

HOME RANGE AND RESIDENCY STATUS OF NORTHERN GOSHAWKS BREEDING IN MINNESOTA

CLINT W. BOAL^{1,3}, DAVID E. ANDERSEN¹ AND PATRICIA L. KENNEDY²

¹USGS-BRD Minnesota Cooperative Fish and Wildlife Research Unit, University of Minnesota,
 St. Paul, MN 55108

²Eastern Oregon Agricultural Research Center, Union Experiment Station, Oregon State University,
 P.O. Box E, Union, OR 97883

Abstract. We used radio-telemetry to estimate breeding season home-range size of 17 male and 11 female Northern Goshawks (*Accipiter gentilis*) and combined home ranges of 10 pairs of breeding goshawks in Minnesota. Home-range sizes for male and female goshawks were 2593 and 2494 ha, respectively, using the minimum convex polygon, and 3927 and 5344 ha, respectively, using the 95% fixed kernel. Home ranges of male and female members of 10 goshawk pairs were smaller than combined home-range size of those pairs (mean difference = 3527 ha; 95% CI = 891 to 6164 ha). Throughout the nonbreeding season, the maximum distance from the nest recorded for all but one goshawk was 12.4 km. Goshawks breeding in Minnesota have home ranges similar to or larger than those reported in most other areas. Home-range overlap between members of breeding pairs was typically $\leq 50\%$, and both members of breeding pairs were associated with breeding home ranges year round. Goshawk management plans based on estimated home-range size of individual hawks may substantially underestimate the area actually used by a nesting pair.

Key words: *Accipiter gentilis*, home range, Minnesota, Northern Goshawk, winter residency.

Rango de Hogar y Estatus de Residencia de Individuos de *Accipiter gentilis* que se Reproducen en Minnesota

Resumen. Utilizamos radioteleetría durante la época reproductiva para estimar el tamaño del rango de hogar de 17 machos y 11 hembras de *Accipiter gentilis* y los rangos de hogar combinados de 10 parejas reproductivas en Minnesota. Los rangos de hogar de machos y hembras fueron de 2593 y 2494 ha, respectivamente, usando el mínimo polígono convexo, y de 3927 y 5344 ha, respectivamente, usando el “kernel” fijo del 95%. Los rangos de hogar de los miembros machos y hembras de las 10 parejas fueron más pequeños que el tamaño del rango de hogar combinado

de dichas parejas (diferencia promedio = 3527 ha; 95% I.C. = 891 a 6164 ha). A través de la época no reproductiva, la distancia máxima desde el nido registrada para todos menos un individuo fue de 12.4 km. Los individuos que se reproducen en Minnesota tienen rangos de hogar similares o mayores que los reportados en la mayoría de otras áreas. La superposición entre los rangos de hogar de miembros de parejas reproductivas fue típicamente $\leq 50\%$, y ambos miembros de las parejas estuvieron asociados con rangos de hogar reproductivos a través del año. Los planes de manejo para *A. gentilis* basados en estimaciones del tamaño del rango de hogar de halcones individuales podrían subestimar sustancialmente el área realmente utilizada por una pareja nidificante.

Potential conflict between Northern Goshawk (*Accipiter gentilis*) habitat requirements and timber harvest practices has led to concern for the status of the species (Kennedy 1997). This has resulted in several studies of goshawk ecology in the last decade, most of which have been conducted in the western United States and western Canada. However, the goshawk is widely distributed in North America (Squires and Reynolds 1997) and much of the existing data may not be relevant to the range of environmental conditions and forest management practices found across the species' distribution. For example, goshawks in western North America typically occupy areas of high elevation (e.g., 1200–3900 m) and substantial topographic relief, with generally warm, dry summers and cool, wet winters (Kennedy et al. 1994, DeStefano and McClosky 1997, Keane 1999). In contrast, the western Great Lakes region is of lower elevation (e.g., 330–560 m), has little topographic relief in most areas, and typically experiences cool, wet summers and long, cold, dry winters (Tester 1995). Forest harvest practices in the western U.S. typically focus on large tracts of land administered by a single public agency or landowner, whereas harvest practices in the midwestern and eastern U.S. focus on smaller tracts of land administered by a mixture of public and private ownerships (Mannan et al. 1994). This has led to increased forest heterogeneity in Midwestern and eastern deciduous forests and, in some cases, an increase in extent of early successional forest types, relative to presettlement landscapes

Manuscript received 27 June 2002; accepted 12 June 2003.

³ Present address: USGS-BRD Texas Cooperative Fish and Wildlife Research Unit, Texas Tech University, Lubbock, TX 79409-2120. E-mail: clint.boal@ttu.edu

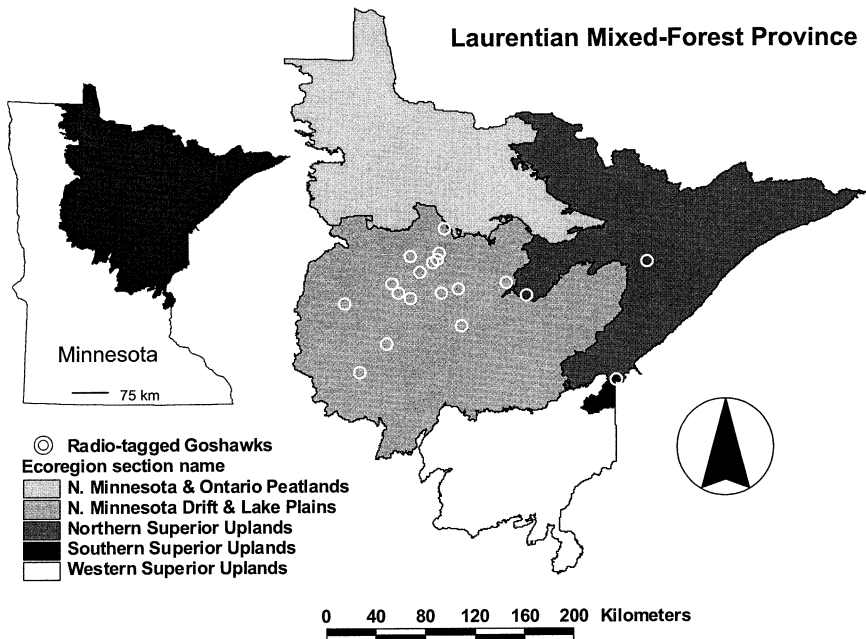


FIGURE 1. Distribution of radio-tracked Northern Goshawks among ecoregion subsections of the Laurentian Mixed-Forest Province, Minnesota, 1998–2000.

(Whitcomb et al. 1981, Minnesota Forest Resources Council 2000, Reich et al. 2001).

Little information exists on home-range size and migration status of goshawks across their range (Squires and Reynolds 1997), but data from the western Great Lakes region are particularly sparse; only a few birds have been sampled, most of which were females (Lapinski 2000). Male goshawks do the majority of foraging during the breeding season, especially when nestlings are young (Boal and Mannan 1996). Thus, female goshawk home-range size estimates alone may be inadequate for developing regional conservation strategies for the species.

Migratory status and seasonal presence or absence should be identified and taken into account when managing for a species. Some goshawk populations consist of seasonal migrants (Doyle and Smith 1994, Squires and Ruggiero 1995), but other populations appear to be resident (Iverson et al. 1996, Keane 1999), or partially migratory (not all birds migrate or migration does not occur in all years; Kenward et al. 1981, Widen 1985). Regardless, winter residency is not well established for most goshawk populations, and goshawk status as residents or seasonal migrants has not been assessed in the western Great Lakes region.

To address these and other information gaps, in 1998 we studied the ecology of Northern Goshawks in Minnesota from 1998–2000. Here we compare home-range sizes among male, female, and breeding pairs of goshawks, and provide evidence suggesting goshawks in Minnesota are year-round residents.

METHODS

Although a majority of the breeding goshawks were on or near the Chippewa National Forest (47°23'N, 94°35'W), the study area encompassed most of northern Minnesota within the Laurentian Mixed-Forest Province (Fig. 1). Study area elevation is 200–400 m. Mean summer and winter temperatures are 18°C and –11°C, respectively, with maximum and minimum temperature records of 40°C and –46°C, respectively. The study area is dominated by pine, mixed-hardwood, boreal, and second-growth forests with wetland community types interspersed among forest stands (Tester 1995).

We searched areas known to have been occupied by nesting goshawks within the last 10 years, areas where large stick nests had been located, and areas where defensive goshawks had been reported. We included goshawks from nests across northern Minnesota to represent the range of landscape types with known nests. Thus, goshawks radio-tracked in this study were selected from among all known nesting goshawks in Minnesota during the 1998–2000 breeding seasons. However, because we did not systematically survey the entire study area for breeding goshawks, known breeding pairs in a single year were likely a relatively small proportion of all goshawks breeding in the study area. Also, as our sample was not randomly selected, our inference is limited to our sample.

We captured breeding goshawks during the nestling stage with dho-gaza traps (Bloom 1987), banded each hawk with a U.S. Fish and Wildlife Service leg band, and outfitted them with a Biotrack, Inc. (Dorset, UK), TW-3 radio-transmitter attached using a backpack har-

ness (Buehler et al. 1995). We began tracking male goshawks within 2 days following radio attachment, and female goshawks once they began moving about in their breeding areas.

In 1998, we attempted to simultaneously triangulate goshawk locations among 3 ground receivers. However, difficulties in approaching goshawks and determining observer locations resulted in large error polygons for some relocation point estimates. To increase location accuracy and efficiency, we began tracking goshawks aerially (Marzluff et al. 1994) late in the 1998 season and for the remainder of the study. We used the homing technique for aerial tracking (Samuel and Fuller 1994) from a fixed-wing aircraft with two wing-mounted Telonics, Inc. (Mesa, Arizona), RA-2A two-element antennas and an Advanced Telemetry Systems, Inc. (Isanti, Minnesota), R4000 receiver. We obtained daily relocations as frequently as weather conditions and aircraft availability allowed. Randomizing the order in which we relocated individual goshawks was not feasible due to internest distances (mean = 28.5 ± 29.6 km). Instead, we flew clockwise and counterclockwise circuits of the radio-tagged goshawks, relocating each goshawk in sequence, but flying at different times of the day throughout the study.

We calculated area observation curves for each goshawk with program BIOTAS 1.0.1a (Ecological Software Solutions 2002). We assumed if the average increase in home-range size did not exceed 5% for the last five locations, that individual's home range had stabilized. If home range increased by more than an average of 5% over the last five locations, data were examined to see if the increase followed a period of stability. If so, the increase may have been due to changes in movement associated with a shift from a nestling or fledgling stage to a postfledging stage (Samuel and Fuller 1994). Thus, we included only those points up to suspected increases in home-range size associated with postfledging activities.

We used program TRIANG (White and Garrott 1990) to derive location coordinates for those relocations obtained by ground-based triangulation. Relocations obtained by aerial telemetry were plotted on aerial photographs carried in the aircraft. Following each flight, we used ArcView 3.1 (Environmental Systems Research Institute 1999) to plot the relocation points onto Digital Orthogonal Quarter Quadrats (Minnesota Department of Natural Resources, St. Paul, Minnesota) to calculate UTM coordinates for each point. Trade name products are mentioned to provide complete descriptions of methods. The authors' institutions neither endorse these products nor intend to discriminate against products not mentioned.

We used the Movement 1.1 ArcView Spatial Analyst Extension to estimate home-range sizes with the 100% minimum convex polygon method (Samuel and Fuller 1994) and the 50% and 95% fixed kernel methods (Seaman and Powell 1996). There are biological and statistical disadvantages of the minimum convex polygon method (Samuel and Fuller 1994), but it is one of the most frequently reported estimates of home range. Therefore, we provide minimum convex polygon estimates for comparison with other studies and with the fixed kernel estimator. The fixed kernel estimator of uti-

lization distributions is a more robust, nonparametric estimator for home range but is sensitive to sample size (Seaman and Powell 1996). Because of small relocation samples for some of the female goshawks and the potential influence of small samples on fixed kernel estimations, we used only the minimum convex polygon estimates of home range for all comparisons.

Only nesting goshawks that reached the nestling stage were included in this analysis. To insure independence of data, we only used data from one breeding season for any individual goshawk. We used correlation analysis to examine possible associations between number of point relocations and home-range-size estimates. Because confidence intervals can be more informative than tests of statistical significance (Johnson 1999), we assessed differences in breeding-season home-range size between male and female goshawks, between male and female members of breeding pairs, and between combined home-range size of pairs versus individuals among pairs, by examining 95% confidence intervals.

Residency status of goshawks in Minnesota was not known, so we used telemetry to monitor presence-absence of goshawks during winter months (December–February) of 1998–1999, 1999–2000, and 2000–2001. For each goshawk we calculated distance from the previous summer's nest to the winter location farthest from that nest. Our sample size of winter relocations was small, so we did not attempt to estimate winter home-range size. Because these data were not normally distributed and could not be normalized with transformations, we used a Wilcoxon rank-sum test to examine differences between male and female goshawks in distance from their respective nests. All values reported in the results section are means \pm SE.

RESULTS

We attached radio-transmitters to 33 adult goshawks (18 males, 15 females). The radio on one of the males failed and two females were depredated before meaningful data could be collected. Also, too few locations were obtained on three females to estimate home range meaningfully. One female goshawk that lost its mate following the 1999 breeding season paired with a male in a different breeding area in 2000. Thus, we considered location data collected for her in the second year as independent from the previous year and included it in the analyses. Over the 3-year period, we estimated breeding-season home ranges for 17 male (mean = 29 ± 1 relocations per male) and 11 female (mean = 22 ± 1 relocations per female) goshawks.

Mean minimum convex polygon home-range sizes for male and female goshawks were 2593 ± 475 ha and 2494 ± 631 ha, respectively. The mean difference between male and female goshawk home range sizes derived from the minimum convex polygon estimates was slight (98.7 ha; 95% CI = -1501 ha to 1698 ha). There also was no notable difference between male (mean = 542 ± 111 ha) and female (mean = 825 ± 275 ha) goshawks when using the 50% fixed kernel home-range estimator (95% CI = -816 ha to 250 ha). Mean home-range size at the 95% fixed kernel appeared to be smaller among male goshawks (3927 ± 638 ha) than female goshawks (5344 ± 5059 ha), but variability in home-range size at this scale was large

TABLE 1. Minimum convex polygon estimates of breeding-season home-range size (ha) for breeding Northern Goshawks in Minnesota, 1998–2000. Estimates are for male and female members of goshawk breeding pairs, the combined locations of both members of a pair, and the proportional increase in home-range size for individuals compared to the pair.

Nesting pair	Home-range size (ha)			% Increase	
	Male	Female	Pair	Male	Female
CROO	965	3864	4784	80	19
DIXO	2446	1670	3175	23	47
DRUM	1556	6616	8870	82	25
ITAS	1961	4657	9549	79	51
JACO	860	732	1552	44	53
LISA	1824	1109	2433	25	54
LOGI	2336	829	3449	32	76
PIPE	4735	174	4735	0	96
STEA	8573	3963	18 112	53	78
WAGN	4864	3240	7101	31	54
Mean \pm SE	3012 \pm 757	2685 \pm 664	6376 \pm 1554	45 \pm 9	55 \pm 7

(95% CI = -4405 to 1570 ha). Further, fixed kernel estimates of female goshawks may be misleading due to small numbers of relocations and a tendency of females to remain in or near the nest stand until late in the nestling cycle.

Mean difference in minimum convex polygon home-range size between male (3012 \pm 757 ha) and female (2685 \pm 665 ha) members of 10 goshawk pairs was small (327 ha; 95% CI = -1941 ha to 2567 ha; Table 1). However, combined home-range size of goshawk pairs (mean = 6376 \pm 1554 ha) was on average 55 \pm 5% greater than home-range sizes of individual male and female members of pairs (2849 \pm 492 ha; 95% CI = 891 ha to 6164 ha; Table 1). Thus, home-range sizes were comparable between the sexes, but home-range overlap between members of a pair was typically \leq 50%.

We relocated all but one of 28 goshawks with active radio-transmitters in the study area during winter. Mean farthest distance from the nest was 6.8 \pm 1.0 km for 13 male goshawks and 13.1 \pm 6.3 km for 13 female goshawks (including one female relocated in two winters). This average distance for female goshawks, however, was influenced considerably by one female, which we found 87 km from her nest. When she was excluded from the sample, mean farthest distance from the nest for females was 6.9 \pm 1.5 km. There was no difference between male and female goshawks in maximum distance from nesting areas in winter, even when this individual was included in the comparison ($T = 170.5$, $P = 0.8$).

DISCUSSION

Breeding-season home-range sizes reported for goshawks in North America range from approximately 500 to 4000 ha depending on sex, habitat, estimation method, and data collection method (Squires and Reynolds 1997). Although methods of home-range estimation vary among studies and, as such, comparisons may be questionable, minimum convex polygon home-range sizes of breeding goshawks in our study appear to fall within the range reported in western North America (Squires and Reynolds 1997, Keane 1999) except Alas-

ka (Iverson et al. 1996). However, the wide range of home-range sizes indicates the need for information at more localized scales. For example, average home-range sizes of breeding male goshawks in our study was 16–44% larger (depending on the estimator) than the estimated home-range size of goshawks that is used for management plans in the southwestern United States (Reynolds et al. 1992). This difference is probably due to factors such as regional differences in forest conditions, spatial distribution of forest stands, climate, topography, and prey availability.

Developing management plans based on estimated home-range sizes of individual goshawks may underestimate the area required for successful nesting. Adult female goshawks typically do not forage for prey until midway through the nestling period (Boal and Mannan 1996). However, we estimated that when the female does start foraging, on average the pair's combined home range is 55% greater than the area used by individual members of pairs. The pair may exploit a greater area to meet the increasing food demands of growing nestling, and therefore combined home-range size of pairs may be a better measure of the area required for successful brood rearing.

Another consideration for goshawk conservation planning is potential overlap of foraging areas between adjacent pairs. We have no information with which to assess this potential, as none of the radio-tagged goshawk pairs in our study overlapped in home ranges with adjacent pairs. This is likely a factor of nesting density, which appeared to be low in our study area. Also, radio-tagged goshawks may have overlapped with adjacent goshawk pairs that were unknown to us.

The relationship between home-range size and landscape features requires stand-scale information across the study area. Although some entities, such as the USDA Forest Service, possess stand age and structure data at a resolution relevant to understanding landscape-level patterns of goshawk habitat use, our study area comprises a myriad of land ownerships. The only available landscape data encompassing all ownerships are derived from remote sensing (e.g., Landsat thematic mapper). Thematic mapper data provide infor-

mation only at the resolution of tree-species composition (Wolter et al. 1995); this is inadequate for examining patterns of goshawk habitat use across our study area. Until stand age and structure data are available for the entire study area, assessment of home-range-size relationships with landscape patterns would be possible for only a few goshawks, which might unpredictably bias inferences.

With few exceptions, breeding adult goshawks in our study appeared to be year-round residents and remained close to their nest stands during three winters. Similar to our study, Keane (1999) found no sex-related differences in winter movement among 18 known breeding goshawks in northern California, with winter ranges including nest stands from the previous breeding season. In contrast, male goshawks radio-tagged in Sweden during late summer and fall tended to remain in the area through the winter, while female goshawks tended to move away (Kenward et al. 1981, Widen 1985). Interpretation of the Swedish data is difficult because the goshawks may have been migrants and had not necessarily bred locally. A small sample of radio-tagged male and female goshawks in Wyoming also moved from their breeding areas during the winter (Squires and Ruggiero 1995).

Inconsistent patterns in winter residency among goshawk populations compound the difficulty in obtaining and interpreting data on winter habitat and prey use. Although data on winter ecology of goshawks is almost nonexistent, we should not assume that breeding-season and winter habitat and prey use are the same for resident populations of goshawks. Acquisition of region-specific winter data for goshawks remains an important missing component of our understanding of goshawk ecology throughout their distribution.

We appreciate the dedication of our field assistants, L. Belmonte, W. Estes, C. Humple, R. Sandstrom, B. Smithers, and A. Wester, and especially the assistance of A. Roberson and M. Solensky. S. Day, D. McConkey, and B. Foster were our pilots. Personnel from our many cooperating agencies and organizations provided assistance and logistical support. Funding for this project was provided by the USDA Chippewa National Forest and Superior National Forest, the National Council for Air and Stream Improvement, Minnesota Department of Natural Resources, Potlatch Corporation, Leech Lake Band of Ojibway, U.S. Fish and Wildlife Service, USGS Minnesota Cooperative Fish and Wildlife Research Unit, The Raptor Center, Minnesota Falconers' Association, and grants from the National Forest Foundation and the National Fish and Wildlife Foundation. T. E. Estabrook, N. C. Parker, K. Titus, T. B. Wigley, and an anonymous referee provided useful comments on the manuscript. This project was approved by the University of Minnesota Animal Care and Use Committee, code number 9904A00003.

LITERATURE CITED

BLOOM, P. H. 1987. Capturing and handling raptors, p. 99–123. *In* B. A. Giron Pendleton, B. A. Millsap, K. W. Cline, and D. M. Bird [EDS.], Raptor management techniques manual. National Wildlife Federation, Washington, DC.

- BOAL, C. W., AND R. W. MANNAN. 1996. Prey sizes of male and female Northern Goshawks. *Southwestern Naturalist* 41:355–358.
- BUEHLER, D. A., J. D. FRASER, M. R. FULLER, L. S. MCALLISTER, AND J. K. D. SEEGAR. 1995. Captive and field-tested radio transmitter attachments for Bald Eagles. *Journal of Field Ornithology* 66: 173–180.
- DESTEFANO, S., AND J. MCCLOSKEY. 1997. Does vegetation structure limit the distribution of Northern Goshawks in the Oregon ranges? *Journal of Raptor Research* 31:34–39.
- DOYLE, F. I., AND J. M. N. SMITH. 1994. Population responses of Northern Goshawks to the 10-year cycle in numbers of snowshoe hares. *Studies in Avian Biology* 16:122–129.
- ECOLOGICAL SOFTWARE SOLUTIONS [ONLINE]. 2002. Biotas. (<http://www.ecostats.com/software/biotas/biotas.htm>) (22 April 2002).
- ENVIRONMENTAL SYSTEMS RESEARCH INSTITUTE. 1999. Getting to know ArcView GIS. 3rd ed. Environmental Systems Research Institute, Inc., Redlands, CA.
- IVERSON, G. C., G. H. HAYWARD, K. TITUS, E. DE-GAYNER, R. E. LOWELL, D. C. CROCKER-BEDFORD, P. F. SCHEMPF, AND J. LINDELL. 1996. Conservation assessment for the Northern Goshawks in southeast Alaska. USDA Forest Service General Technical Report PNW-GTR-387.
- JOHNSON, D. H. 1999. The insignificance of statistical significance testing. *Journal of Wildlife Management* 63:763–772.
- KEANE, J. J. 1999. Ecology of the Northern Goshawk in the Sierra Nevada, California. Ph.D. dissertation, University of California, Davis, CA.
- KENNEDY, P. L. 1997. The Northern Goshawk (*Accipiter gentilis atricapillus*): is there evidence of a population decline? *Journal of Raptor Research* 31:95–106.
- KENNEDY, P. L., J. M. WARD, G. A. RINKER, AND J. A. GESSAMAN. 1994. Post-fledging areas in Northern Goshawk home ranges. *Studies in Avian Biology* 16:75–82.
- KENWARD, R. E., V. MARCSTROM, AND M. KARLBOM. 1981. Goshawk winter ecology in Swedish pheasant habitats. *Journal of Wildlife Management* 45: 397–408.
- LAPINSKI, N. W. 2000. Habitat use and productivity of the Northern Goshawk in the Upper Peninsula of Michigan. M.Sc. thesis, Northern Michigan University, Marquette, MI.
- MANNAN, R. W., R. N. CONNER, B. MARCOT, AND J. M. PEEK. 1994. Managing forestlands for wildlife, p. 689–721. *In* T. A. Bookhout [ED.], Research and management techniques for wildlife and habitats. 5th ed. The Wildlife Society, Bethesda, MD.
- MARZLUFF, J. M., M. S. VEKASY, AND C. COODY. 1994. Comparative accuracy of aerial and ground telemetry locations of foraging raptors. *Condor* 96:447–454.
- MINNESOTA FOREST RESOURCES COUNCIL. 2000. Minnesota north central landscape: current conditions and trends assessment. Minnesota Forest Resources Council Document LT-0500.

- REICH, P. B., P. BAKKEN, D. CARLSON, L. E. FRELICH, S. K. FRIEDMAN, AND D. F. GRIGAL. 2001. Influence of logging, fire, and forest type on biodiversity and productivity in southern boreal forests. *Ecology* 82:2731–2748.
- REYNOLDS, R. T., R. T. GRAHAM, M. H. REISER, R. L. BASSETT, P. L. KENNEDY, D. A. BOYCE JR., G. GOODWIN, R. SMITH, AND E. L. FISHER. 1992. Management recommendations for the Northern Goshawk in the southwestern United States. USDA Forest Service General Technical Report RM-GTR-217.
- SAMUEL, M. D., AND M. R. FULLER. 1994. Wildlife radiotelemetry, p. 370–418. In T. A. Bookhout [ED.], Research and management techniques for wildlife and habitats. 5th ed. The Wildlife Society, Bethesda, MD.
- SEAMAN, D. E., AND R. A. POWELL. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* 77:2075–2085.
- SQUIRES, J. R., AND R. T. REYNOLDS. 1997. Northern Goshawk (*Accipiter gentilis*). In A. Poole and F. Gill [EDS.], The birds of North America, No. 298. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.
- SQUIRES, J. R., AND L. F. RUGGIERO. 1995. Winter movements of adult Northern Goshawks that nested in southcentral Wyoming. *Journal of Raptor Research* 29:5–9.
- TESTER, J. R. 1995. Minnesota's natural heritage: an ecological perspective. University of Minnesota Press, Minneapolis, MN.
- WHITCOMB, R. F., C. S. ROBBINS, J. F. LYNCH, B. L. WHITCOMB, M. K. KLIMKIEWICZ, AND D. BYSTRAK. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forests, p. 125–205. In R. L. Burgess and D. M. Sharp [EDS.], Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York.
- WHITE, G. C., AND R. A. GARROTT. 1990. Analysis of wildlife radio tracking data. Academic Press, London, UK.
- WIDEN, P. 1985. Breeding and movements of goshawks in boreal forests in Sweden. *Holarctic Ecology* 8: 273–279.
- WOLTER, P. T., D. J. MLADENOFF, G. E. HOST, AND T. R. CROW. 1995. Improved forest classification in the northern lake states using multi-temporal Landsat imagery. *Photogrammetric Engineering and Remote Sensing* 61:1129–1143.

The Condor 105:816–821
© The Cooper Ornithological Society 2003

EFFECTS OF PATERNITY AND MATE AVAILABILITY ON MATE SWITCHING IN HOUSE WRENS

NICOLE E. POIRIER¹, LINDA A. WHITTINGHAM² AND PETER O. DUNN

Department of Biological Sciences, University of Wisconsin-Milwaukee, Milwaukee, WI 53211

Abstract. We studied within-season mate switching in House Wrens (*Troglodytes aedon*) from 1998 to 2000. Males initiated mate switching, but mate switching was not related to the male's paternity in the first brood, his body condition, or his breeding experience. Males were more likely to switch mates when unmated females were nearby. Males that switched mates sired a similar number of young as males that stayed with the same mate, and, thus, males did not appear to benefit directly from switching mates. In contrast, half of the females that were deserted did not find a second mate during the breeding season, and, thus, incurred a reproductive cost.

Key words: House Wren, mate switching, paternity, reproductive success, *Troglodytes aedon*.

Efectos de la Paternidad y Disponibilidad de Pareja sobre el Cambio de Parejas en *Troglodytes aedon*

Resumen. Estudiamos el cambio de pareja dentro de una misma estación reproductiva en *Troglodytes aedon* entre 1998 y 2000. Los machos iniciaron el cambio de pareja, pero este cambio no estuvo relacionado con la paternidad del macho en la primera nidada, ni con su condición corporal, ni con su experiencia de cría previa. Los machos presentaron una mayor probabilidad de cambiar de pareja cuando se encontraban hembras no apareadas en las cercanías. Los machos que cambiaron de pareja engendraron un número similar de crías al de los machos que permanecieron con la misma pareja, por lo que los machos no parecieron beneficiarse directamente con el cambio de pareja. En

Manuscript received 20 September 2002; accepted 6 June 2003.

¹ Present address: Department of Biology, Tufts University, Medford, MA 02155.

² Corresponding author. E-mail: whitting@uwm.edu

contraste, la mitad de las hembras que fueron abandonadas no encontraron una segunda pareja durante el periodo reproductivo, y por lo tanto incurrieron en un costo reproductivo.

Mate switching, also referred to as mate desertion or divorce, is a common reproductive strategy in which at least one member of a mated pair severs the pair bond and mates with a new partner (Black 1996). Over 90% of bird species are described as socially monogamous (Lack 1968), and in many of these species individuals switch mates. Mate switching can occur either between breeding seasons, even though both individuals survive between years (Dhindsa and Boag 1992, Dhondt and Adriaensen 1994), or within a breeding season between first and second broods (reviewed in Burns 1983). Numerous hypotheses have been proposed to explain which ecological or social factors precipitate mate switching, and which sex benefits from mate switching and is likely to initiate it (Choudhury 1995).

Two of these hypotheses have been the focus of recent work attempting to explain why mate switching may be adaptive in birds. The "incompatibility hypothesis" predicts that divorce is precipitated by poor breeding performance and that both members of the pair benefit from switching mates (Coulson and Thomas 1983, Dhondt and Adriaensen 1994). The "better options hypothesis" predicts that individuals of one sex improve their reproductive success by obtaining a better mate (Ens et al. 1993). In addition, there are several nonadaptive hypotheses which suggest that individuals do not choose to switch mates, but that it occurs for other reasons such as territory usurpation (Ens et al. 1993), or rapid territory settlement following migration (Bensch and Hasselquist 1991).

Most studies show that nest failure or reduced nesting success (i.e., reduced clutch size or fledging success) is associated with mate switching between breeding seasons (Mills 1973, Lindén 1991, Streif and Rasa 2001) or within seasons (Pinkowski 1977, Nolan 1978, Shields 1984, Wunderle 1984), from which females usually benefit. Other studies have found that mate switching occurs between and within seasons in relation to other factors. For example, females may switch mates to breed with older males (Grant and Grant 1987), males of higher social rank (Otter and Ratcliffe 1996), or males on better territories (Baeyens 1981, Matthyens 1990). In other cases, individuals may desert their mate in response to the availability of unmated individuals in the population (Székely et al. 1999, Pilastro et al. 2001).

Recent comparative work suggests that mate switching is more common in species with higher levels of extra-pair paternity (Cézilly and Nager 1995). This correlation is expected if extra-pair mating allows females paired socially to poor quality males to produce young sired by higher quality extra-pair males and then later switch to a better mate for the next reproductive episode (Wagner 1992, Ramsay et al. 2000). Alternatively, we would also predict a positive correlation between mate switching and extra-pair paternity if males that have reduced paternity in their first brood are more likely to desert that mate and seek a new female for the second brood.

House Wrens (*Troglodytes aedon*) have been a popular species for the study of within-season mate switching in birds (Kendeigh 1941, Burns 1983, Bart 1990, Drilling and Thompson 1991), and recent work has revealed a moderate level of extra-pair paternity in this species (27% of broods; Soukup and Thompson 1997, Poirier et al., in press). Although both sexes may initiate mate switching, the benefits of doing so have remained elusive, and the role of paternity has not been examined. The goal of this study was to identify the factors associated with within-season mate switching in House Wrens and the costs and benefits for each sex following mate switching.

METHODS

House Wrens are secondary cavity nesters that readily nest in boxes (Kendeigh 1941, 1952). House Wren males build a nest cup of sticks that the female lines with grass. Clutch size is 4–8 eggs and only the female incubates (Kendeigh 1941). Both males and females feed the young. Fieldwork was conducted during the 1998–2000 breeding seasons (May–August) at the University of Wisconsin–Milwaukee Field Station (43°23'N, 88°01'W), where 180 nest boxes were placed 25 m apart along deciduous forest edges (see Drilling and Thompson 1984 for nest box design). To deter predators, the fence post supporting each nest box was covered with a greased PVC pipe (10 cm diameter). Nest boxes were checked daily to determine the breeding stage at each nest as well as to monitor the presence of banded adults at each box.

All birds in the population were banded with a U.S. Fish and Wildlife Service aluminum band, and all adults were banded with three color bands arranged in a unique combination. Adult males were captured in mist nets as soon as they were observed singing at and defending a nest box, and adult females were captured in their nest boxes during incubation. All nestlings were banded seven full days after they hatched (hatching = day 0). Body mass (to the nearest 0.1 g), tarsus length (to the nearest 0.1 mm), wing chord, and tail length (to the nearest 1.0 mm) were recorded for all adults, and on day 7 for nestlings. We estimated adult body condition as the residuals of body mass regressed against tarsus length and date of capture to correct for body size and time of season. Nestling condition was calculated as a regression of body mass on tarsus length, and means for each brood were used in analyses. The interbrood interval was defined as the period between fledging of the first brood and laying of the first egg of the second brood (Drilling and Thompson 1991).

BEHAVIORAL OBSERVATIONS

Male and female feeding rates to nestlings were recorded during 20-min observation sessions when nestlings were 4, 6, 8, and 10 days old (1998–2000). In 2000, we included an additional 20-min session at 2 days old to monitor male and female provisioning rates while the female was brooding. Feeding observations were recorded from 06:45 to 16:30 (mean = 10:50). Female feeding rates to nestlings declined with time of day ($r^2 = 0.05$, $F_{1, 388} = 20.8$, $P < 0.001$), and thus we used the residuals of a linear regression of female feeding rate and time of day for feeding rate analyses. Time of day did not affect male feeding rate to nestlings ($r^2 < 0.01$, $F_{1, 388} = 2.5$, $P > 0.1$).

PARENTAGE ANALYSES

To determine the relationship between extra-pair paternity and mate switching, we examined the parentage of 190 nestlings from 36 broods using microsatellite DNA. Microsatellite amplification and analysis followed the methods of Poirier et al. (in press). Briefly, parentage of young was determined using four microsatellite loci originally developed from other avian species (McDonald and Potts 1994, Primmer et al. 1996, Double et al. 1997, Dawson et al. 2000). Sizes of microsatellite alleles were determined using an ABI 373 automated sequencer and Genotyper software (Applied Biosystems, Foster City, California).

Unrelated adults ($n = 104$) were genotyped to determine levels of polymorphism at each locus. The four microsatellite loci were highly polymorphic (number of alleles per locus was 12 to 20) and had a combined probability of paternal exclusion of 0.997 (range 0.63 to 0.86 for each locus; Poirier et al., in press). All nestlings shared an allele with their putative mother at each locus. Extra-pair young mismatched the paternal allele of their putative father at two or more loci; there were no cases in which young mismatched the paternal allele at only one locus. Extra-pair sires were assigned only when they matched the paternal allele of extra-pair young at all four loci.

STATISTICAL ANALYSES

JMP (version 4.0, SAS Institute Inc. 2000) was used for all statistical analyses. All means are reported \pm SE, and all tests are two-tailed. For an overall assessment of the factors that may have influenced mate switching we performed a series of multiple logistic regressions that included the following predictors: availability of unmated females, interbrood interval, male breeding experience, male and female body condition, female parental care (at the first nest), laying date of the first clutch, and number of young fledged at the first nest. For multivariate analyses, the test statistic was the log likelihood chi-square and interactions among terms were not significant unless noted otherwise. For bivariate analyses, Wilcoxon rank-sum tests were used with a Z-approximation. In some cases, sample sizes differ among analyses because it was not possible to collect all data from all nests and individuals.

RESULTS

Males, rather than females, initiated mate switching in our population. Males that eventually switched mates began advertising for a new mate at a second nest box during the incubation or early nestling period at his first nest. All males that deserted their first mate successfully paired with a second female during the nestling or fledgling period of the first nest. There were no cases in which a female deserted her mate with young at the first nest.

Over the three years of this study, 68 different males bred in our population: 39 males were single brooded, 11 males were polygynous (i.e., no interbrood interval between primary and secondary females), and 18 males were sequentially monogamous. No males were sequentially monogamous in more than one year. Sequentially monogamous males had two broods during a breeding season that did not overlap temporally (i.e., there was an interbrood interval). Of these 18 males,

10 males switched mates within a breeding season while eight males stayed with the same female for both broods. Regardless of whether males switched mates, first and second broods were always raised in different nest boxes and a new nest was built in each box.

FACTORS INFLUENCING MALE MATE SWITCHING

There was very little extra-pair paternity in broods of sequentially monogamous males, and males that switched mates did not improve their paternity in their second brood. In fact, there were no extra-pair young in first broods, and only two extra-pair young occurred in second broods of males that switched mates (one each in 2 of 18 second broods). Furthermore, sequentially monogamous males did not excel as extra-pair sires in other broods. Over three years, 59 of 584 nestlings were extra-pair young (Poirier et al., in press). Only two of these extra-pair young were sired by two sequentially monogamous males that did not switch mates, whereas three extra-pair young were sired by two males that did switch mates.

Next, we examined the relationship between mate switching and the availability of unmated females and the interbrood interval. Both of these factors have been associated previously with mate switching in House Wrens. In our population, males that switched mates traveled an average of 90 ± 28 m (range 25–325 m) between their first and second nest box, and most (90%) traveled 125 m or less. This is approximately the distance between five nest boxes in our population. Thus, we estimated the availability of unmated females as the number of known unmated females within 125 m of a male's first nest during the average interbrood interval (15 days). Known unmated females included banded females with independent young from an earlier nest and unbanded females that had arrived recently. Males were more likely to switch mates when there were more unmated females nearby (log likelihood $\chi^2_1 = 6.1$, $P < 0.01$). The interbrood interval did not differ between males that switched mates (17.5 ± 2.4 days) and males that stayed with the same female (13.3 ± 2.9 days; $Z = 1.5$, $n_1 = 8$, $n_2 = 10$, $P = 0.1$). Presence/absence of male breeding experience in our population was not related to male mate switching ($\chi^2_1 = 0.1$, $P = 0.7$). Only the availability of unmated females was a significant predictor of male mate switching in any model (all log likelihood $\chi^2 > 13.7$, all $P < 0.01$).

COSTS AND BENEFITS OF MATE SWITCHING

For males, switching mates between first and second broods did not improve their reproductive success. Overall, males that switched mates fledged a similar number of young (within-pair and extra-pair) as males that did not switch mates ($Z = 0.8$, $P = 0.4$; Table 1). When extra-pair young were excluded from total fledging success, males that switched mates fledged significantly fewer young from second broods than males that stayed with their mate ($Z = 2.1$, $P = 0.03$; Table 1). In addition, there was a tendency for males that switched mates to have smaller clutches in both first and second broods (Table 1). These deficits were apparently ameliorated by higher hatching success for males that switched, at least in first broods ($Z = 1.9$, $P = 0.05$; Table 1). Thus, the total number of within-pair young males produced was not affected by mate switching (Ta-

TABLE 1. Reproductive success of monogamous male House Wrens that did ($n = 10$ males) or did not ($n = 8$ males) switch mates between first and second broods. P -values are from Wilcoxon rank-sum tests with a Z -approximation.

	First nests			Second nests		
	Switched mates	Did not switch	P	Switched mates	Did not switch	P
Clutch size	6.7 \pm 0.1	6.9 \pm 0.2	0.06	4.5 \pm 0.3	5.5 \pm 0.3	0.04
Young sired (%)	100 \pm 0	100 \pm 0	1.0	93 \pm 5	100 \pm 0	0.2
Hatching success (%)	99 \pm 1	91 \pm 4	0.05	96 \pm 6	96 \pm 3	0.7
Fledging success (%)	100 \pm 0	100 \pm 0	1.0	98 \pm 2	96 \pm 3	0.7
No. fledged	6.5 \pm 0.2	6.3 \pm 0.4	0.7	4.1 \pm 0.3	5.1 \pm 0.4	0.06
No. fledglings sired ^a	6.5 \pm 0.2	6.3 \pm 0.4	0.7	3.9 \pm 0.4	5.1 \pm 0.4	0.03
Total fledglings sired ^b	10.9 \pm 0.4	11.6 \pm 0.6	0.4			

^a Within-pair young that fledged from the male's own broods.

^b Total number of within-pair young from both broods, plus number of extra-pair young.

ble 1). Males did not switch to females in better condition ($Z = 1.6$, $P = 0.1$) or to a female that fed nestlings more frequently ($Z = 1.4$, $P = 0.2$). As a result, males that switched mates did not produce nestlings that were in better condition than nestlings in their first brood ($Z = 0.04$, $P = 0.9$), or than nestlings in second broods of males that did not switch ($Z = 0.5$, $P = 0.6$).

In contrast to males, mate switching had a considerable negative effect on female reproductive success. Of the 10 females that were deserted, only five mated with another male and produced a second brood. The five females that produced two broods fledged significantly more young (12.2 ± 0.2) than the five females that produced only one brood (6.4 ± 0.2 ; $Z = 2.6$, $P < 0.01$; Fig. 1). In a multivariate analysis, the likelihood of a deserted female obtaining a second mate and producing a second brood was not related to her condition, the clutch size of the first brood, or the date the first brood

fledged (all $\chi^2_1 \leq 1.9$, all $P \geq 0.2$). Among females that produced two broods, there was no difference in fledging success in relation to whether they remained with the same male (11.4 ± 0.6) or had different mates (12.2 ± 0.2 ; $Z = 1.0$, $n_1 = 8$, $n_2 = 5$, $P = 0.3$; Fig. 1). One of the five females that produced only one brood left the study area and may have nested again elsewhere.

DISCUSSION

Overall, males that switched mates and those that did not switch mates had similar reproductive success. We found no obvious reproductive benefits to males from switching mates. In fact, males that switched mates had reduced clutch size in their second broods and a tendency to fledge fewer young from their second broods than males that did not switch mates. Furthermore, there was no indication that males gained a better mate or produced better young by switching mates. Our results do not support either the incompatibility or better options hypothesis.

The incompatibility hypothesis predicts that both sexes benefit from switching, which obviously was not the case in our population of wrens. Although we found no clear benefits to males from switching mates, the cost to deserted females was potentially substantial in terms of reduced reproductive success. Few studies have found that both sexes initiate and benefit from mate switching, other than in long-lived birds in which new pairs have lower reproductive success than established pairs with prior breeding experience (Mills 1973, Coulson and Thomas 1983, Rowley 1983, Ens et al. 1993).

In most studies at least one sex appears to gain reproductive benefits from mate switching; the exception seems to be House Wrens. In Illinois, where most House Wrens are double brooded, both sexes switched mates (55% of individuals), but neither sex appeared to gain a reproductive benefit from switching (Drilling and Thompson 1991). In our population, few males are double brooded, but almost half of them initiated mate switching with no apparent benefit to the male and a potential cost to the deserted female. Further evidence that switching may not be adaptive in House Wrens comes from studies in Minnesota and Ohio where male reproductive success was reduced following mate

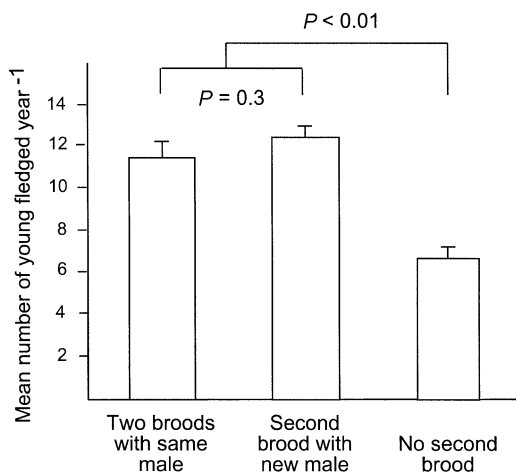


FIGURE 1. Mean (\pm SE) number of young fledged for females that had the same mate for both broods ($n = 8$), females that had different mates for each brood ($n = 5$) and females that did not have a second brood after they were deserted by their first mate ($n = 5$).

switching (Burns 1983). It is possible that the benefits of mate switching may not be realized immediately (e.g., in second broods) but may occur in subsequent years if the pair remains together (McNamara et al. 1999). Such a scenario seems unlikely in Wisconsin because the annual return rate of adults was low (26%), and when both members of a pair returned they did not re-pair in four of seven cases (57%).

Reproductive success of males may be improved by switching mates if paternity varies among broods. For example, male Pied Flycatchers (*Ficedula hypoleuca*) were more likely to switch mates in response to reduced paternity in earlier broods (Lifjeld et al. 1998). Although monogamous male House Wrens had a substantial level of extra-pair young in Illinois (26% of broods; Soukup and Thompson 1997), in our study just 5% of broods of sequentially monogamous males contained extra-pair young. As a result, paternity was not a factor influencing male mate switching in our population.

An important factor influencing mate switching for House Wrens appears to be the availability of unmated females. In Illinois, mate switching was examined in both low and high quality habitats (Drilling and Thompson 1991). Individuals of both sexes were less likely to switch mates in the poorer habitat, where there were fewer unmated individuals available. Habitat quality in our study area was fairly uniform, yet males still switched mates when the number of unmated females in the area increased. Mate switching in response to the availability of unmated individuals has been found more commonly in polyandrous species (Székely et al. 1999, Pilastro et al. 2001).

In summary, we found no support for the hypothesis that males switched mates in response to cuckoldry. However, males did switch mates when unmated females were available nearby. We also found that deserted females incurred a reproductive cost, namely, fewer second broods, while males did not appear to gain a reproductive benefit from switching, even after considering the paternity of young in their own nests and the extra-pair young sired in other nests.

We thank S. Valkenaar and L. Belli for help in the field as well as J. Johnson and T. DeRoos for help in the lab. We also thank A. Brylawski, J. Nooner, and S. Tarof for comments on the manuscript. We are grateful to C. F. Thompson for sharing his enthusiasm and knowledge of wrens, and to the staff at the University of Wisconsin-Milwaukee Field Station for their logistical support. Financial support for this study was provided by Sigma Xi Grants-in-Aid of Research, a FORWARD in Science Engineering and Mathematics grant, and the National Science Foundation (IBN-98-05973). This work was conducted under UWM Animal Care and Use Committee permits 97-98#35, 98-99#26 and 99-00#19.

LITERATURE CITED

- BAEYENS, G. 1981. Functional aspects of serial monogamy: the magpie pair-bond in relation to its territorial system. *Ardea* 69:145–166.
- BART, J. 1990. Male care, mate switching, and future reproductive success in a double-brooded passer-

ine. *Behavioral Ecology and Sociobiology* 26: 307–313.

- BENSCH, S., AND D. HASSELQUIST. 1991. Territory infidelity in the polygynous Great Reed Warbler *Acrocephalus arundinaceus*: the effect of variation in territory attractiveness. *Journal of Animal Ecology* 60:857–872.
- BLACK, J. M. 1996. Partnerships in birds: the study of monogamy. Oxford University Press, New York.
- BURNS, J. T. 1983. Mate switching in House Wrens. Ph.D. dissertation, University of Minnesota, Minneapolis, MN.
- CÉZILLY, F., AND R. G. NAGER. 1995. Comparative evidence for a positive association between divorce and extra-pair paternity in birds. *Proceedings of the Royal Society of London Series B* 262:7–12.
- CHOUHURY, S. 1995. Divorce in birds: a review of the hypotheses. *Animal Behaviour* 50:413–429.
- COULSON, J. C., AND C. S. THOMAS. 1983. Mate choice in the kittiwake gull, p. 361–376. In P. Bateson [ED.], *Mate choice*. Cambridge University Press, Cambridge, UK.
- DAWSON, D. A., O. HANNOTE, C. GREG, I. R. K. STEWART, AND T. BURKE. 2000. Polymorphic microsatellites in the Blue Tit *Parus caeruleus* and their cross-species utility in 20 songbird families. *Molecular Ecology* 9:1941–1944.
- DHINDSA, M. S., AND D. A. BOAG. 1992. Patterns of nest site, territory, and mate switching in Black-billed Magpies (*Pica pica*). *Canadian Journal of Zoology* 70:633–640.
- DHONDT, A. A., AND F. ADRIAENSEN. 1994. Causes and effects of divorce in the Blue Tit *Parus caeruleus*. *Journal of Animal Ecology* 63:979–987.
- DOUBLE, M. C., D. DAWSON, T. BURKE, AND A. COCKBURN. 1997. Finding the fathers in the least faithful bird: a microsatellite-based genotyping system for the Superb Fairy-wren *Malurus cyaneus*. *Molecular Ecology* 6:691–693.
- DRILLING, N. E., AND C. F. THOMPSON. 1984. The use of nest boxes to assess the effect of selective logging on House Wren populations, p. 188–196. In W. C. McComb [ED.], *Proceedings of a workshop on management of non-game species and ecological communities*. University of Kentucky, Lexington, KY.
- DRILLING, N. E., AND C. F. THOMPSON. 1991. Mate switching in multibrooded House Wrens. *Auk* 108:60–70.
- ENS, B., U. N. SAFRIEL, AND M. P. HARRIS. 1993. Divorce in the long-lived and monogamous Oystercatcher, *Haematopus ostralegus*: incompatibility or choosing the better option? *Animal Behaviour* 45:1199–1217.
- GRANT, B. R., AND P. R. GRANT. 1987. Mate choice in Darwin's finches. *Biological Journal of the Linnean Society* 32:247–270.
- KENDEIGH, S. C. 1941. Territorial and mating behavior of the House Wren. *Illinois Biological Monographs* 18:1–120.
- KENDEIGH, S. C. 1952. Parental care and its evolution in birds. *Illinois Biological Monographs* 22:1–358.

- LACK, D. 1968. Ecological adaptations for breeding in birds. Methuen & Co., London.
- LIFJELD, J. T., T. SLAGSVOLD, AND H. ELLEGREN. 1998. Experimental reduced paternity affects parental effort and reproductive success in Pied Flycatchers. *Animal Behaviour* 55:319–329.
- LINDÈN, M. 1991. Divorce in Great Tits: chance or choice? An experimental approach. *American Naturalist* 138:1039–1048.
- MATTHYSEN, E. 1990. Behavioral and ecological correlates of territory quality in the Eurasian Nuthatch (*Sitta europea*). *Auk* 107:86–95.
- MCDONALD, D. B., AND W. K. POTTS. 1994. Cooperative display and relatedness among males in a lek-mating bird. *Science* 266:1030–1032.
- MENAMARA, J. M., P. FORSLUND, AND A. LANG. 1999. An ESS model for divorce strategies in birds. *Philosophical Transactions of the Royal Society of London Series B* 354:223–236.
- MILLS, J. A. 1973. The influence of age and pair-bond on the breeding biology of the Red-billed Gull, *Larus novaehollandiae scopulinus*. *Journal of Animal Ecology* 42:147–162.
- NOLAN, V., JR. 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor*. *Ornithological Monographs* 26.
- OTTER, K., AND L. M. RATCLIFFE. 1996. Female initiated divorce in a monogamous songbird: abandoning mates for males of higher quality. *Proceedings of the Royal Society of London Series B* 263:351–355.
- PILASTRO, A., L. BIDDAU, G. MARIN, AND T. MINGOZZI. 2001. Female brood desertion increases with number of available mates in the Rock Sparrow. *Journal of Avian Biology* 32:68–72.
- PINKOWSKI, B. C. 1977. Breeding adaptations in the Eastern Bluebird. *Condor* 79:289–302.
- POIRIER, N. E., L. A. WHITTINGHAM, AND P. O. DUNN. In press. Males achieve greater reproductive success through multiple broods than through extra-pair mating in House Wrens. *Animal Behaviour*.
- PRIMMER, C. R., A. P. MØLLER, AND H. ELLEGREN. 1996. A wide-range survey of cross-species microsatellite amplification in birds. *Molecular Ecology* 5:365–378.
- RAMSAY, S. M., K. A. OTTER, D. J. MENNILL, L. M. RATCLIFFE, AND P. T. BOAG. 2000. Divorce and extra-pair mating in female Black-capped Chickadees (*Parus atricapillus*): separate strategies with a common target. *Behavioral Ecology and Sociobiology* 49:18–23.
- ROWLEY, I. 1983. Re-mating in birds, p. 331–360. In P. Bateson [ED.], *Mate choice*, Cambridge University Press, Cambridge, UK.
- SAS INSTITUTE INC. 2000. JMP 4.0. SAS Institute, Inc., Cary, NC.
- SHIELDS, W. M. 1984. Factors affecting nest and site fidelity in Adirondack Barn Swallows (*Hirundo rustica*). *Auk* 101:780–789.
- SOUKUP, S. S., AND C. F. THOMPSON. 1997. Social mating system affects the frequency of extra-pair paternity in House Wrens. *Animal Behaviour* 54:1089–1105.
- STREIF, M., AND A. RASA. 2001. Divorce and its consequences in the Common Blackbird *Turdus merula*. *Ibis* 143:554–560.
- SZÉKELY, T., I. C. CUTHILL, AND J. KIS. 1999. Brood desertion in the Kentish Plover: sex differences in remating opportunities. *Behavioral Ecology* 2:185–190.
- WAGNER, R. H. 1992. The pursuit of extra-pair copulations by monogamous Razorbills: how do females benefit? *Behavioral Ecology and Sociobiology* 29:455–464.
- WUNDERLE, J. M., JR. 1984. Mate switching and a seasonal increase in polygyny in the Bananaquit. *Behaviour* 88:123–144.

The Condor 105:821–825
© The Cooper Ornithological Society 2003

STASIS IN THE MORPH RATIO CLINE IN THE BANANAQUIT ON GRENADA, WEST INDIES

ANDREW D. C. MACCOLL^{1,3} AND IAN R. STEVENSON²

¹University of Sheffield, Department of Animal and Plant Sciences, Western Bank, Sheffield S10 2TN, UK

²Institute of Biological Sciences, University of Stirling, Stirling FK9 4LA, UK

Abstract. Bananaquits (*Coereba flaveola*) on the island of Grenada in the West Indies have a plumage

color polymorphism in which individuals are either yellow and black or all black. In the southwest of the island there is a cline in plumage morphs in which the frequency of black individuals increases with distance from the island's southwestern tip. We describe the present position (September 2002) and form of this cline in comparison to when it was last mapped, 21

Manuscript received 6 December 2002; accepted 17 July 2003.

³E-mail: a.maccoll@sheffield.ac.uk

years ago. There has been no net movement of the cline during this period. We suggest that previous movement in the cline could have been related to long-term variation in rainfall.

Key words: *Bananaquit*, *Coereba flaveola*, *Grenada*, *plumage polymorphism*, *rainfall*, *single-locus cline*.

Estasis en la Clina de Formas de *Coereba flaveola* en Grenada, Antillas

Resumen. Los individuos de *Coereba flaveola* de la isla de Grenada en las Antillas presentan un polimorfismo en el color del plumaje, en el cual existen individuos de color amarillo y negro e individuos totalmente negros. Al sudeste de la isla existe una clina de tipos de plumaje en la cual la frecuencia de individuos negros se incrementa con la distancia desde el extremo sudoccidental de la isla. Describimos la forma y posición actual de esta clina en comparación a cuando fue mapeada hace veinte años, y mostramos que no ha ocurrido un desplazamiento neto durante este período. Sugerimos que los movimientos anteriores de esta clina podrían estar relacionados con variaciones a largo plazo de la precipitación.

The two Bananaquit color morphs and the morph-ratio cline on Grenada have been described in detail by Wunderle (1981, 1983): a black and yellow morph ("yellow") ubiquitous in the Caribbean and much of Latin America, and an all-black ("black") morph found only on Grenada, St Vincent, and two small islands off the Venezuelan coast (Theron et al. 2001). This system is particularly useful for the study of avian clines because the color difference between the morphs is encoded by two alleles at a single locus, with black dominant to yellow (Theron et al. 2001); the clines are narrow and therefore easy to study; they are replicated; and there are some good historical data on their position.

Clines have attracted substantial theoretical study, and can be categorized as equilibrium or dynamic. Equilibrium clines are maintained by a balance between selection and dispersal, and show no long-term directional movement (Endler 1977). Clines in which a wave of new alleles moves through a population are designated as dynamic (Fisher 1937). The cline described in this note is known to have undergone previous movements, consistent with a dynamic spread of the yellow allele into previously all-black populations (Wunderle 1981, 1983). The aim of this study was to determine whether this spread has continued, or whether some other interpretation of the previous movements, consistent with an equilibrium cline, is possible.

METHODS

We carried out fieldwork in the cline during September 2002. In common with Wunderle (1983), we censused different sites by walking slowly and observing Bananaquits along trails and roads in southwestern Grenada (12°01'N, 61°45'W; Fig. 1). We also mist netted and banded Bananaquits at seven sites across the cline. At each of these sites, a total of approximately 40 m of five-shelf net in four or five lengths was set from about 07:30 until about 15:30 for 2–3 days. Two tape recorders placed below the nets were used to play back

short sections of Bananaquit song, and were moved regularly between the sections of net. Observational and netting data were collected, where possible, at Wunderle's (1983) sites, but, where there had been changes in access or habitat, we substituted sites at equivalent points in the cline. Data were used only from sites where at least 10 Bananaquits were caught or seen. The straight-line distance from Point Salines lighthouse to each site was measured from a 1:25 000 map (Ordnance Survey International 1988). We used data from Wunderle (1983) to compare the position of the cline in 1981 and 2002. Following Wunderle (1981), our sites can be considered as belonging mainly to two transects following the northern and southern sides of the southwestern peninsula. All data were collected between 30 August and 28 September 2002, and sites were visited in haphazard order with respect to their likely morph ratio.

STATISTICAL ANALYSES

The data were analyzed with logistic regression models using PROC GENMOD in SAS (SAS Institute Inc. 1999). In these models the response variable had the number of black birds caught or seen at a site as the numerator, and the total number of bananaquits caught or seen as the denominator.

RESULTS

Table 1 shows the sample sizes and percentages of black morphs recorded by us at different sites, excluding observational data that was gathered at the same locations as netting data. We were able to record data at or close to 12 of the 15 sites recorded by Wunderle (1983) in 1981. We also recorded data at another 11 sites. At one of Wunderle's sites ("Golf Course") we netted in two areas about 250 m apart, in scrub woodland on the north and south sides of the golf course itself. Having done so we found that the morph ratios in the two places were significantly different ($\chi^2_1 = 10.4$, $P = 0.001$), and so we considered these as two separate sites. We do not know how they compare to the exact location of Wunderle's golf course site, although when we combine our data from the two sites the ratio is 71% black, very similar to that obtained by Wunderle (67% black).

There was no change in the position or slope of the cline between 1981 and 2002 (Fig. 2). In a logistic regression model, distance from Point Salines was highly significant ($\chi^2_1 = 365.0$, $P < 0.001$), there was no effect of year ($\chi^2_1 = 0.3$, $P > 0.5$) or the interaction between distance and year ($\chi^2_1 = 0.3$, $P > 0.5$). In contrast to Wunderle (1981), we found a small but significant difference in ratios between netted samples and observations (for the difference in intercepts for models of netted and observed ratios $\chi^2_1 = 5.3$, $P = 0.02$). This difference was consistent with a slight over-recording of the rarer morph at the extremes of the cline in observational samples. The cline was significantly less steep along the south coast than along the north coast of the peninsula ($\chi^2_1 = 4.5$, $P < 0.05$), such that the widths of the cline (between ratios 0.2 and 0.8) were 3.4 km and 3.2 km respectively. Our estimate of the width of the cline through the southern transect was 0.9 km less than Wunderle's (1983) estimate, but the difference was not significant ($\chi^2_1 = 0.8$,

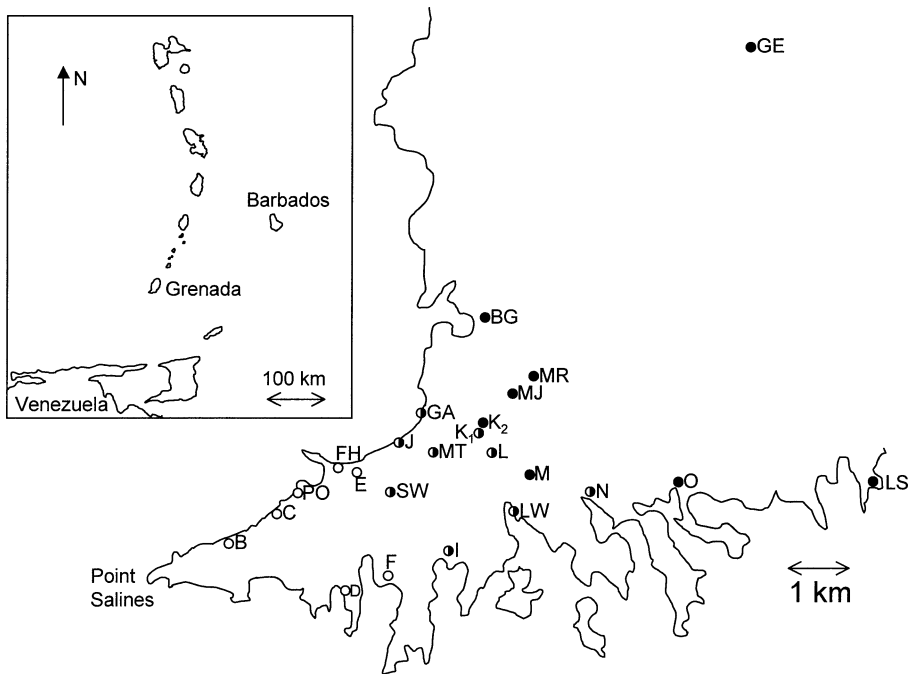


FIGURE 1. The location of Bananquit sampling sites on the Point Salines peninsula in southwestern Grenada, with (inset) the Lesser Antilles showing the position of Grenada. Circles indicate approximate proportion of black-morph birds at a site in 2002: unfilled: = <20% black morph, half-filled = 20–80%; filled = >80%. Table 1 contains exact values for each site. We split Wunderle's (1983) site K into K_1 (Golf Course South) and K_2 (Golf Course North) owing to differences in morph ratio in the two areas. Single-letter codes are sites originally sampled by Wunderle (1983); see Table 1 for full names of all sites.

$P = 0.39$). The width of the northern cline is very similar to Wunderle's estimate of 3.0 km.

The percentage of black morphs at different sites is strongly related to rainfall (Wunderle 1981), with the black morph more common in wetter areas farther from Point Salines. Therefore, we explored the possibility that previous variation in the position of the cline might have been related to temporal variation in rainfall. Available rainfall data for Grenada do not cover a sufficiently long period, so instead we examined data for neighbouring parts of the Caribbean. The data are from the global precipitation dataset (gu23wld0098.dat, Version 1.0), constructed and supplied by Dr. Mike Hulme at the Climatic Research Unit, University of East Anglia, UK (Hulme et al. 1998, Hulme 2000). Figure 3 shows variation in five-year mean rainfall for Barbados from 1900 to 1996. Barbados is 270 km from Grenada to the northeast, and is the nearest West Indian island with available long-term rainfall data. We also examined data for coastal Venezuela, approximately the same distance from Grenada as Barbados, in the opposite direction. Annual rainfall in the two areas is strongly correlated for the period ($r = 0.65$, $P < 0.001$; Sokal and Rohlf 1981), and we are therefore confident that these data are a reasonable indicator of long-term rainfall patterns in Grenada. The rainfall records from both Barbados and Venezuela indicate that this part of

the Caribbean was exceptionally dry in the late 1920s, the early 1960s, and the late 1970s (Fig. 3).

DISCUSSION

The movement of the cline recorded between 1978 and 1981 (Wunderle 1983) has not continued. There are at least two possible explanations for this. First, the cline may have become trapped in a region of low density or at a habitat barrier (Barton and Hewitt 1985). However Bananquits have broad habitat preferences (as shown by their ubiquitous distribution, from beaches to mountain rainforest) and there are no large habitat discontinuities or obvious barriers to dispersal in this part of Grenada. Nor do there appear to be any obvious large-scale variations in Bananquit density, although it is impossible to be certain about this.

Second, the cline may be in equilibrium, maintained by a balance between selection and dispersal (Endler 1977). In the late nineteenth century there were very few yellow birds in Grenada, and these were confined to the extreme southwest (Wunderle 1981). However, the distribution of yellow birds expanded during the early part of the twentieth century, equivalent to a north-eastern movement of the cline (Wunderle 1981). This pattern, and Wunderle's (1983) observation of another significant movement of the cline to the northeast between 1978 and 1981, argues against it being in equi-

TABLE 1. The percentage of black-morph Bananaquits at 24 sites in Grenada, September 2002. Single-letter site codes were originally used by Wunderle (1983). Two-letter site codes are other sites surveyed by us. Where we gathered netting and observational data at the same site, we included only the netting data in this table. Sites are listed in order of distance from Point Salines (Fig. 1).

Site name	Site code	Transect	Method	% Black morph	Sample size
Pinguin	B	North and South	Net	3	34
Parc a Boeuf	C	North	Observation	13	16
Portici	PO	North	Observation	10	10
True Blue	D	South	Observation	13	15
Flamboyant Hotel	FH	North	Observation	8	12
Blue Horizons	E	North	Net	15	33
Lance aux Epines	F	South	Observation	18	11
South Winds	SW	North	Net	40	15
Grenada Grand	J	North	Observation	35	17
Mt. Hartman Estate	I	South	Observation	71	14
Mont Tout	MT	North	Net	58	24
Grand Anse North	GA	North	Net	50	34
Golf Course South	K ₁	North	Net	45	20
Golf Course North	K ₂	North	Net	87	31
Lower Woburn	LW	South	Observation	67	12
Woodlands Estate	L		Observation	53	15
Woburn	M	South	Observation	82	11
Morne Jaloux	MJ	North	Observation	91	22
Botanic Gardens	BG	North	Observation	100	13
Calivigny	N	South	Observation	64	11
Morne Jaloux Ridge	MR	North	Observation	100	10
Westerhall Estate	O	South	Observation	91	22
La Sagesse	LS	South	Observation	100	10
Grand Etang	GE		Net	100	13

librium. Nevertheless, the cline could still be in equilibrium, with movements linked to changes in a selection regime associated with environmental conditions.

It is clear that the relative proportions of the two morphs at different sites is strongly related to spatial variation in rainfall, with yellow birds occurring in

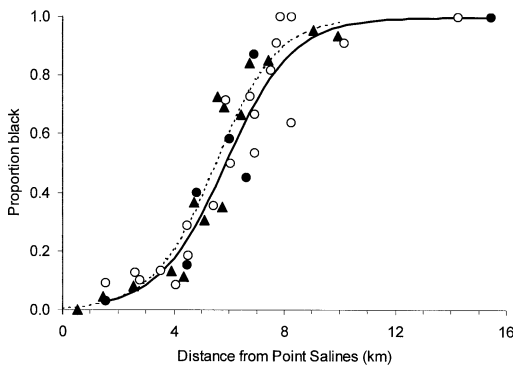


FIGURE 2. The relationship between the percentage of black-morph Bananaquits at sampling sites and their distance from Point Salines lighthouse, Grenada. Triangles and the dashed line indicate Wunderle's 1981 data (Wunderle 1983). Circles and the continuous line correspond to our 2002 data. Filled circles are data from netting, unfilled circles are observational data.

only the driest areas (Wunderle 1981). This suggests the possibility that the observed movements of the cline have been related to temporal variation in rainfall. In this case, we would expect drier conditions to favor the spread of the yellow allele. Observed movements of the cline are consistent with rainfall data in this respect since the large spread in yellow birds that was recorded in 1929 (Wunderle 1981) came immediately after a very dry period, and the similar spread of yellow alleles between 1978 and 1981 followed the very dry period that this part of the Caribbean experienced in the late 1970s. Although the movement of the cline at this time did not exactly match the period of low rainfall, we believe that it is likely that there would be lag in the response of the Bananaquit pop-

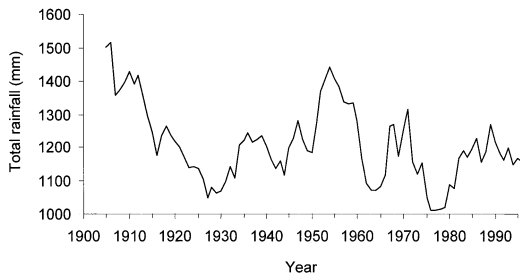


FIGURE 3. Average annual rainfall in the previous five years against year for Barbados, 1905 to 1996.

ulation to changes in rainfall, which could amount to several breeding seasons.

It has previously been shown that Bananaquits on another Caribbean island, Puerto Rico, suffered a large population decline during a drought there in the mid-1970s, and that there was a lag in the response to rainfall (Faaborg et al. 1984). The size of the Bananaquit population was most closely related to rainfall two years previously. This provides strong support for our suggestion that drought could have perturbed the Bananaquit population in Grenada. If black birds are more strongly affected by drought than yellow birds, as is suggested by their relative rarity in the driest areas of Grenada, then it seems likely that drought could result in movement of the cline. If movement in the cline is caused by variation in rainfall acting with a lag, then the cline should have moved to the southwest during the late 1950s, following a wet period in the mid-1950s. We have been unable to find data to test this prediction.

In summary, the Bananaquit morph-ratio cline has not experienced any net movement in 20 years, which is approximately 20 generations. This suggests that the cline is in equilibrium. Previous movements of the cline may have been the result of long-term variation in rainfall.

We thank the Ministry of Agriculture, Forestry, Lands and Fisheries, Grenada, for permission to carry out the work. We also thank C. Macpherson, M. Phillip, D. Ramsier, and M. Sousa for assistance in Grenada; Blue Horizons Hotel and Mr. Ross for permission to mist net on their land, and B. Hatchwell and J. Wunderle for comments on a previous version of the manuscript. The work was funded by the British Ecological Society.

LITERATURE CITED

- BARTON, N. H., AND G. M. HEWITT. 1985. Analysis of hybrid zones. *Annual Review of Ecology and Systematics* 16:113–148.
- ENDLER, J. A. 1977. *Geographic variation, speciation, and clines*. Princeton University Press, Princeton, N.J.
- FAABORG, J., W. J. ARENDT, AND M. S. KAISER. 1984. Rainfall correlates of bird population fluctuations in a Puerto Rican dry forest—a nine year study. *Wilson Bulletin* 96:575–593.
- FISHER, R. A. 1937. The wave of advance of advantageous genes. *Annals of Eugenics* 7:355–369.
- HULME, M. [ONLINE]. 2000. Datasets/global precipitation: global land precipitation. (<http://www.cru.uea.ac.uk/~mikeh/datasets/global>) (5 June 2003).
- HULME, M., T. J. OSBORN, AND T. C. JOHNS. 1998. Precipitation sensitivity to global warming: comparison of observations with HadCM2 simulations. *Geophysical Research Letters* 25:3379–3382.
- ORDNANCE SURVEY INTERNATIONAL. 1988. Grenada south. Ordnance Survey International, Southampton, UK.
- SAS INSTITUTE INC. 1999. OnlineDoc. Version 8.0. SAS Institute Inc., Cary, NC.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*. W. H. Freeman, New York.
- THERON, E., K. HAWKINS, E. BERMINGHAM, R. E. RICKLEFS, AND N. I. MUNDY. 2001. The molecular basis of an avian plumage polymorphism in the wild: a melanocortin-1-receptor point mutation is perfectly associated with the melanic plumage morph of the Bananaquit, *Coereba flaveola*. *Current Biology* 11:550–557.
- WUNDERLE, J. M. 1981. An analysis of a morph ratio cline in the Bananaquit (*Coereba flaveola*) on Grenada, West Indies. *Evolution* 35:333–344.
- WUNDERLE, J. M. 1983. A shift in the morph ratio cline in the Bananaquit on Grenada, West Indies. *Condor* 85:365–367.

The Condor 105:825–829

© The Cooper Ornithological Society 2003

WING SHAPE IN HOUSE FINCHES DIFFERS RELATIVE TO MIGRATORY HABIT IN EASTERN AND WESTERN NORTH AMERICA

JEREMY R. EGBERT AND JAMES R. BELTHOFF¹

Department of Biology, Boise State University, Boise, ID 83725

Abstract. We investigated whether wing morphology differed between the sedentary House Finches

(*Carpodacus mexicanus*) of western North America and the introduced population of eastern North America, as the latter has developed migratory behavior since its inception. Wing morphology differed between eastern and western House Finches. Eastern House Finches had shorter proximal primaries and a longer outer primary, perhaps reflecting a thinner and more pointed wing, although no disparity in wing length was

Manuscript received 24 December 2002; accepted 4 June 2003.

¹ Corresponding author. E-mail: jbeltho@boisestate.edu

detected. Since we interpret these differences in wing shape as modifications for flight capability, we believe that initial evidence for morphological divergence relative to migratory habit between eastern and western House Finches has been established here. Confirmatory studies to determine if wing morphology varies according to the gradient in expression of migratory behavior throughout the range of eastern House Finches are now warranted.

Key words: *Carpodacus mexicanus*, House Finch, intraspecific variation, morphology, partial migration, wing shape.

La Forma Alar en *Carpodacus mexicanus* Difiere en Relación a los Hábitos Migratorios entre el Este y Oeste de Norte América

Resumen. Investigamos si la morfología del ala difería entre individuos sedentarios de *Carpodacus mexicanus* del oeste de Norte América y la población introducida en el este de Norte América, la cual ha desarrollado un comportamiento migratorio desde su inserción. La morfología del ala difirió entre las poblaciones de *C. mexicanus* del este y del oeste. Los individuos del este tuvieron primarias proximales más cortas y primarias externas más largas, lo que quizás refleja un ala más fina y más puntiaguda, aunque no se detectó una diferencia en el largo del ala. Ya que interpretamos estas diferencias en la forma del ala como modificaciones para la capacidad del vuelo, creemos que se ha establecido una evidencia inicial de divergencia morfológica en relación con el hábito migratorio entre las poblaciones de *C. mexicanus* del este y del oeste de Norte América. Actualmente, son necesarios estudios que confirmen y determinen si la morfología del ala varía de acuerdo al gradiente de expresión del comportamiento migratorio a través del rango de distribución de la población de *C. mexicanus* del este.

One of the most notable ornithological events of the twentieth century in North America was the introduction of House Finches (*Carpodacus mexicanus*) into the eastern United States from native western populations and their subsequent spread (Hill 1993). The eastern population is believed to have originated from the release of a small but unknown number of captive birds on Long Island, New York, around 1940 (Elliot and Arbib 1953), and the source of the birds is presumed to be the Los Angeles area of southern California (Mundinger 1975). After a decade or so of local increases in the vicinity of western Long Island, the introduced population grew exponentially and rapidly expanded its range across the continent (Veit and Lewis 1996). House Finches are now naturalized and common throughout most of the eastern and midwestern United States, and in southern Canada.

As House Finches in the native range are essentially sedentary, one striking outcome of the introduction has been the appearance and increased frequency of migratory behavior in the eastern population of House Finches (Belthoff and Gauthreaux 1991, Able and Belthoff 1998). In fact, the eastern House Finch pro-

vides one of the very few cases in which the establishment of a large-scale pattern of migratory behavior has been documented under natural conditions in our lifetime. Over the 60 or so generations since their introduction, a complex system of seasonal migration has evolved in House Finches (Able and Belthoff 1998) in a remarkably brief and perhaps unprecedented period of time, something that studies on captive birds suggest can occur under strong selection (Berthold et al. 1990, Berthold 1996).

Wings of migrant species often are characterized by long distal primaries and short proximal primaries, resulting in relatively long and thin wings (compared with nonmigratory species; Rayner 1988, Winkler and Leisler 1992, Alerstam 1993, Lockwood et al. 1998), and a wing tip close to the leading edge. A pointed tip may reduce drag associated with the wing tip vortex (Lockwood et al. 1998). Even within species, comparisons between sedentary and migratory individuals or populations show that the migratory representatives indeed have wing features more characteristic of migration (Senar et al. 1994, Copete et al. 1999, Perez-Tris and Telleria 2001).

Wilson (1975) pointed out that behavior is the part of the phenotype that is most likely to change in response to long-term environmental change, such that behavior will usually be altered first and physical structure second. Thus, given that selection has apparently favored migratory behavior in eastern House Finches since their introduction, we investigated whether corresponding changes in wing morphology have arisen as well.

METHODS

We captured a sample of western House Finches ($n = 60$) with mist nets and baited traps at several suburban locations in Boise, Idaho (43°34'N, 116°13'W) from May to November 2002 (most were captured September–November 2002). Eastern House Finches ($n = 92$) were trapped at several locations near Ithaca, New York (42°27'N, 6°29'W) in mist nets and baited traps in October–November 2002. All captured finches received U.S. Geological Survey aluminum leg bands for individual identification. At the time of capture, sex and age were determined where possible. However, because we could not age many birds, we pooled individuals of all ages for analyses. Birds showing signs of wing molt (primaries or secondaries) were excluded from our study. JRE measured the wings of all captured House Finches with a ruler and digital calipers to determine wing length (to nearest 0.25 mm) and the differences between the tip of the longest primary and the tips of each of the other eight primaries (to nearest 0.01 mm). This was done with the wing in a consistent, folded position such that the primaries were partially stacked on top of each other as in Senar et al. (1994). We refer to these measurements for the nine primaries as primary distances. We then calculated the length of each primary (P1 through P9, where P1 is the most proximal primary) by subtracting each primary distance from the maximum wing length according to the formula $P_i \text{ length} = (\text{wing length}) - (\text{primary distance of } P_i)$ (see Evered 1990). As Senar et al. (1994) suggest, we then corrected these primary lengths for body

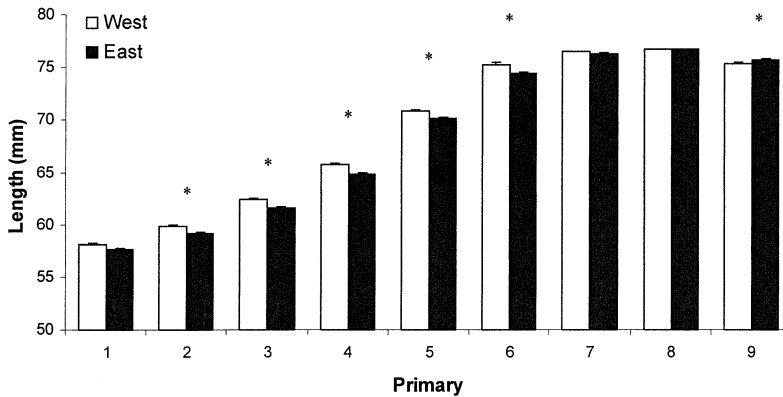


FIGURE 1. Standardized primary lengths of House Finches in two populations in the eastern and western United States (Ithaca, New York, $n = 92$ birds, and Boise, Idaho, $n = 60$ birds). Asterisks above bars indicate primaries for which the two samples differed significantly using one-way ANOVA and sequential Bonferroni corrections following a significant MANOVA.

size by taking into account allometric relationships using the SIZESTD program (Leonart et al. 2000), which produced a standardized length for each primary. Briefly, this program transformed feather length as follows:

$$P'_{ji} = P_{ji}(l_0/l_i)^{b_j}$$

where P_{ji} is the original measurement of the primary j in individual i , l_i is the wing length (an indication of body size) of individual i , l_0 is a standard wing length (taken as 76.81 mm, the mean wing length of the House Finches in our study) to which all individuals are reduced (or increased), and b_j is the allometry coefficient of primary j according to the growth model of Senar et al. (1994). These corrected measurements formed the basis of a multivariate analysis of wing-shape variation using principal components analysis (PCA), which was shown to be an accurate analysis of wing shape by Chandler and Mulvihill (1988).

STATISTICAL ANALYSIS

Wing length in eastern and western House Finches was compared using ANOVA. We compared transformed primary lengths (P1' through P9') between sexes and populations using two-way multivariate analysis of variance (MANOVA) followed by inspection of univariate tests to determine which transformed primary lengths contributed to overall range differences. Because sex did not affect P1' through P9', and sex did not interact with range in either multivariate or univariate analyses, we pooled sexes for all subsequent analyses and used all 152 captured individuals. To help control for inflated Type I errors following the initial MANOVA, follow-up univariate ANOVAs were evaluated using sequential Bonferroni corrections (Rice 1989), in which alpha was $0.05/9 (= 0.0055)$ for the first comparison and sequentially adjusted. We conducted PCA on the standardized primary lengths and compared PC scores between House Finches in the eastern and western populations using ANOVA with sequential Bonferroni corrections. Analyses were con-

ducted using SAS (Version 8.2, SAS Institute Inc. 2000), and all results are reported as means \pm SE.

RESULTS

Despite the prediction relative to migratory habit, there was no difference in mean wing length between the eastern (76.7 ± 0.2 mm) and western (76.9 ± 0.3 mm) House Finches in our sample ($F_{1,150} = 0.2$, $P = 0.68$). However, there was a significant difference in standardized primary lengths between populations (MANOVA: Wilks' lambda = 0.79, $F_{9,142} = 4.1$, $P < 0.001$). Follow-up univariate ANOVAs revealed that mean P2' through P6' were greater in western House Finches, whereas average P9' was greater in eastern House Finches (Fig. 1).

The first three principal components (PCs) explained 73% of the variation in transformed primary lengths (Table 1). The first axis, PC1, represented increasing proximal primary (P2'–P6') lengths. PC2 represented increasing distal primary length (P8' and P9'), and P6' loaded most highly on PC3 (Table 1). Eastern and western House Finches differed significantly along PC1 ($F_{1,150} = 25.9$, $P < 0.001$). Eastern House Finches ($PC1 = -0.64 \pm 0.20$) had shorter proximal primary lengths than western House Finches ($PC1 = 0.98 \pm 0.25$), and this contributed to wings of eastern House Finches being thinner and somewhat more pointed (Fig. 2, 3). Eastern and western House Finches did not differ along PC2 (0.08 ± 0.12 and -0.12 ± 0.14 , respectively; $F_{1,150} = 1.1$, $P = 0.29$) or along PC3 (-0.10 ± 0.10 and 0.16 ± 0.12 , respectively; $F_{1,150} = 2.6$, $P = 0.11$).

DISCUSSION

Results of our study indicate that the wings of the more migratory eastern House Finches tended to be more pointed than those of western House Finches. The shorter proximal primaries of eastern House Finches perhaps reflected a thinner wing proximally. In accordance with another prediction of morphology based on migration, the transformed length of P9 also was

TABLE 1. Results of a principal components (PC) analysis on standardized primary lengths (P1' through P9') of House Finches from eastern and western North American populations ($n = 152$). P1' represents standardized length of the most proximal primary.

Variable	Factor loadings		
	PC1	PC2	PC3
P1'	0.353	0.058	-0.383
P2'	0.430	0.116	-0.216
P3'	0.451	0.140	-0.088
P4'	0.436	0.093	0.118
P5'	0.398	0.100	0.278
P6'	0.186	-0.165	0.666
P7'	0.292	-0.253	-0.121
P8'	-0.051	0.707	0.397
P9'	-0.124	0.595	-0.303
Eigenvalue	4.29	1.27	1.01
% Variance explained	48	14	11
Cumulative variance explained (%)	48	62	73

significantly longer in eastern House Finches, which may represent the wing point being closer to the leading edge.

While we observed wing-shape differences consistent with each population's migratory habit, the predicted increase in the overall wing length of the more migratory (eastern) population was not observed. It is possible that this is related to the short amount of time that selection has had to operate on wing morphology. Longitudinal studies of wing morphology in House Finches could help document these changes over time. Alternatively, decreased wing lengths in at least one population of eastern House Finches have been documented after the recent mycoplasmal conjunctivitis outbreak (Nolan et al. 1998), so differences in wing lengths may have been more apparent before the outbreak. Finally, we were uncertain if the eastern House Finches we sampled were actually migratory or sedentary, as House Finches in the East are partial migrants (Belthoff and Gauthreaux 1991, Able and Belthoff 1998). A future study in which the migration distance of individuals is known might uncover a significant difference in wing length between the two populations. Nevertheless, the patterns of wing-shape

differences between regions (east and west) that we observed despite the lack of differences in overall wing length indicate potential changes in wing morphology consistent with a more migratory habit in eastern House Finches.

An alternative hypothesis for the pattern of wing-shape differences we observed between eastern and western House Finches is that the measured morphological features of eastern House Finches also may be characteristic of the southern California source population from which the eastern population presumably arose. That is, southern California House Finches could have shorter proximal primaries and longer distal primaries than the sample of western House Finches we measured from Idaho for the current study, and these differences carried over via their introduction to the East.

In conclusion, we interpret the differences that were detected in wing shape between eastern and western House Finches as initial evidence for morphological divergence as a result of migratory habit. However, our study was limited to single populations in the East and the West. Confirmatory tests should include measurements of wing morphology in populations throughout both the sedentary and migratory ranges of House Finches. For instance, Able and Belthoff (1998) showed that populations colonized most recently, and farther from the origin of the eastern population, had the greatest propensity to migrate. Considering this gradient in the expression of migratory behavior, we hypothesize that wing morphology will vary accordingly within the eastern population of House Finches.

We thank the Cornell Laboratory of Ornithology's House Finch Project personnel, C. Moulton, and J. Soules for assistance in the field. We especially thank A. Dhondt for his assistance, hospitality, and many stimulating and interesting discussions. We also thank J. C. Senar and J. Leonart for providing the SIZESTD program for use in this study, and J. C. Senar and two anonymous referees for helpful comments on our manuscript. Finally we thank Sigma Xi, The Scientific Research Society, and Boise State University for provid-

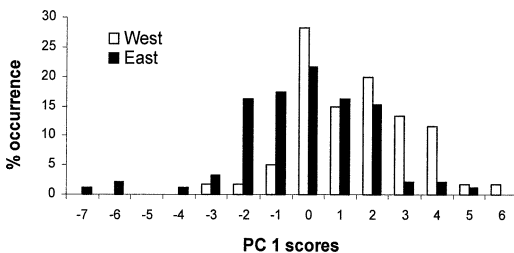


FIGURE 2. Frequency distribution (% occurrence) of eastern-U.S. ($n = 92$) and western-U.S. ($n = 60$) House Finches along the first axis generated by a principal components analysis of standardized primary lengths (Table 1). Increasing PC1 score corresponds to increasing lengths of proximal primaries.

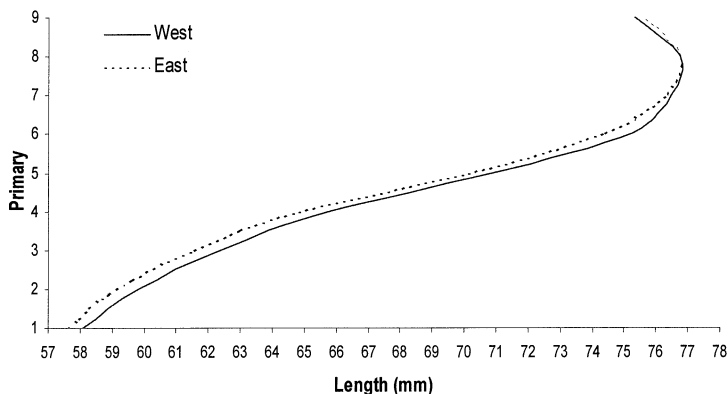


FIGURE 3. Graphical representation of distal wing segments produced using mean standardized primary lengths to visualize differences in wing morphology between eastern and western House Finches (note that these are not wing tracings). Wings are less rounded proximally (thinner) and more pointed distally in eastern House Finches, which appears to correlate with their more migratory habit.

ing financial or logistical support. This research was completed in partial fulfillment of requirements for undergraduate research credit at Boise State University for JRE.

LITERATURE CITED

- ABLE, K. P., AND J. R. BELTHOFF. 1998. Rapid 'evolution' of migratory behaviour in the introduced House Finch of eastern North America. *Proceedings of the Royal Society of London Series B* 265:2063–2071.
- ALERSTAM, T. 1993. *Bird migration*. Cambridge University Press, Cambridge, UK.
- BELTHOFF, J. R., AND S. A. GAUTHREAUX JR. 1991. Partial migration and differential winter distribution of House Finches in eastern United States. *Condor* 93:374–382.
- BERTHOLD, P. 1996. *Control of bird migration*. Chapman & Hall, London.
- BERTHOLD, P., G. MOHR, AND U. QUERNER. 1990. Steuerung und potentielle Evolutionsgeschwindigkeit des obligaten Teilziehverhaltens: Ergebnisse eines Zweiweg-Selections experiments mit der Mönchsgrasmücke (*Sylvia atricapilla*). *Journal für Ornithologie* 131:33–45.
- CHANDLER, C. R., AND R. S. MULVIHILL. 1988. The use of wing shape indices: an evaluation. *Ornis Scandinavica* 19:212–216.
- COPETE, J. C., R. MARINE, D. BIGAS, AND A. MARTINEZ-VILALTA. 1999. Differences in wing shape between sedentary and migratory Reed Buntings *Emberiza schoeniclus*. *Bird Study* 46:100–103.
- ELLIOT, J. J., AND R. S. ARBIB JR. 1953. Origin and status of the House Finch in the eastern United States. *Auk* 70:31–37.
- EVERED, D. S. 1990. Measures of wing area and wing span from wing formula data. *Auk* 107:784–787.
- HILL, G. E. 1993. House Finch (*Carpodacus mexicanus*). In A. Poole and F. Gill [EDS.], *The birds of North America*, No. 46. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.
- LLEONART, J., J. SALAT, AND G. J. TORRES. 2000. Removing allometric effects of body size in morphological analysis. *Journal of Theoretical Biology* 205:85–93.
- LOCKWOOD, R., J. P. SWADDLE, AND M. V. RAYNER. 1998. Avian wingtip shape reconsidered: wingtip shape indices and morphological adaptations to migration. *Journal of Avian Biology* 29:273–292.
- MUNDINGER, P. M. 1975. Song dialects and colonization of the House Finch *Carpodacus mexicanus* on the East Coast. *Condor* 77:407–422.
- NOLAN, R. M., G. E. HILL, AND A. M. STOEHR. 1998. Sex, size, and plumage redness predict House Finch survival in an epidemic. *Proceedings of the Royal Society of London Series B* 265:961–965.
- PEREZ-TRIS, J., AND J. L. TELLERIA. 2001. Age-related variation in wing shape of migratory and sedentary Blackcaps *Sylvia atricapilla*. *Journal of Avian Biology* 32:207–213.
- RAYNER, J. M. V. 1988. Form and function in avian flight. *Current Ornithology* 5:1–66.
- RICE, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
- SAS INSTITUTE INC. 2000. *SAS/STAT user's guide*. Version 8. SAS Institute Inc., Cary, NC.
- SEAR, J. C., J. LLEONART, AND N. B. METCALFE. 1994. Wing-shape variation between resident and transient wintering Siskins *Carduelis spinus*. *Journal of Avian Biology* 25:50–54.
- VEIT, R. R., AND M. S. LEWIS. 1996. Dispersal, population growth, and the Allee effect: dynamics of the House Finch invasion of eastern North America. *American Naturalist* 148:255–274.
- WILSON, E. O. 1975. *Sociobiology: the new synthesis*. Harvard University Press, Cambridge, MA.
- WINKLER, H., AND B. LEISLER. 1992. On the ecomorphology of migrants. *Ibis* 134:21–28.

DIGESTIVE ENZYMES IN TWO SPECIES OF MARINE CINCLODES (PASSERIFORMES: FURNARIIDAE)

PABLO SABAT¹ AND SANDRA P. GONZALEZ

*Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Casilla 653,
Santiago, Chile*

Abstract. Changes in digestive enzyme activity along the intestine may be related to changes in substrate concentration in the intestine. We examined the distribution of digestive enzymes along the intestine in two species of carnivorous passerine birds from the genus *Cinclodes*. Both species lacked sucrase activity, suggesting that these species are unable to feed on sucrose-rich diets. Distribution of maltase and aminopeptidase-N activity differed from that found in other passerines, including omnivorous species, but resembled those found in herbivorous and frugivorous birds. We hypothesize that the type of prey items that *Cinclodes* consume may explain the pattern of maltase and aminopeptidase-N expression.

Key words: *Aminopeptidase-N*, *Cinclodes*, *digestion*, *disaccharidases*, *nutrition*.

Enzimas Digestivas en Dos Especies de *Cinclodes* Marinos (Passeriformes: Furnariidae)

Resumen. Los cambios en los niveles de actividad enzimática digestiva a lo largo del intestino de aves pueden estar relacionados con cambios en la concentración de sustratos en el intestino. En este estudio examinamos la distribución de enzimas digestivas a lo largo del intestino en dos especies de aves passeriformes del género *Cinclodes*. Ambas especies carecen de actividad de sacarasa lo que sugiere que estas especies son incapaces de consumir dietas ricas en sacarosa. La distribución de la actividad de maltasa y aminopeptidasa-N difiere de la documentada para otros passeriformes, incluyendo especies omnívoras, y es similar a la encontrada en aves herbívoras y frugívoras. Se sugiere que el tipo de presas consumidas por *Cinclodes* explicaría el patrón de expresión de maltasa y aminopeptidasa-N.

Levels of intestinal hydrolase activity affect digestion rates and digestive efficiency in birds (Karasov 1996). Complex nutrients such as carbohydrates and proteins need to be degraded to simple monomers before they can be absorbed by the intestine. The last step of carbohydrate digestion is carried out by sucrase-isomal-

tase and maltase-glucoamilase, yielding glucose (Vonk and Western 1984, Caviedes-Vidal and Karasov 1996). Proteins, which are initially transformed to oligopeptides by acid and pancreatic enzymes, are subsequently degraded by exopeptidases into amino acids prior to absorption. The most important exopeptidase in the small intestine of birds, often used as an index for protein digestive capacity, appears to be aminopeptidase-N (Vonk and Western 1984).

The expression and activity of digestive enzymes are often correlated with diet (Martínez del Río and Stevens 1989, Martínez del Río et al. 1992, Sabat et al. 2001). In many species of birds, disaccharidase activity decreases distally along the small intestine (Martínez del Río 1990, Martínez del Río et al. 1995), seemingly as a consequence of a decreasing substrate concentration along the gut (Hume 1998). The opposite pattern from the typical decrease in disaccharidase activity along the gut has been found for aminopeptidase-N (Meynard et al. 1999, McWilliams et al. 1999). Although the biochemistry of digestion in omnivorous, granivorous, and herbivorous birds has received some attention (Martínez del Río et al. 1995, Sabat et al. 1998, Caviedes-Vidal et al. 2000), the intestinal biochemistry of insectivorous and carnivorous species remains poorly understood (Sabat 2000, Witmer and Martínez del Río 2001).

The objective of this study was to characterize digestive enzyme profiles along the small intestine of two marine passerine species from the genus *Cinclodes* (Furnariidae) inhabiting central Chile, the Gray-flanked *Cinclodes* (*C. oustaleti*) and the Dark-bellied *Cinclodes* (*C. patagonicus*). *Cinclodes* species eat insects and other aquatic invertebrates (Paynter 1971, Hockey et al. 1987). We used disaccharidases (sucrase and maltase) and aminopeptidase-N activity as an index of the ability to digest carbohydrates and proteins respectively (Vonk and Western 1984). A previous report (Sabat 2000) indicated that *C. patagonicus* and the Sea-side *Cinclodes* (*C. nigrofumosus*) lack sucrase activity. We therefore measured sucrase activity in *C. oustaleti* to determine whether the lack of ability to digest sucrose is common to another member of the Furnariidae.

METHODS

Adult birds were collected using mist nets or shot at El Quisco, a coastal locality in central Chile (33°34'S, 71°37'W) during austral autumn (May and June) 2000

Manuscript received 27 August 2002; accepted 5 June 2003.

¹ E-mail: psabat@uchile.cl

after the end of the breeding season and before migration (Sielfeld et al. 1996, Jorge et al. 1998). Individuals were captured between 07:00 and 12:00, while they foraged at the shore. Mist-netted birds were killed by decapitation. Birds were weighted (to the nearest 0.05 g), and their small intestine and stomachs (proventriculus and gizzard) immediately removed. In order to examine the current diet of our specimens, stomach contents were deposited in a petri dish for analysis. Prey items were separated, weighed with an electronic balance (to the nearest 0.0005 g), and identified to the lowest taxonomic level possible. Intestines were separated into five sections of similar length, washed with a 0.9% NaCl solution, and immediately frozen in liquid nitrogen. Tissues were thawed and homogenized (30 sec in an ULTRA TURRAX T25 homogenizer at maximum setting) in 20 volumes of 0.9 % NaCl solution. Disaccharidase activity was determined according to the method described by Martínez del Rio et al. (1995). Briefly, tissue homogenates (100 μ L) were incubated at 40°C with 100 mL of 56 mmol L⁻¹ sugar solutions in 0.1 M Maleate/NaOH buffer, pH 6.5. After 10 min incubation, reactions were stopped by adding 3 mL of a stop/develop Glucose-Trinder (one bottle of Glucose Trinder 500 reagent (Sigma Diagnostics, Saint Louis, Missouri) in 250 mL 0.1 mol L⁻¹ TRIS/HCl, pH 7 plus 250 mL of 0.5 NaH₂PO₄, pH 7). Absorbance was measured at 505 nm with a Sequoia Turner 390 spectrophotometer after 18 min at 20°C. Aminopeptidase-N assays were done using L-alanine-p-nitroanilide as a substrate. Briefly, 100 μ L of homogenate diluted with 0.9% NaCl solution were mixed with 1 mL of assay mix (2.04 mmol L⁻¹ L-alanine-p-nitroanilide in 0.2 mol L⁻¹ NaH₂PO₄/Na₂HPO₄, pH 7). The reaction was incubated at 40°C and arrested after 10 min with 3 mL of ice-cold acetic acid 2 N, and absorbance was measured at 384 nm. On the basis of absorbance, standardized intestinal enzymatic activities were calculated. The selected pHs for measuring the activities were the optimum for each enzyme. The activity of enzymes is presented as standardized hydrolytic activity, (UI per g wet tissue, where UI = μ mol hydrolyzed per min; see Martínez del Rio et al. 1995 for a detailed explanation). We statistically evaluated enzyme activity as a function of intestinal position by repeated measures ANOVA using bird species as a factor. Statistical analyses were performed using Statistica (StatSoft Inc. 1997) statistical package for Windows 95. Data are reported as means \pm SD.

RESULTS

The two *Cinclodes* species differed considerably in mass. Body mass was 40.6 \pm 1.6 g for *C. patagonicus* ($n = 5$) and 28.7 \pm 1.9 g for *C. oustaleti* ($n = 4$). Neither species showed measurable sucrase activity. Maltase activity in both *C. patagonicus* and *C. oustaleti* peaked in the proximal small intestine and declined significantly in the distal small intestine (repeated-measures ANOVA: $F_{1,2} = 7.3$, $P < 0.001$; Fig. 1), and there was neither an effect of species ($F_{1,6} = 0.2$, $P > 0.5$) nor a significant species \times gut position interaction ($F_{1,2} = 0.5$, $P > 0.5$). There was, however, a significant decrease in maltase activity in the distal section of the small intestine in the two species (Tukey

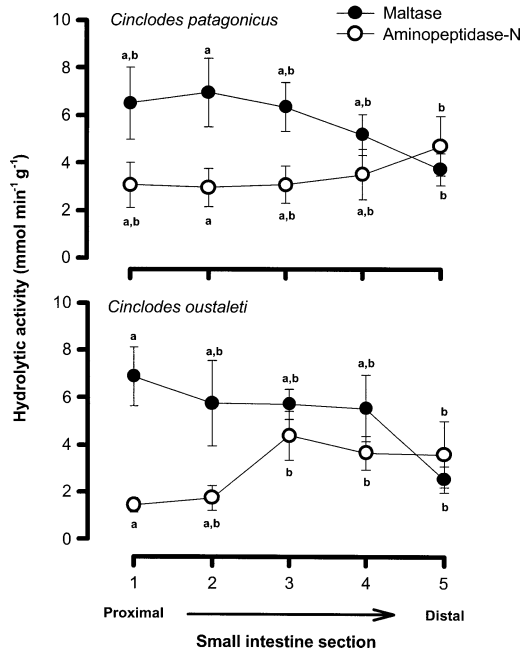


FIGURE 1. Intestinal brush-border enzyme hydrolysis rates in *Cinclodes patagonicus* ($n = 5$) and *Cinclodes oustaleti* ($n = 4$) as a function of the position along the small intestine. Maltase activity declined, whereas aminopeptidase-N activity increased with distance along the small intestine. Similar letters indicate nonsignificant differences among segments (Tukey test) after repeated-measures ANOVA.

test; $P < 0.05$). The pattern of aminopeptidase-N activity along the intestine showed an opposite trend. In both species, activity was low in the first section and tended to increase distally (repeated-measures ANOVA: $F_{1,2} = 4.1$, $P < 0.05$; results of the Tukey test are shown in Fig. 1). There was no effect of species ($F_{1,6} = 0.59$, $P > 0.5$) nor interaction ($F_{1,2} = 2.1$, $P > 0.1$). In agreement with previous reports, dietary analysis of *Cinclodes* revealed that both species were consuming exclusively animal prey (marine invertebrates and insects). For five individuals of *C. patagonicus*, the mean percentage by weight of gut content was 55% insect (39% Diptera adults, 16% other), 34% crustacean (20% amphipod, 4% isopod, 10% other), and 11% mollusk. For four individuals of *C. oustaleti*, the gut contents were 89% insect (Diptera adults and larvae), 10% mollusk, and 1% crustacean.

DISCUSSION

Our findings that sucrase activity was absent in *C. oustaleti* support the hypothesis that the genus *Cinclodes* entirely lacks the sucrase-isomaltase enzyme complex, suggesting that species are unable to feed on sucrose-rich diets. Maltase activity measurements revealed the presence of the maltase-isomaltase enzyme complex, which hydrolyzes maltose, a product of the hydrolysis of both plant (starch) and animal (glycogen) carbohy-

drate. Because of the carnivorous habits of *Cinclodes*, it is likely that the presence of intestinal maltase activity relates to glycogen digestion from marine invertebrates and insects. Thus, the lack of sucrase-isomaltase in the genus *Cinclodes* may be related to their highly specialized carnivorous diet (Sabat 2000). Alternatively, as in other groups of birds that include omnivorous and frugivorous species, the lack of sucrase activity may be related to phylogenetic constraints, rather than trophic specialization (Martínez del Río 1990, Martínez del Río et al. 1995). Whether the lack in sucrase activity is due to a phylogenetic constraint in the genus *Cinclodes* will only be elucidated on the basis of studies that include other members of the group.

Sucrase and maltase are usually highest in the proximal intestine, where most disaccharides are present (Levey and Martínez del Río 1999, McWhorter and Martínez del Río 2000, Witmer and Martínez del Río 2001). The distal segment of the intestine exhibits minimal levels of activity. Interestingly, *Cinclodes* species exhibited relatively constant levels of maltase activity; a decrease was apparent only in the most distal section of the small intestine. Meynard et al. (1999) reported a similar pattern in the herbivorous Rufous-tailed Plantcutter (*Phytotoma rara*). Despite the probable decrease of sugar (maltose) concentration along the small intestine, high levels of enzyme activity may compensate for the short retention time and highly diluted plant material consumed by this herbivorous bird (López-Calleja and Bozinovic 1999). In addition, Witmer and Martínez del Río (2001) observed an increase in aminopeptidase-N activity in distal segments of the small intestine in the frugivorous Cedar Waxwing (*Bombycilla cedrorum*), but not in the omnivorous thrushes American Robin (*Turdus migratorius*), Wood Thrush (*Hylocichla mustelina*), Hermit Thrush (*Catharus guttatus*), Gray-cheeked Thrush (*C. minimus*), and Swainson's Thrush (*C. ustulatus*). The authors hypothesized that differences in the profiles of this enzyme may be related to the contrasting strategies of digestion of proteins from dilute, aqueous, sugary diets in the frugivore and from fatty diets in omnivores.

Our results do not support this hypothesis. Distribution of aminopeptidase-N along the small intestine in carnivorous *Cinclodes* resembles the situation found in the frugivorous Cedar Waxwing and the herbivorous Rufous-tailed Plantcutter. It is possible that such a trend relates more to specific digestion strategies than to the chemical composition of natural diets. We suggest that water content of prey items consumed by *Cinclodes* (e.g., mollusks and crustaceans are more than 80% water, Vonk and Western 1984) may dilute and thereby reduce the turnover time of food (see Afik and Karasov 1995, Karasov 1996, McWilliams and Karasov 2001). This hypothesis would explain why *Cinclodes* profiles of enzymes resemble profiles of herbivorous and frugivorous birds. Finally, dietary composition may also influence the pattern of enzyme activities (Afik et al. 1995). Profiles of enzyme activities of birds eating natural and controlled diets are needed to know how levels of dietary substrates may affect these profiles.

We thank Francisco Bozinovic, Todd McWhorter, Rodrigo Medel, and two anonymous referees for useful

comments on the early version of the manuscript. This research was funded by FONDECYT grant No. 1010647 to PS.

LITERATURE CITED

- AFIK, D., E. CAVIEDES-VIDAL, C. MARTÍNEZ DEL RÍO, AND W. H. KARASOV. 1995. Dietary modulation of intestinal hydrolytic enzymes in Yellow-rumped Warblers. *American Journal of Physiology* 269: R423–R420.
- AFIK, D., AND W. H. KARASOV. 1995. The trade-offs between digestion rate and efficiency in warblers and their ecological implications. *Ecology* 76: 2247–2257.
- CAVIEDES-VIDAL, E., AND W. H. KARASOV. 1996. Glucose and amino acid absorption in House Sparrow intestine and its dietary modulation. *American Journal of Physiology* 271:R561–R568.
- CAVIEDES-VIDAL, E., D. AFIK, C. MARTÍNEZ DEL RÍO, AND W. H. KARASOV. 2000. Dietary modulation of intestinal enzymes of the House Sparrow (*Passer domesticus*): testing an adaptive hypothesis. *Comparative Biochemistry and Physiology A* 125: 11–24.
- HOCKEY, P. A. R., A. L. BOSMAN, AND P. G. RYAN. 1987. The maintenance of polymorphism and cryptic mimicry in the limpet *Scurria variabilis* by two species of *Cinclodes* (Aves: Furnariidae) in central Chile. *Veliger* 30:5–10.
- HUME, I. D. 1998. Optimization in design of the digestive system, p. 212–219. In E. R. Weibel, C. R. Taylor, and L. Bolis [EDS.], *Principles of animal design*. Cambridge University Press, Cambridge, UK.
- JORGE, R., E. TABILO-VALDIVIESO, AND V. MONDACA. 1998. Avifauna de la bahía de Coquimbo, Chile. *Boletín Chileno de Ornitología* 5:2–9.
- KARASOV, W. H. 1996. Digestive plasticity in avian energetics and feeding ecology, p. 61–84. In C. Carey [ED.], *Avian energetics and nutritional ecology*. Chapman and Hall, New York.
- LEVEY, D. J., AND C. MARTÍNEZ DEL RÍO. 1999. Test, rejection, and reformulation of a chemical reactor-based model of gut function in a fruit-eating bird. *Physiological and Biochemical Zoology* 72:369–383.
- LÓPEZ-CALLEJA, M. V., AND F. BOZINOVIC. 1999. Feeding behavior and assimilation efficiency of the Rufous-tailed Plantcutter: a small avian herbivore. *Condor* 101:705–710.
- MARTÍNEZ DEL RÍO, C. 1990. Dietary and phylogenetic correlates of intestinal sucrase and maltase activity in birds. *Physiological Zoology* 63:987–1011.
- MARTÍNEZ DEL RÍO, C., H. G. BAKER, AND I. BAKER. 1992. Ecological and evolutionary implication of digestive processes: bird preferences and the sugar constituents of floral nectar and fruit pulp. *Experientia* 48:544–540.
- MARTÍNEZ DEL RÍO, C., E. BRUGGER, J. L. RIOS, M. E. VERGARA, AND M. WITMER. 1995. An experimental and comparative study of dietary modulation of intestinal enzymes in European Starlings (*Sturnus vulgaris*). *Physiological Zoology* 68:490–511.

- MARTÍNEZ DEL RIO, C., AND B. R. STEVENS. 1989. Physiological constraint on feeding behavior: intestinal membrane disaccharidases of the Starling. *Science* 243:794–796.
- MCWHORTER, T., AND C. MARTÍNEZ DEL RIO. 2000. Does gut function limit hummingbird food intake? *Physiological and Biochemical Zoology* 73:313–324.
- MCWILLIAMS, S. R., E. CAVIEDES-VIDAL, AND W. H. KARASOV. 1999. Digestive adjustments in Cedar Waxwings to high feeding rate. *Journal of Experimental Zoology* 283:394–407.
- MCWILLIAMS, S. R., AND W. H. KARASOV. 2001. Phenotypic flexibility in digestive system structure and function in migratory birds and its ecological significance. *Comparative Biochemistry and Physiology A* 128:579–593.
- MEYNARD, C., M. V. LOPEZ-CALLEJA, F. BOZINOVIC, AND P. SABAT. 1999. Digestive enzymes of a small avian herbivore, the Rufous-tailed Plantcutter. *Condor* 101:904–907.
- PAYNTER, R. A., JR. 1971. Nasal glands in *Cinclodes nigrofumosus*, a maritime passerine. *Bulletin of the British Ornithological Club* 91:11–12.
- SABAT, P. 2000. Intestinal disaccharidases and aminopeptidase-N in two species of *Cinclodes* (Passerine: Furnariidae). *Revista Chilena de Historia Natural* 73:345–350.
- SABAT, P., F. F. NOVOA, F. BOZINOVIC, AND C. MARTÍNEZ DEL RIO. 1998. Dietary flexibility and intestinal plasticity in birds: a field and laboratory study. *Physiological Zoology* 71:226–236.
- SABAT, P., F. F. NOVOA, AND M. PARADA. 2001. Digestive constraints and nutrient hydrolysis in nestlings of two flamingo species. *Condor* 103:396–399.
- SIELFELD, W., N. AMADO, J. HERREROS, R. PEREDO, AND A. REBOLLEDO. 1996. La avifauna del salar de Huasco: Primera Región, Chile. *Boletín Chileno de Ornitología* 3:17–24.
- STATSOFT INC. 1997. *Statistica* release 5 (quick reference) for the Windows 95 operating system. StatSoft, Inc., Tulsa, OK.
- VONK, H. J., AND J. H. R. WESTERN. 1984. *Comparative biochemistry and physiology of enzymatic digestion*. Academic Press, London.
- WITMER, M. C., AND C. MARTÍNEZ DEL RIO. 2001. The membrane-bound intestinal enzymes of waxwings and thrushes: adaptive and functional implications of pattern of enzyme activity. *Physiological and Biochemical Zoology* 74:584–593.