving the nest within 3 hr of the last egg hatching (Graul 1973, Knopf 1996) and move with the adult up to 2 km from the nest in the first 2 days (Knopf 1996). Chicks have been reported to fledge at 33–34 days (Graul 1975) and 36 days (Miller and Knopf 1993).

METHODS

The model assumes there are k sampling occasions. Broods can be added to or removed from the data set at any occasion. Adults attending young must be uniquely marked, and that mark must be read without error each time the adult is resighted. The young do not need any type of mark. The notation used here is similar to that used by Schwarz and Stobo (1999) because our model shares some of the characteristics of their tag-misread model. Model notation is presented in Table 1.

STATISTICAL MODEL AND ASSUMPTIONS

Several assumptions underlie the model. First, broods are assumed to be independent, so that no brood influences the fate of any other brood. Here we make an assumption about broods, but inference remains at the level of individual chicks. Second, individual chicks within a brood are assumed to be exchangeable. This means that all chicks within a brood have the same survival probability at a given time. Third, survival of chicks is assumed to be equal across broods at a given age and time interval. We address some ways of relaxing these assumptions in the discussion.

To extend the CJS model to broods rather than individual birds it is necessary to switch to matrix notation to account for all of the possible outcomes of the survival and detection of chicks within a brood. For example, there are six possible ways to observe two chicks from a brood of three. One chick may have died and the remaining two chicks survived and were detected; this could happen with three different combinations of chicks. Otherwise, three chicks could have survived, but only two chicks were detected; this can also happen three ways. For example, if the encounter history (3, 2, 3, 1) is observed, the observations before the second count of three chicks provide information about detection probability because all chicks are known to be alive. Observations beyond the second three chicks provide information about survival. While this model appears similar to a multistate model, it is different in the way the detection probability is handled. Matrices used here are given in the Appendix.

Upon completion of the study each brood will have an encounter history; for example $\mathbf{h} = (3, 2, 3, 1)$ for a study with $k = 4$ sampling occasions and $m = 3$ initial chicks. The overall probability of this encounter history is

$$P[\mathbf{h}] = [1 \ 0 \ 0 \ 0] \phi_1 \mathbf{D}(\mathbf{p}_2, 2) \phi_2 \mathbf{D}(\mathbf{p}_3, 3) \\ \times \phi_3 \mathbf{D}(\mathbf{p}_4, 1) \begin{bmatrix} 1 \\ 1 \\ 1 \\ 1 \end{bmatrix}$$

The row vector [1 0 0 0] is needed to denote that the brood began with three chicks. If only two of three eggs hatched the vector would be [0 1 0 0]. For computing purposes, it is most efficient to set m to the maximum number of eggs observed in any nest and use row vector to assign the number of eggs hatching from each individual nest. The final column vector [1 1 1 1]^T is required to sum over all possible outcomes of the survival and resighting processes because it is unknown how many chicks survived to the k^{th} sampling occasion.

The likelihood function is proportional to the multinomial probability function

$$L(\phi, p | n, \mathbf{h}) \propto \prod_{i=1}^n P[\mathbf{h}_i].$$

The likelihood can be optimized numerically to obtain parameter estimates. We used the quasi-Newton optimization routine in SAS PROC IML (SAS Institute 2002). The variance-covariance matrix may be obtained from the numerically estimated information matrix. The variance of each parameter could also be estimated by bootstrapping on broods (Efron and Tibshirani 1993). SAS code is available from the first author.

The ϕ and p parameters can be modeled as functions of covariates through a link function as is common in general linear models (McCullagh and Nelder 1989) and in program MARK (White and Burnham 1999). It is important to note that covariates of individual chicks cannot be used with this model because individual chicks are not known uniquely. Brood-specific covariates, environmental covariates, and any form of grouping may be used to build biologically relevant models.

MOUNTAIN PLOVER EXAMPLE

Our study was conducted in Weld County, Colorado (40°37'N, 103°58'W) during the spring and summer of 2002. Mountain Plover nests were found by locating adults and watching them until they returned to their nest. The number of eggs that hatched per nest was counted. The adult plover attending each nest was trapped and fit with a back-mounted radio just before the eggs hatched (as determined by egg flotation). Adults were located by radio-telemetry daily after the eggs hatched. The number of chicks seen with each adult was recorded. If the adult could not be located (due to adverse weather conditions for example), a “.” was assigned to the encounter history for that occa-

TABLE 1. Definitions of parameters and statistics used to estimate survival of unmarked dependent chicks.

Parameter	Definition
ϕ_i	The probability of survival of an individual chick from time i to time $i + 1$ given the chick is alive at time i and remains on the study area.
p_i	The probability that a chick will be resighted given it is alive and the adult was resighted at time i .
Statistic	
m	The maximum number of chicks in a brood.
$h = \{h_1, h_2, \dots, h_k\}$	Number of chicks seen on each sampling occasion for a given brood. Each h_i value takes on one of the following codes: 0, 1, 2, ..., m , "...". A "." represents a brood that was not sampled on a given occasion. This is distinctly different from a zero, which indicates a brood that was sampled (i.e., the adult was seen), but no chicks were detected.
n	The number of broods sampled. This is also equal to the number of adults marked for a species with uniparental care.
$D(p, h_i)$	An operator that returns the appropriate capture probability matrix given the value of the encounter history at time i . See Appendix for matrix definitions.

sion. Nineteen adults and their broods were monitored for up to 40 days after hatching. An adult whose radio failed during the course of the study was removed from the analysis after the time of radio failure. Broods that fledged were also removed from analysis at the time of fledging.

We constructed models to examine several hypotheses about survival. Models included ϕ constant across time ($\phi(\cdot)p(\cdot)$), ϕ at the first period (day) after hatching different from subsequent $\phi(\phi(H1)p(\cdot))$, ϕ at the first two periods after hatching equal but different from subsequent $\phi(\phi(H2)p(\cdot))$, ϕ at the first three periods and after hatching equal but different from subsequent $\phi(\phi(H3)p(\cdot))$. The constant ϕ model represents a situation where survival is close enough to constant that we can estimate it with a single parameter given the data available. The next three models represent either survival changing with the age of the chicks or heterogeneity in survival among chicks. These two hypotheses cannot be separated with these data and likely occur simultaneously. Detection probability was held constant in all models. Our model set is intentionally small and simple because only 19 broods were sampled. Therefore, not much information about detection probability is available to inform model selection and the chance for spurious results is high. Many other biologically reasonable models could be examined, such as trends in survival and variation in detection probability, but large model sets are dangerous with small sample sizes (Burnham and Anderson 2002). Model selection was based on information-theoretic methods and scored using Akaike's Information Criterion adjusted for small sample size (AIC_c). Parameter estimates and variances were model averaged (Burnham and Anderson 2002).

Goodness-of-fit was considered using a χ^2 test. Due to the sparsity of the data relative to the number of

possible capture histories, data were pooled over five consecutive encounters, such that the highest number of chicks detected during that 5-occasion period was used as the number of chicks detected. A general time-varying model was fit to the pooled data. Expected cell counts were generated and a standard χ^2 test generated from summed (observed - expected)²/expected values.

RESULTS

The goodness-of-fit statistics suggested the model fit the data well, except for a single encounter of a chick within one brood. Excluding the outlying value, the χ^2_{20} value was 20.5, ($P = 0.57$). The sampling protocol met the model assumptions, further supporting an adequate fit of the model to the data.

Model $\phi(H1)p(\cdot)$ was selected as the best model by AIC_c (Table 2). Models $\phi(H2)p(\cdot)$ and $\phi(H1)p(\cdot)$ both had considerable support ($\Delta AIC_c < 2$). Model $\phi(\cdot)p(\cdot)$ had essentially no support from the data. The model-averaged estimate of survival probability for the first day after hatching was 0.88 ± 0.05 . The model-averaged survival estimates increase each day after hatching up to the fourth day at which survival was modeled as constant and equaled 0.98 ± 0.01 (Table 3).

DISCUSSION

Allowing for imperfect detection of chicks is important for species whose chicks are difficult to detect. Previous methods assumed that all chicks in a brood were counted each time the adult was resighted. This is very difficult for some species, such as the Mountain Plover, where the chicks hide when alerted by the adult (Sordahl 1991).

The model presented here does not allow for brood mixing. Therefore, the adult bird is assumed to be caring only for young from the nest it was tending. This is a reasonable assumption for many species, but is

TABLE 2. Summary of model selection results for Mountain Plovers in Weld County, Colorado in 2002. Maximized log likelihoods, number of parameters (K), sample size (n), ΔAIC_c and Akaike weights for models listed by order of AIC_c from best to worst approximating model. ΔAIC_c is the difference between model i and the best approximating model.

Model	Log-likelihood	K	n	ΔAIC_c^a	AIC_c weight
$\phi(H1)p(\cdot)$	-447.42	3	19	0.00	0.49
$\phi(H3)p(\cdot)$	-448.03	3	19	1.22	0.27
$\phi(H2)p(\cdot)$	-448.16	3	19	1.48	0.23
$\phi(\cdot)p(\cdot)$	-452.34	2	19	6.99	0.01

^a The lowest AIC_c value in the analysis was 902.44.

less so for other species, such as waterfowl. Flint et al. (1995) and Manly and Schmutz (2001) present methods for dealing with brood mixing, but assume that all chicks are detected.

Our model allows for adults to be marked in any way that allows for individual identification. The example Mountain Plover data used radio-tagged adults, which allowed adults to be located easily and therefore increased capture probability. This resulted in precise estimates of survival of the young. In situations where adults are only banded, our model remains applicable but precision will likely be worse if the adults are difficult to resight.

In some species there may be dependence in fate across broods. In Mountain Plovers, males and females independently brood clutches and raise young from separate nests. Some clutches may therefore be highly related. One would expect the survival of chicks in a clutch to be more similar to closely related clutches than to distantly related clutches. Using a bootstrapped variance (Efron and Tibshirani 1993) can help account for the lack of independence within broods.

Survival probability may vary among chicks within a brood. If this is true, then one would expect the chicks with the lowest survival probability to die first and the chicks with the highest survival probability to die last. The result appears much like increasing survival probability with age of chicks. Therefore, an age or heterogeneity model may be constructed in the same manner as was done with models H1–H4 in our example. Unfortunately, when chicks are not individually marked, there is no information to separate these two hypotheses. These age/heterogeneity models fit Mountain Plover survival well and would likely be useful for other species. Mountain Plovers show increased survival with time since hatch up to at least 4 days of

age suggesting either an age differences or individual heterogeneity in survival.

The pooling for the goodness-of-fit test was admittedly *ad hoc*, but it appeared to provide useful information about model fit. Much of capture-recapture statistics suffers from problems with goodness-of-fit testing and our model is no exception. One could generalize Test 2 and Test 3 from Burnham et al. (1987) to examine data for this model, but it would result in very small expected values in most cells and therefore the test would be unreliable. Our goal in this paper was to present a new model structure applicable to avian studies, not to expand goodness-of-fit theory. Therefore, we feel the fit statistic used here was adequate.

The model can estimate the survival of young in broods of any number, but in practice smaller broods (<5 young per brood) will produce better estimates. As the broods get larger, the number of possible outcomes with nearly the same probability becomes large. This results in the likelihood surface flattening and estimation being unreliable without very large sample sizes. With simulated broods similar to that of the Mountain Plover, the estimator performs well.

A standard CJS model estimates apparent survival, the probability that an individual remains alive and available for recapture. We suggest that the estimator presented here gives true survival in many situations, such as with the Mountain Plover, because chicks have little or no chance of surviving if they leave the adult. As long as the chick is with the adult, it remains available for recapture because the adult may be found with telemetry.

We presented the model in the language of avian biology, and Mountain Plover chicks were the motivation for the development of the model, but the model applies to a wide array of taxa for which young stay

TABLE 3. Model-specific and model-averaged estimates of survival \pm SE for individual Mountain Plovers for days 1, 2, 3 and 4+ after hatching.

Model	Day 1	Day 2	Day 3	Day 4+
$\phi(\cdot)p(\cdot)$	0.97 \pm 0.01	0.97 \pm 0.01	0.97 \pm 0.01	0.97 \pm 0.01
$\phi(H1)p(\cdot)$	0.86 \pm 0.05	0.98 \pm 0.01	0.98 \pm 0.01	0.98 \pm 0.01
$\phi(H2)p(\cdot)$	0.90 \pm 0.03	0.90 \pm 0.03	0.98 \pm 0.01	0.98 \pm 0.01
$\phi(H3)p(\cdot)$	0.91 \pm 0.03	0.91 \pm 0.03	0.91 \pm 0.03	0.98 \pm 0.02
Model-averaged estimate	0.88 \pm 0.05	0.94 \pm 0.04	0.96 \pm 0.03	0.98 \pm 0.01

near the adult and are hard to detect, including bear cubs and other species.

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APPENDIX

It is necessary to use matrix notation to describe all possible outcomes of the survival and capture processes. We follow a notation similar to that of Schwarz and Stobo (1999). See Table 1 for definitions of parameters and statistics

Φ_i an $m + 1 \times m + 1$ matrix with elements describing all possible outcomes of the survival process. Rows represent the number of chicks alive at encounter occasion i and columns represent the number of chicks alive at $i + 1$.

$$\begin{bmatrix} \Phi_i^m & \binom{m}{m-1} \Phi_i^{m-1} (1 - \Phi_i) & \binom{m}{m-2} \Phi_i^{m-2} (1 - \Phi_i)^2 & \dots & \binom{m}{0} (1 - \Phi_i)^m \\ 0 & \Phi_i^m & \binom{m-1}{m-2} \Phi_i^{m-2} (1 - \Phi_i) & \dots & \binom{m-1}{0} (1 - \Phi_i)^{m-1} \\ 0 & 0 & \Phi_i^{m-2} & \dots & \binom{m-2}{0} (1 - \Phi_i)^{m-2} \\ \vdots & \vdots & & & \vdots \\ 0 & 0 & \dots & 0 & 1 \end{bmatrix}$$

\mathbf{p}_i an $m + 1 \times m + 1$ matrix with elements describing all possible outcomes of the detection process:

$$\begin{bmatrix} p_i^m & 0 & 0 & \dots & 0 \\ 0 & 0 & & & \\ 0 & & \ddots & & \vdots \\ \vdots & & & & \\ 0 & & & & 0 \end{bmatrix} \text{ if } h_i = m, \quad \begin{bmatrix} \binom{m}{m-1} p_i^{m-1} (1 - p_i) & 0 & 0 & \dots & 0 \\ 0 & p_i^{m-1} & 0 & \dots & 0 \\ 0 & 0 & 0 & \dots & 0 \\ \vdots & & & \ddots & \vdots \\ 0 & & & \dots & 0 \end{bmatrix} = \text{if } h_i = m - 1,$$

... \mathbf{p}_i matrices follow this pattern for all other values of h_i .

$$\begin{bmatrix} 1 & 0 & \dots & 0 & 0 \\ 0 & 1 & & 0 & 0 \\ \vdots & & \ddots & & \vdots \\ 0 & 0 & & 1 & 0 \\ 0 & 0 & \dots & 0 & 0 \end{bmatrix} \text{ if } h_i \text{ is observed } (\cdot).$$