SHORT COMMUNICATIONS

The Condor 106:386–390

FACULTATIVE REST-PHASE HYPOTHERMIA IN FREE-RANGING WHITE-THROATED SPARROWS

ANDREW S. DOLBY[1], JOHN G. TEMPLE, LAURA E. WILLIAMS, EMILY K. DILGER, KATRINA M. STECHLER AND VANESSA S. DAVIS
Department of Biological Sciences, Mary Washington College, 1301 College Avenue, Fredericksburg, VA 22401

Abstract. Shallow facultative rest-phase hypothermia has been reported in a number of passerine families, but few published data exist about its use by free-ranging birds. We used temperature-sensitive radio-transmitters to determine whether White-throated Sparrows (*Zonotrichia albicollis*) employ nocturnal hypothermia during winter. We measured skin temperatures of 24 free-ranging sparrows between 13:00 and 14:00 and between 02:00 and 03:00 for each of three days and nights per subject. The average nightly skin-temperature reduction per individual was 3.4 ± 1.0°C (SD). Skin temperature reductions ranged from 0.2°C to 7.0°C among all individuals. There was a significant negative correlation between the magnitude of skin temperature decline and nighttime ambient temperature. Additionally, we found a negative trend between depth of hypothermia and a body density index.

Key words: hypothermia, thermoregulation, White-throated Sparrow, Zonotrichia albicollis.

Fase de Reposo Hipotérmica Facultativa en Individuos de *Zonotrichia albicollis* que se Desplazan Libremente

Resumen. La fase de reposo facultativa somera ha sido mencionada para un número de familias de paseriformes, pero existen pocos datos publicados sobre su uso por parte de aves que se desplazan libremente. Usamos radio transmisores sensibles a la temperatura para determinar si *Zonotrichia albicollis* emplea hipotermia nocturna durante el invierno. Medimos la temperatura de la piel de 24 individuos que se desplazan libremente entre las 13:00 y 14:00 y entre las 02:00 y 03:00 durante tres días y tres noches por individuo. La reducción nocturna promedio de la temperatura de la piel por individuo fue 3.4 ± 1.0°C (DE). Las reducciones de la temperatura de la piel variaron entre 0.2°C y 7.0°C considerando todos los individuos. Hubo una correlación negativa significativa entre la disminución de la magnitud de la temperatura de la piel y la temperatura ambiental nocturna. Adicionalmente, encontramos una tendencia negativa entre la profundidad de la hipotermia y el índice de densidad corporal.

Body temperature maintenance entails considerable metabolic cost for endothermic animals. When metabolic demand exceeds energy supply, some birds use facultative hypothermic responses to reduce energy expenditure (McKechnie and Lovegrove 2002). Such circumstances may arise when food supplies are insufficient or unpredictable, when weather is cold, or when foraging is inhibited for prolonged periods (Reinertsen 1996).

Avian facultative hypothermic responses occur in a broad range of depths and bout lengths, ranging from seasonal hibernation, exhibited by Common Poorwill (*Phalaenoptilus nuttallii*), to shallow rest-phase hypothermia observed in an array of avian families (McKechnie and Lovegrove 2002). They are generally most pronounced among nonpasserine nectarivores and aerial-feeding insectivores whose food sources are ephemeral and dependent upon weather (McKechnie and Lovegrove 2002). Among such taxa (e.g., Apodidae, Trochilidae, and Caprimulgidae), body temperature (T_b) reductions exceeding 10°C are common, and individuals often enter torpor (Geiser and Ruf 1995, Reinertsen 1996, Körtner et al. 2000, Barclay et al. 2001). In contrast, most passerines examined maintain nocturnal T_b within 10°C of active-phase normothermic T_b and typically do not become torpid (Reinertsen 1996, McKechnie and Lovegrove 2003). A notable exception is the nectarivorous Malachite Sunbird (*Nectarinia famosa*; Downs and Brown 2002). However, while relatively modest in depth, facultative rest-phase

---

Manuscript received 17 October 2003; accepted 20 January 2004.

[1] E-mail: adolby@mwc.edu

hypothermia likely affords passerines biologically significant energetic savings (Dawson and Whittow 2000).

Much about passerines' use of this energy-saving strategy remains unknown. Most research has been conducted on captive subjects (McKechnie and Lovegrove 2003), or has targeted nonpasserines (Brigham 1992, Bech et al. 1997). Our first objective was therefore to determine whether it occurs in a free-ranging temperate-zone species, the White-throated Sparrow (*Zonotrichia albicollis*).

White-throated Sparrows are winter residents of the Mid-Atlantic region of the eastern United States. They are regularly exposed to nighttime ambient temperatures (T_a) at or below those known to produce hypothermia in other passerines (Reinertson and Haftorn 1986, Clemens 1989). Furthermore, since they are primarily ground-feeding granivores (Falls and Kopachena 1994), their food supply may be periodically obscured by snow and ice, possibly subjecting them to short-term food limitation.

Another poorly understood facet of avian thermoregulation relates to the factors that produce intraspecific variability. Such factors may include both environmental and physiological variables (Reinertsen 1996). A number of studies have reported relationships between T_a and the depth of hypothermia bouts, but few have examined the effects of T_a on free-ranging birds (Brigham 1992). Moreover, the effects of individuals' energetic status on the depth of hypothermia have generally been addressed via food deprivation experiments in the laboratory (Ketterson and King 1977, Graf et al. 1989, McKechnie and Lovegrove 2003). Data for individuals in the field are needed to understand the effects of energy reserves on facultative rest-phase hypothermic strategies.

Thus, our second objective was to determine whether T_a or stored energy predict the depth of facultative rest-phase hypothermia. We predicted that magnitude of skin temperature (T_{sk}) depression would be negatively correlated with both T_a and fat supply, estimated using a body density index. Additionally, we predicted that there would be an interaction between these variables.

METHODS

We conducted our study 7–21 January 2002 and from 10 January to 3 February, 2003, on the Mary Washington College grounds and adjacent residential neighborhood of Fredericksburg, Virginia (38°10′N, 77°35′W). The area contains a mixture of lawns and hedgerows, as well as unmanaged Eastern deciduous forest fragments. Bird feeders were present in the study area. During the day, we typically observed White-throated Sparrows in loosely structured social groups foraging in leaf litter. At night, sparrows most frequently roosted in broad-leaved evergreens (e.g., *Ilex opaca*, *Photinia serrulata*, and *Ligustrum lucidum*).

We mist-netted 24 adult sparrows opportunistically and weighed and measured the wing chords of each. Body masses ranged from 23.3 to 32.8 g (mean ± SD = 27.9 ± 2.7 g), and wing chords ranged from 65.5 to 78.0 mm (mean ± SD = 71.6 ± 3.0 mm). From these measurements, we calculated a body density index by dividing body mass by the cube of wing chord length. This index is frequently used as an indicator of physical condition in birds, and variation among individuals is indicative of variation in fat supply (Pravosudov et al. 1999, Ekman and Hake 1990).

We sexed 18 individuals based on wing chord length (Piper and Wiley 1991). The wing chord lengths of six individuals were within the published range of overlap between males and females (Piper and Wiley 1991, Falls and Kopachena 1994), and consequently, we could not sex them with certainty.

Each bird was fitted with two colored leg bands to permit individual identification. We affixed a temperature-sensitive radio-transmitter (Model BD-2AT; 0.7 g; Holohil Systems Ltd., Carp, Ontario, Canada) to the interscapular apteria of each bird using Skin-Bond® latex cement (Smith & Nephew® Inc., Largo, Florida).

We measured T_{sk} of birds between 13:00 and 14:00 and between 02:00 and 03:00 during the next three consecutive days and nights by timing the interpulse interval and comparing it with the calibration curves provided by the manufacturer. We based the timing of our T_{sk} measurements on data for six individuals whose T_{sk} we measured every 3 hr also over 3 days and nights. From these pilot observations, we determined that we reliably captured maximum diurnal T_{sk} and minimum nocturnal T_{sk} during these hours. To verify that transmitters were properly attached following the third night's reading, we measured T_{sk} the next afternoon. If a transmitter detached from a bird at any time, we attached it to a new subject. We obtained six T_{sk} measurements for 12 sparrows each winter. Observations were spread as evenly as possible across calendar dates each year.

Since we were interested in measuring temperature changes only, and not absolute body temperature (T_b) values, we did not record subjects' cloacal temperatures immediately after applying transmitters. Brigham (1992) found that cloacal and interscapular T_{sk} temperatures in Common Poorwills are tightly correlated ($r^2 = 0.99$). We assumed that T_{sk} changes would reflect T_b changes in our White-throated Sparrows with a similar degree of precision. Moreover, the diurnal T_{sk} in our sample averaged 40.9 ± 1.6°C (SD), which is within one degree of the mean T_b typical of passerines (Prinzinger et al. 1991). It is possible that T_{sk} measurements are affected by ambient cooling (Willis and Brigham 2003). However, even though the daytime T_a range was nearly equivalent to nighttime range, there was only a 0.02°C change in daytime T_{sk} measurements for every 1.0°C change in daytime T_a. Thus, it appears that T_a had little direct effect on T_{sk} measurements. We therefore feel that our use of external transmitters was a valid means of assessing T_b fluctuations.

When we measured T_{sk}, we also recorded T_a and wind speed (m sec^{-1}). T_a ranged from −7°C to 12°C (mean ± SD = 5.0 ± 4.3°C) during the day, and −8°C to 7°C at night (−1.6 ± 4.7°C). T_a averages were consistent with historical T_a averages for the region. Wind speeds were negligible during both years in the vicinity of sparrows' nocturnal roost sites. Thus, we excluded wind speed from our analyses. Snow and ice cover were also insignificant during our observation period.

STATISTICAL ANALYSES

We used ANCOVA to test our predictions (SPSS 11.0 for windows). To eliminate pseudoreplication, we cal-

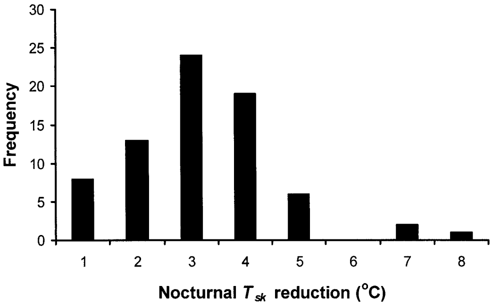

FIGURE 1. Frequency distribution of rest-phase skin temperature (T_{sk}) reduction in White-throated Sparrows ($n = 24$ individuals; three observations per subject).

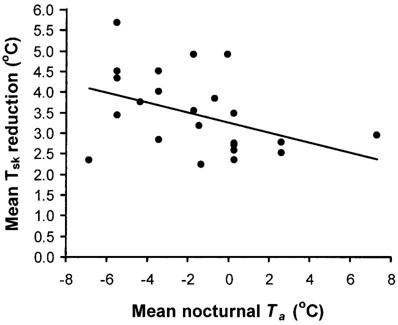

FIGURE 2. Significant negative correlation between mean rest-phase skin temperature (T_{sk}) reduction and the average nocturnal ambient temperature (T_a) in 24 White-throated Sparrows ($r = -0.42$, $P = 0.05$). Each data point represents the mean of three T_{sk} measurements of an individual.

culated the average nocturnal T_{sk} reduction exhibited by each individual. Our response variable, therefore, comprised the mean of the three diurnal-nocturnal T_{sk} differences recorded per individual. We also averaged the T_a for the three nights corresponding to when each subject's nocturnal T_{sk} readings were taken. Since the predicted interaction term was not significant, we removed it from our final model. We performed a separate, but identical analysis on the 18 birds that we could sex reliably. Values represent means ± SD.

RESULTS

Overall nocturnal T_{sk} reduction ranged from 0.2°C to 7.3°C (mean 3.5 ± 1.4°C; Fig. 1), while per-subject average T_{sk} reductions ranged between 2.2°C and 5.7°C (mean 3.4 ± 1.0°C). Twelve of 24 sparrows exhibited mean T_{sk} decreases $\geq$3.0°C.

We found a significant negative correlation between average per-subject T_{sk} reduction and T_a ($F_{1,21} = 4.5$, $P = 0.05$; Fig. 2). Additionally, average T_{sk} reduction tended to be negatively related to body density ($F_{1,21} = 3.9$, $P = 0.06$; Fig. 3). Both variables accounted for approximately one-third of the variation among individuals' mean nocturnal T_{sk} decline and significantly predicted the depth of hypothermia ($R^2 = 0.30$, $P = 0.02$).

In our analysis of those individuals that we could sex reliably, we found no difference in depth of hypothermia between seven males and 11 females after controlling for the effects of T_a and body density ($F_{1,14} = 1.1$, $P = 0.32$).

DISCUSSION

White-throated Sparrows in our study exhibited nocturnal T_{sk} depression that varied among individuals. Half of our 24 subjects reduced their T_{sk} by $\geq$3.0°C, enough to suggest use of facultative rest-phase hypothermia (Prinzinger et al. 1991), likely to lessen thermoregulatory costs. To our knowledge, these data represent the first evidence of facultative rest-phase hypothermia in a free-ranging emberizid. They are consistent, however, with laboratory evidence that most passerines are capable of only modest rest-phase temperature reduction (McKechnie and Lovegrove 2002).

The average T_{sk} reduction we recorded was greater than that of well-fed captive White-crowned Sparrows (*Z. leucophrys*), a congener of equal body mass, whose T_b dropped by less than 1.0°C between night and day at a mean T_a of about 7.0°C (Ketterson and King 1977). In fact, the average T_{sk} decline we recorded was comparable to those of captive White-crowned Sparrows (T_b decline = 3.4°C) fasted for 56 hr, also at T_a = 7.0°C, during which birds lost more than 20% of their body mass (Ketterson and King 1977).

The average nocturnal T_a in our study was nearly 9.0°C lower than in Ketterson and King's (1977) food deprivation experiment (−1.6°C versus 7.0°C). We did record 14 T_{sk} observations when the T_a was comparable (i.e., 4.0°C to 7.0°C). Under these conditions, T_{sk} reduction was still within 0.5°C (mean 3.1 ± 1.0°C) of the T_b declines reported by Ketterson and King (1977) for severely fasted White-crowned Sparrows. Thus, our data are consistent with recent arguments that laboratory studies underestimate the amplitude of circadian T_b fluctuations typical of free-ranging birds (Geiser et al. 2000, McKechnie and Lovegrove 2002).

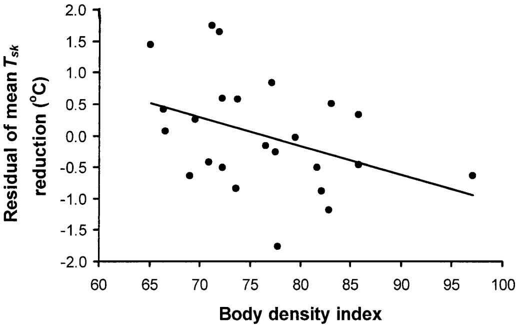

FIGURE 3. Negative relationship between rest-phase skin temperature (T_{sk}) reduction and an index of body density in White-throated Sparrows, after controlling for ambient temperature (T_a) ($r_{\text{partial}} = -0.40$, $P = 0.06$). Each data point represents the ANCOVA residual of rest-phase skin temperature (T_{sk}) reduction after we removed the effects of T_a (Fig. 2).

Variability in depth of T_{sk} reduction was at least partially explained by T_a. As T_a declines, energetic costs associated with thermoregulation should increase, creating greater need for conservation (Reinertsen and Haftorn 1983, Merola-Zwartjes 1998). The variation in nocturnal T_{sk} reduction we found was also partly explained by our body density index, although our observed negative correlation was only marginally significant. This relationship suggests that birds with lower fat reserves have greater need to reduce thermoregulatory costs.

We must interpret this trend with caution. Additional variables such as muscle mass and gut contents affect the density index. Furthermore, consistent relationships between energy limitation and depth of hypothermia have not been found in the field (Dawson and Whittow 2000). Birds that are not obviously energy limited may still enter rest-phase hypothermia or even become torpid. Brigham (1992) found that food supply did not reliably predict torpor use by free-ranging Common Poorwills. Willow Tits (*Poecile montanus*; Reinertsen and Haftorn 1983) regularly fell into hypothermia despite access to adequate food. Furthermore, the biological consequences of hypothermia for our subjects cannot be quantified based on our data.

There was no interaction between T_a and body density index, perhaps because these variables exert independent effects on subjects' thermoregulatory strategies. Alternatively, climatic conditions during our study, although typical of the region, may not have been sufficient to cause birds to thermoregulate differently depending upon their energetic status. Finally, physiological differences among individuals not captured by our body density index may have had overriding effects on thermoregulation as T_a declined.

In summary, we provide evidence that free-ranging White-throated Sparrows use facultative rest-phase hypothermia to a greater extent than would be predicted by previous laboratory work. Additional factors such as diurnal T_a, wind exposure, nocturnal predation risk, social status, and energetic quality of food consumed by birds may influence White-throated Sparrow nocturnal thermoregulation. Furthermore, much debate currently exists regarding heterothermy terminology and the physiological significance of rest-phase hypothermia (Geiser and Ruf 1995, Barclay et al. 2001, Lovegrove and Smith 2003). Nonetheless, our results reinforce the conclusion by others (McKechnie and Lovegrove 2002) that more field studies are needed to understand passerine rest-phase thermoregulation.

We thank Sigma Xi, the Virginia Academy of Science, and Mary Washington College for project funding. We also thank Dr. Debra Hydorn for statistical advice, and the E. G. Thornton family for access to their private property. Helpful comments by R. M. Brigham and an anonymous reviewer improved this manuscript.

LITERATURE CITED

BARCLAY, R. M. R., C. L. LAUSEN, AND L. HOLLIS. 2001. What's hot and what's not: defining torpor in free-ranging birds and mammals. Canadian Journal of Zoology 79:1885–1890.

BECH, C., A. S. ABE, J. F. STEFFENSEN, AND M. BERGER. 1997. Torpor in three species of Brazilian hummingbirds under semi-natural conditions. Condor 99:780–788.

BRIGHAM, R. M. 1992. Daily torpor in a free-ranging goatsucker, the Common Poorwill (*Phalaenoptilus nuttallii*). Physiological Zoology 65:457–472.

CLEMENS, D. T. 1989. Nocturnal hypothermia in rosy finches. Condor 91:739–741.

DAWSON, W. R., AND G. C. WHITTOW. 2000. Regulation of body temperature, p. 343–390. *In* P. D. Sturkie [ED.], Avian physiology. Academic Press, New York.

DOWNS, C. T., AND M. BROWN. 2002. Nocturnal heterothermy and torpor in the Malachite Sunbird (*Nectarinia famosa*). Auk 119:251–260.

EKMAN, J. B., AND M. K. HAKE. 1990. Monitoring starvation risk: adjustments of body reserves in Greenfinches (*Carduelis chloris* L.) during periods of unpredictable foraging success. Behavioral Ecology 1:62–67.

FALLS, J. B., AND J. G. KOPACHENA. 1994. White-throated Sparrow (*Zonotrichia albicollis*). *In* A. Poole and F. Gill [EDS.], The birds of North America, No. 167. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.

GEISER, F., J. C. HOLLOWAY, G. KORTNER, T. A. MADDOCKS, C. TURBILL, AND R. M. BRIGHAM. 2000. Do patterns of torpor differ between free-ranging and captive mammals and birds?, p. 95–102. *In* G. Heldmaier and M. Klingenspor [EDS.], Life in the cold: 11th International Hibernation Symposium. Springer, Berlin.

GEISER, F., AND T. RUF. 1995. Hibernation versus daily torpor in mammals and birds: physiological variables and classification of torpor patterns. Physiological Zoology 68:935–966.

GRAF, R., S. KRISHNA, AND F. HEPPNER. 1989. Regulated nocturnal hypothermia induced in pigeons by food deprivation. American Journal of Physiology 256:R733–R738.

KETTERSON, E. D., AND J. R. KING. 1977. Metabolic rate and behavioral responses to fasting in the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*). Physiological Zoology 50:115–129.

KÖRTNER, G., R. M. BRIGHAM, AND F. GEISER. 2000. Winter torpor in a large bird. Nature 407:318.

LOVEGROVE, B. G., AND G. A. SMITH. 2003. Is 'nocturnal hypothermia' a valid physiological concept in small birds?: a study on Bronze Mannikins *Spermestes cucullatus*. Ibis 145:547–557.

MEROLA-ZWARTJES, M. 1998. Metabolic rate, temperature regulation, and the energetic implications of roost sites in the Bananaquit (*Coereba flaveola*). Auk 115:780–786.

MCKECHNIE, A. E., AND B. G. LOVEGROVE. 2002. Avian facultative hypothermic responses: a review. Condor 104:705–724.

MCKECHNIE, A. E., AND B. G. LOVEGROVE. 2003. Facultative hypothermic responses in an Afrotropical arid-zone passerine, the Red-headed Finch (*Amadine erythrocephala*). Journal of Comparative Physiology B 173:339–346.

PIPER, W. H., AND R. H. WILEY. 1991. Effects of laparotomies on wintering White-throated Sparrows and the usefulness of wing chord as a criterion for sexing. Journal of Field Ornithology 62:40–45.

PRAVOSUDOV, V. V., T. C. GRUBB JR., P. F. DOHERTY JR., C. L. BRONSON, E. V. PRAVOSUDOVA, AND A. S. DOLBY. 1999. Social dominance and energy reserves in wintering woodland birds. Condor 101: 880–884.

PRINZINGER, R., A. PREßMAR, AND E. SCHLEUCHER. 1991. Body temperature in birds. Comparative Biochemistry and Physiology 99A:499–506.

REINERTSEN, R. E. 1996. Physiological and ecological aspects of hypothermia, p. 125–157. *In* C. Carey [ED.], Avian energetics and nutritional ecology. Chapman & Hall, New York.

REINERTSEN, R. E., AND S. HAFTORN. 1983. Nocturnal hypothermia and metabolism in the Willow Tit *Parus montanus* at 63°N. Journal of Comparative Physiology 156:655–663.

REINERTSEN, R. E., AND S. HAFTORN. 1986. Different metabolic strategies of northern birds for nocturnal survival. Journal of Comparative Physiology 156:655–663.

SPSS INC. 2003. SPSS for Windows, Release 11.0. SPSS Inc., Chicago.

WILLIS, C. K. R., AND R. M. BRIGHAM. 2003. Defining torpor in free-ranging bats: experimental evaluation of external temperature-sensitive radiotransmitters and the concept of active temperature. Journal of Comparative Physiology B 173:379–389.

The Condor 106:390–395

YOU CAN'T JUDGE A PIGMENT BY ITS COLOR: CAROTENOID AND MELANIN CONTENT OF YELLOW AND BROWN FEATHERS IN SWALLOWS, BLUEBIRDS, PENGUINS, AND DOMESTIC CHICKENS

KEVIN J. MCGRAW[1,8], KAZUMASA WAKAMATSU[2], SHOSUKE ITO[2], PAUL M. NOLAN[3], PIERRE JOUVENTIN[4], F. STEPHEN DOBSON[3], RICHARD E. AUSTIC[5], REBECCA J. SAFRAN[6], LYNN M. SIEFFERMAN[3], GEOFFREY E. HILL[3] AND ROBERT S. PARKER[7]

[1]*Department of Neurobiology and Behavior, Cornell University, Ithaca, NY 14853*
[2]*Fujita Health University, School of Health Sciences, Toyoake, Aichi 470-1192, Japan*
[3]*Department of Biological Sciences, Auburn University, 331 Funchess Hall, Auburn, AL 36849*
[4]*Centre d'Ecologie Fonctionnelle et Evolutive, Centre National de la Recherche Scientifique, 1919 Route de Mende, Montpellier, France*
[5]*Department of Animal Science, Cornell University, Ithaca, NY 14853*
[6]*Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY 14853*
[7]*Division of Nutritional Sciences, Cornell University, Ithaca, NY 14853*

Abstract. The two main pigment types in bird feathers are the red, orange, and yellow carotenoids and the black, gray, and brown melanins. Reports conflict, however, regarding the potential for melanins to produce yellow colors or for carotenoids to produce brown plumages. We used high-performance liquid chromatography to analyze carotenoids and melanins present in the yellow and brown feathers of five avian species: Eastern Bluebirds (*Sialia sialis*), Barn Swallows (*Hirundo rustica*), King Penguins (*Aptenodytes patagonicus*), Macaroni Penguins (*Eudyptes chrysolophus*), and neonatal chickens (*Gallus domesticus*). In none of these species did we detect carotenoid pigments in feathers. Although carotenoids are reportedly contained in the ventral plumage of European Barn Swallows (*Hirundo rustica rustica*), we instead found high concentrations of both eumelanins and phaeomelanins in North American Barn Swallows (*H. r. erythrogaster*). We believe we have detected a new form of plumage pigment that gives penguin and domestic-chick feathers their yellow appearance.

Key words: Aptenodytes patagonicus, *carotenoids,* Eudyptes chrysolophus, Gallus domesticus, Hirundo rustica, *melanins,* Sialia sialis.

No Puedes Juzgar un Pigmento por su Color: Contenido de Carotenoide y Melanina de Plumas Amarillas y Marrones en Golondrinas, Azulejos, Pingüinos y Gallinas Domésticas

Resumen. Los dos tipos principales de pigmentos que las aves incorporan en sus plumas son carotenoi-

---

Manuscript received 16 June 2003; accepted 19 January 2004.

[8] Present address: Dept. of Animal Science, University of California-Davis, One Shields Ave., Davis, CA 95616. E-mail: kjmcgraw@davis.edu

des, para desarrollar plumajes rojo, naranja o amarillo, y melaninas, para adquirir coloración negra, marrón, gris o tonalidades color tierra. Sin embargo, existe información conflictiva sobre la potencial coloración de plumas amarillas basadas en melanina y la presencia de caroteniodes en el plumaje marrón de ciertas especies. En este estudio, usamos cromatografía líquida de alto rendimiento para analizar los tipos y cantidades de carotenoides y melaninas presentes en las plumas amarillas y marrones de cinco especies de aves: el azulejo *Sialia sialis* y la golondrina *Hirundo rustica*, los pingüinos *Aptenodytes patagonicus* y *Eudyptes chrysolophus* y el plumón natal amarillo de la gallina doméstica *Gallus domesticus*. En ninguna de estas especies detectamos pigmentos carotenoides en las plumas. A pesar de que los carotenoides han sido encontrados en el plumaje ventral de la golondrina *Hirundo rustica rustica*, nosotros en cambio encontramos altas concentraciones de eumelaninas y feomelaninas en *H. r. erythrogaster* y en azulejos que variaron entre individuos y regiones de plumaje. Creemos que hemos detectado una nueva forma de pigmento de plumaje que le da a las plumas de pingüinos y pollos domésticos su apariencia amarilla.

Carotenoids and melanins are the two primary types of pigment incorporated into bird feathers (Fox 1976). Red, orange, and yellow plumage colors are typically the result of carotenoid pigments, whereas black, brown, gray, and earth-toned colors are created by the presence of melanins (Fox and Vevers 1960). Many classes of carotenoids exist, based on their molecular structure (e.g., carotenes, xanthophylls), and these may confer different colors on an animal (Goodwin 1984). In contrast, melanin pigments come in only two main forms, eumelanin and phaeomelanin, and the relative ratio of these two melanins can influence feather coloration (e.g., domestic pigeons [*Columba livia*]; Haase et al. 1992). Black and gray feathers are typically thought to contain predominantly eumelanins, whereas earth-toned feathers are dominated by phaeomelanins, much like red human hair (Fox and Vevers 1960).

Interestingly, some have attributed the yellow color of feathers in certain species to melanins. Völker (1934), for example, classified the yellow plumage pigmentation of domestic chicks (*Gallus domesticus*) as melanin based. Still others have reported that brown plumage, particularly in the Barn Swallow (*Hirundo rustica rustica*), contains a host of colorful carotenoid pigments (Stradi 1998, Camplani et al. 1999, Saino et al. 1999). These biochemical reports seem to contradict the normal appearance of the respective plumage colors, so we investigated both the carotenoid and melanin content of yellow and brown feathers from five avian species, including these two mentioned above. We sampled feathers from wild Eastern Bluebirds (*Sialia sialis*) and Barn Swallows from North America (*Hirundo rustica erythrogaster*), from wild King Penguins (*Aptenodytes patagonicus*) and Macaroni Penguins (*Eudyptes chrysolophus*) on the Crozet archipelago, and from domestic chicks. We used high-performance liquid chromatography (HPLC) to determine whether carotenoids, melanins, or both types of pigment were present in the colorful plumage of these species.

METHODS

SPECIES DESCRIPTIONS AND FEATHER COLLECTION

Barn Swallows. The ventral plumage of North American Barn Swallows is rufous or chestnut colored (Brown and Brown 1999). This trait honestly signals mate quality in both males and females and varies most among individuals in the color of specific body regions (e.g., throat, breast, belly, vent; Safran and McGraw 2004). As part of an ongoing study of Barn Swallows in Tompkins County, New York (42°27′N, 76°29′W), RJS collected up to 10 pigmented ventral feathers from three males and three females in March and April 2001. Feathers were stored attached to index cards in the dark at room temperature and analyzed for carotenoids in October 2001 and melanins in December 2001 and January 2002. Carotenoid analyses were performed on a group of five feathers from each bird; the remaining feathers from each body region were pooled for all birds to understand the variation in eumelanin and phaeomelanin pigmentation across the colored plumage areas.

Eastern Bluebirds. Eastern Bluebirds display orange-red plumage on the breast (Gowaty and Plissner 1998) and exhibit marked within- and between-sex variation in the size of this feather patch (Siefferman and Hill 2004). We characterized the pigment composition from a standardized location on the breast patch (the center). As part of a study of bluebirds in Lee County, Alabama (32°36′N, 85°30′W), LMS collected three pigmented breast feathers from six males and six females in March 2002. These feathers were stored in envelopes in the dark at room temperature and analyzed for the presence of carotenoids (in three males and three females) and melanins (the remaining three of each sex) in April and May 2002.

King and Macaroni Penguins. King Penguins have flashy auricular and chest patches of yellow-orange feathers (Jouventin 1982). Macaroni penguins develop yellow-orange filamentous forehead plumes (Warham 1975, Jouventin 1982). As part of a study of penguins on Possession Island, Crozet Archipelago in the Indian Ocean (46°27′S, 51°51′E), PMN and FSD collected ca. 100 breast and auricular feathers from three King Penguins and single feather plumes from two Macaroni Penguins (all of unknown sex) in November–December 2001. These feathers were folded within index cards and stored in sealed plastic packets at 22°C until pigment analysis in March–May 2002. We separately analyzed ca. 10 breast and 10 auricular feathers from all King Penguins and halves of each Macaroni Penguin forehead plume for carotenoids and melanins.

Domestic chicks. Yellow downy feathers were collected from two 1-day-old single-comb white leghorn domestic chicks (Cornell K-strain; one in February 2002 and one in May 2002). All feathers were stored in the dark in a plastic bag. In March 2002 and again June 2002, ca. 10 feathers from each bird were analyzed for both carotenoids and melanins.

CAROTENOID EXTRACTION AND CHROMATOGRAPHY

All carotenoid analyses were conducted in the laboratory of RSP. We used both thermochemical (Hudon and Brush 1992) and mechanical (Stradi et al. 1995) extraction techniques to isolate carotenoid pigments from bird feathers. Prior to both procedures, feathers from all species were washed separately in ethanol and hexane for 30 min each and blotted dry. We trimmed 3–5 mg of pigmented barbules and split them into equal portions for the two extractions. For the thermochemical method, we placed the colored barbules in 1 mL acidified pyridine (3 drops HCl in 50 mL pyridine) and held them at 95°C under argon for 4 hr. The solution was then cooled to room temperature, and we twice extracted the lipids with 1 mL distilled water and 5 mL hexane:*tert*-butyl methyl ether (1:1, v/v). We centrifuged the mixture for 5 min at 3000 rpm, removed the supernatant, and evaporated the solvent to dryness under a stream of nitrogen. For the mechanical extraction, we ground the trimmed barbules for 15 min at 30 Hz in a Retsch® MM200 mixer mill (Retsch Inc., Irvine, California) using a zirconia grinding jar and balls (fitted with a Teflon® O-ring) and in the presence of 3 mL methanol. Again, the solution was centrifuged for 5 min at 3000 RPM and the supernatant removed and evaporated under nitrogen. For both extraction procedures, we ran a positive control (yellow, carotenoid-pigmented contour feathers from American Goldfinches [*Carduelis tristis*]; McGraw et al. 2001, McGraw, Hill, et al. 2002) along with our samples.

For HPLC analysis, the purified extracts were redissolved in 200 μL HPLC mobile phase (acetonitrile:methanol:chloroform, 46:46:8, v/v/v) and 50 μL was injected into a Waters™ 717plus Autosampler HPLC (Millipore Corp., Bedford, Massachusetts) fitted with a Develosil RPAqueous RP-30 column (250 × 4.6 mm ID; Nomura Chemical Co. Ltd., Aichi, Japan) and an Eppendorf TC-50 column heater (Hamburg, Germany) set at 32°C (McGraw, Adkins-Regan, and Parker 2002). We used an isocratic system (Hewlett-Packard 1050 Series Isocratic Pump) at a constant flow rate of 1.2 mL min^{-1} for 90 min to allow sufficient time for both xanthophylls and carotenes to elute. Data were collected from 250–600 nm using a Waters™ 996 photodiode array detector (Waters Chromatography, Milford, Massachusetts). The minimum detection limit of this instrument is 0.0001 absorbance units, which amounts to approximately 0.005 mg of carotenoid per gram of pigmented feather portion using this protocol.

MELANIN EXTRACTION AND CHROMATOGRAPHY

All melanin procedures were performed in the laboratory of SI and KW. Methods of analyzing both phaeomelanins and eumelanins in bird feathers follow those in Haase et al. (1992). To determine eumelanin content, colored feather barbules were homogenized in water (1:100, w/v) and 400 μL of the homogenate were added to 800 μL 1 M H_2SO_4, oxidized with 3% $KMnO_4$. The resulting oxidation product (pyrrole-2,3,5-tricarboxylic acid; PTCA) was analyzed via HPLC (Ito and Fujita 1985, Ito and Wakamatsu 1994). Phaeomelanins were examined by hydrolyzing 200 μL feather homogenate with 500 μL 57% hydriodic acid at 130°C in the presence of H_3PO_2 for 24 hr, and subsequently analyzing the product (4-amino-3-hydroxyphenylalanine; 4-AHP) using HPLC with electrochemical detection (Wakamatsu et al. 2002). Amounts of eumelanin and phaeomelanin were obtained by multiplying the amount of PTCA and 4-AHP by conversion factors of 50 and 9, respectively (Ito and Fujita 1985, Wakamatsu and Ito 2002). Analyses of all samples were performed in duplicate, and we report averages of these values here.

RESULTS

In none of the feathers from the five species studied did we detect carotenoid pigments. Lipid-soluble extracts were colorless; brown and yellow feathers retained their respective hues. In contrast, our feather standards from American Goldfinches yielded 0.2–6 mg carotenoid per g of feather (McGraw, Hill, et al. 2002).

In the chestnut ventral feathers from both Eastern Bluebirds and Barn Swallows, we found substantial amounts of both eumelanin and phaeomelanin (Table 1). Eumelanin concentrations were higher than phaeomelanin in all bluebird and swallow samples except one: Barn Swallow throat feathers. Throat feathers in Barn Swallows also contained the highest concentration of pigments among the four plumage regions we sampled in this species. In our bluebird samples, male feathers tended to contain more pigments overall, and a higher percentage of eumelanin pigments, than those of females (Table 1).

In the breast and auricular feathers of King Penguins, we also detected a small amount of melanin, primarily eumelanin (Table 1). However, there remained much yellow pigment in the feather that could not be accounted for by either carotenoids or melanins. Yellow plumes from Macaroni Penguins similarly contained very low levels of melanin (Table 1) and remained brilliant yellow after pigment analyses. The same was true for the yellow natal down of domestic chicks, as we were unable to detect any appreciable amounts of melanins or carotenoids in these feathers (Table 1).

DISCUSSION

The aim of this study was to analyze the extent to which carotenoid and melanin pigments determine yellow and brown feather coloration in a diverse group of bird species. Although carotenoids and melanins are not the only two forms of yellow or brown pigments in animals (Needham 1974, Brush 1978), several recent behavioral-ecology studies in birds have assumed that yellow integumentary features (e.g., feathers, beaks) are carotenoid based (e.g., Irwin 1994, Massaro et al. 2003), and that certain rust-colored plumage colors contain a high concentration of carotenoid pigments (e.g., Møller and Mousseau 2001).

We first characterized the plumage pigments contained within the chestnut ventral feathers of male and female Barn Swallows and Eastern Bluebirds from North America. We found no carotenoid pigments in the colorful throat, breast, belly, or vent feathers of North American swallows or in the breast feathers of bluebirds. This was a surprising result, as it is reported in the literature that the chestnut-colored facial and throat plumage in the European subspecies of Barn Swallows (*H. r. rustica*) contains carotenoid pigments (e.g., Stradi 1998, Camplani et al. 1999, Saino et al. 1999). Stradi (1998) first published a complete HPLC chromatogram profiling the suite of hydroxy- and keto-carotenoid pigments that are found in the rust-colored

TABLE 1. Mean eumelanin and phaeomelanin concentrations (mg pigment per g pigmented feather barbule) in yellow and brown feathers from swallows, bluebirds, penguins, and domestic chicks. Blank entries indicate that pigment concentrations were below our detection limit (0.01 mg g^{-1}).

Species (Plumage color)	Bird ID	Sex	Body region	Eumelanin	Phaeomelanin
Barn Swallow[a]	pooled	pooled	throat	3.2	6.6
(chestnut or rufous)	pooled	pooled	breast	1.0	0.5
	pooled	pooled	belly	0.7	0.4
	pooled	pooled	vent	1.3	1.0
Eastern Bluebird	1	male	breast	4.5	2.8
(orange-red)	2	male	breast	4.6	2.0
	3	male	breast	4.4	2.9
	4	female	breast	2.8	0.9
	5	female	breast	3.0	0.7
King Penguin	1	unknown	breast	0.4	0.04
(yellow-orange)	1	unknown	auricular	0.4	0.04
	2	unknown	breast	0.2	0.02
	2	unknown	auricular	0.2	0.02
	3	unknown	breast	0.4	0.02
	3	unknown	auricular	0.7	0.05
Macaroni Penguin	1	unknown	head plume		0.16
(yellow-orange)	2	unknown	head plume	0.3	0.2
Domestic chicken	1	unknown	natal down		
(yellow)	2	unknown	natal down	0.06	

[a] North American subspecies. Ventral feathers were pooled from 3 males and 3 females and analyzed by body region.

throat feathers of European *H. rustica*. Saino et al. (1999) later asserted, however, that this reddish color ‘‘is mainly caused by melanin, although small amounts of lutein have also been found in these feathers (R. Stradi, unpubl. data)’’ (p. 442).

In fact, we isolated a high concentration of melanin pigments in the chestnut ventral plumage of male and female Barn Swallows and Eastern Bluebirds from North America. Both phaeomelanins and eumelanins were present, and this is typical of brown feathers in other species (e.g., pigeons, ducks; Haase et al. 1992, 1995). Compared to swallows, bluebirds exhibited a richer chestnut hue in the ventral plumage we examined, and these feathers contained a higher overall concentration of melanins. Among the body regions we studied in Barn Swallows, the throat feathers yielded the highest concentration of melanins, and this is invariably the most deeply colored ventral region of plumage in both sexes (Safran and McGraw 2004). Eumelanins are typically darker than phaeomelanins (Ito and Fujita 1985), however, and yet the dark throat plumage in Barn Swallows also yielded the highest percentage of phaeomelanins compared to other feather regions.

Ventral plumage color is a sexually selected trait in North American Barn Swallows (Safran and McGraw 2004) and in Eastern Bluebirds (Siefferman and Hill 2004), with the most colorful birds breeding earliest and producing the most offspring in a year. To reinforce the honesty of these mating signals, there may be physiological costs to producing brightly colored plumage. Animals synthesize melanins from nutritionally dispensable amino acids (e.g., tyrosine; Meister 1965), but phaeomelanin and eumelanin biosynthesis follow markedly different biochemical pathways (Land and Riley 2000) that appear to be differentially sensitive to levels of circulating sex steroids in certain species (Haase et al. 1995). In Mallard drakes (*Anas platyrhynchos*), for example, androgen treatment stimulates phaeomelanogenesis, but not eumelanogenesis, in feather tracts and results in more phaeomelanic head plumage and undertail coverts (Haase et al. 1995). Thus, there may be important and fine-tuned enzymatic and hormonal control over the production and deposition of these two forms of melanin pigments in feathers, so that birds may manufacture optimal levels of phaeomelanins and eumelanins to express bright plumage coloration. There may be sex-related differences in phaeomelanin or eumelanin biosynthesis as well, as suggested by the fact that male bluebird feathers in this study had higher melanin levels, and a higher relative amount of phaeomelanins, than those of females.

Next, we investigated the biochemical nature of yellow feathers in two sub-Antarctic penguin species and from domestic chicks. Again, despite the widespread view that yellow plumage is derived from carotenoids in birds (e.g., in finches, sparrows, woodpeckers; Fox 1976, Stradi 1998), we found that yellow feathers in penguins and domestic chicks lacked carotenoids entirely. We also investigated the possibility that these yellow plumage colors could be attributed to the presence of melanins, as there is evidence in mammals that yellow fur contains melanins (primarily phaeomelanin; Cone et al. 1996, Miltenberger et al. 1999) and as some have speculated about the melanic nature of yellow chick feathers (Völker 1934). In King Penguin feathers, we indeed found small amounts of melanin pigments. These were primarily eumelanins, but occurred nearly one order of magnitude less in concentration than in the brown feathers described above for bluebirds and swallows. Pigmented plumage regions in King Penguins have been occasionally described as orange (Jouventin 1982), and in the hand individual feathers appear yellow at the base but tipped with small amounts of brown. This small amount of melanin is presumably what gives King Penguin feathers their brown edges.

In contrast to King Penguin plumage, only trace amounts of melanin were quantified from yellow Macaroni Penguin and domestic chick feathers. However, like King Penguin feathers, a substantial amount of yellow pigment remained after analysis that could not be classified as either melanin or carotenoid. At present, the only other yellow pigments that have been described from bird feathers are the psittacofulvins found in the plumage of parrots (Stradi 1998) and pterin pigments in the yellow, orange, and red irises of blackbirds, starlings, owls, and pigeons (e.g., Oehme 1969, Oliphant 1988, Oliphant et al. 1992, Oliphant and Hudon 1993, Hudon and Muir 1996). We have gathered preliminary biochemical evidence that these yellow penguin and chick pigments are soluble in mild acids and bases and fluoresce strongly under UV light, characteristics that typify pterins (Needham 1974). This suggests that penguins and domestic chicks color themselves with a class of pigments never before described from bird feathers.

We thank F. Bath and Retsch Inc. for loaning the mixer mill that was used to grind feathers, four anonymous referees for helpful comments on the manuscript, and the American Museum of Natural History, Sigma Xi, the Environmental Protection Agency (grants to KJM), the National Science Foundation (IBN 97122971 to GEH and OPP0128913 to PMN and FSD), and the Ministry of Education, Science, Sports and Culture of Japan (Grant # 14570829 to KW and SI) for funding this research.

LITERATURE CITED

BROWN, C. R., AND M. B. BROWN. 1999. Barn Swallow (*Hirundo rustica*). *In* A. Poole and F. Gill [EDS.], The birds of North America, No. 452. The Birds of North America, Inc., Philadelphia, PA.

BRUSH, A. H. 1978. Avian pigmentation, p. 141–161. *In* A. H. Brush [ED.], Chemical zoology. Vol. X. Academic Press, New York.

CAMPLANI, A., N. SAINO, AND A. P. MØLLER. 1999. Carotenoids, sexual signals and immune function in Barn Swallows from Chernobyl. Proceedings of the Royal Society of London Series B 266:1111–1117.

CONE, R. D., D. S. LU, S. KOPPULA, D. I. VAGE, H. KLUNGLAND, B. BOSTON, W. B. CHEN, D. N. ORTH, C. POUTON, AND R. A. KESTERSON. 1996. The melanocortin receptors: agonists, antagonists, and the hormonal control of pigmentation. Recent Progress in Hormone Research 51:287–318.

FOX, D. L. 1976. Animal biochromes and structural colors. University of California Press, Berkeley, CA.

FOX, H. M., AND G. VEVERS. 1960. The nature of animal colours. Sidwick and Jackson Limited, London.

GOODWIN, T. W. 1984. The biochemistry of the carotenoids. Vol. II. Animals. Chapman and Hall, London.

GOWATY, P. A., AND J. H. PLISSNER. 1998. Eastern Bluebird (*Sialia sialis*). *In* A. Poole and F. Gill [EDS.], The birds of North America, No. 381. The Birds of North America, Inc., Philadelphia, PA.

HAASE, E., S. ITO, A. SELL, AND K. WAKAMATSU. 1992. Melanin concentrations in feathers from wild and domestic pigeons. Journal of Heredity 83:64–67.

HAASE, E., S. ITO, AND K. WAKAMATSU. 1995. Influences of sex, castration, and androgens on the eumelanin and phaeomelanin contents of different feathers in wild Mallards. Pigment Cell Research 8:164–170.

HUDON, J., AND A. H. BRUSH. 1992. Identification of carotenoid pigments in birds. Methods in Enzymology 213:312–321.

HUDON, J., AND A. D. MUIR. 1996. Characterization of the reflective materials and organelles in the bright irides of North American blackbirds (Icterinae). Pigment Cell Research 9:96–104.

IRWIN, R. 1994. The evolution of plumage dichromatism in the New World blackbirds: social selection on female brightness. American Naturalist 144: 890–907.

ITO, S., AND K. FUJITA. 1985. Microanalysis of eumelanin and phaeomelanin in hair and melanomas by chemical degradation and liquid chromatography. Analytical Biochemistry 144:527–536.

ITO, S., AND K. WAKAMATSU. 1994. An improved modification of permanganate oxidation that gives constant yield of pyrrole-2,3,5-tricarboxylic acid. Pigment Cell Research 7:141–144.

JOUVENTIN, P. 1982. Visual and vocal signals in penguins: their evolution and adaptive characters. P. Parey, Berlin.

LAND, E. J., AND P. A. RILEY. 2000. Spontaneous redox reactions of dopaquinone and the balance between the eumelanic and phaeomelanic pathways. Pigment Cell Research 13:273–277.

MASSARO, M., L. S. DAVIS, AND J. T. DARBY. 2003. Carotenoid-derived ornaments reflect parental quality in male and female Yellow-eyed Penguins (*Megadyptes antipodes*). Behavioral Ecology and Sociobiology 55:169–175.

MCGRAW, K. J., E. ADKINS-REGAN, AND R. S. PARKER. 2002. Anhydrolutein in the Zebra Finch: a new, metabolically derived carotenoid in birds. Comparative Biochemistry and Physiology B 132:811–818.

MCGRAW, K. J., G. E. HILL, R. STRADI, AND R. S. PARKER. 2001. The influence of carotenoid acquisition and utilization on the maintenance of species-typical plumage pigmentation in male American Goldfinches (*Carduelis tristis*) and Northern Cardinals (*Cardinalis cardinalis*). Physiological and Biochemical Zoology 74:843–852.

MCGRAW, K. J., G. E. HILL, R. STRADI, AND R. S. PARKER. 2002. The effect of dietary carotenoid access on sexual dichromatism and plumage pigment composition in the American Goldfinch. Comparative Biochemistry and Physiology B 131: 261–269.

MEISTER, A. 1965. Biochemistry of the amino acids. 2nd ed. Academic Press, New York.

MILTENBERGER, R. J., R. L. MYNATT, B. D. BRUCE, W. O. WILKISON, R. P. WOYCHIK, AND E. J. MICHAUD. 1999. An agouti mutation lacking the basic domain induces yellow pigmentation but not obesity in transgenic mice. Proceedings of the National Academy of Sciences 96:8579–8584.

MØLLER, A. P., AND T. A. MOUSSEAU. 2001. Albinism and phenotype of Barn Swallows (*Hirundo rustica*) from Chernobyl. Evolution 55:2097–2104.

NEEDHAM, A. E. 1974. The significance of zoochromes. Springer-Verlag, New York.

OEHME, H. 1969. Vergleichende untersuchungen uber die farbung der vogeliris. Biologisches Zentralblatt 88:3–35.

OLIPHANT, L. W. 1988. Cytology and pigments of non-melanophore chromatophores in the avian iris, p. 65–82. *In* J. T. Bagnara [ED.], Advances in pigment cell research. Liss, New York.

OLIPHANT, L. W., AND J. HUDON. 1993. Pteridines as reflecting pigments and components of reflecting organelles in vertebrates. Pigment Cell Research 6:205–208.

OLIPHANT, L. W., J. HUDON, AND J. T. BAGNARA. 1992. Pigment cell refugia in homeotherms—the unique evolutionary position of the iris. Pigment Cell Research 5:367–371.

SAFRAN, R. J., AND K. J. MCGRAW. 2004. Plumage coloration, not length or symmetry of tail-streamers, is a sexually selected trait in North American Barn Swallows. Behavioral Ecology, in press.

SAINO, N., R. STRADI, P. NINNI, E. PINI, AND A. P. MØLLER. 1999. Carotenoid plasma concentration, immune profile, and plumage ornamentation of male Barn Swallows (*Hirundo rustica*). American Naturalist 154:441–448.

SIEFFERMAN, L. M., AND G. E. HILL. 2004. Structural and phaeomelanin colors indicate male quality in the Eastern Bluebird (*Sialia sialis*). Behavioral Ecology 14:855–861.

STRADI, R. 1998. The colour of flight. Solei Gruppo Editoriale Informatico, Milan, Italy.

STRADI, R., G. CELENTANO, AND D. NAVA. 1995. Separation and identification of carotenoids in bird's plumage by high-performance liquid chromatography—diode-array detection. Journal of Chromatography B 670:337–348.

VÖLKER, O. 1934. Die Abhangigkeit der Lipochrombildung bei Vögeln von Pflanzlichen Carotinoiden. Journal für Ornithologie 82:439–450.

WAKAMATSU, K., AND S. ITO. 2002. Advanced chemical methods in melanin determination. Pigment Cell Research 15:174–183.

WAKAMATSU, K., S. ITO, AND J. L. REES. 2002. The usefulness of 4-amino-3-hydroxyphenylalanine as a specific marker of phaeomelanin. Pigment Cell Research 15:225–232.

WARHAM, J. 1975. The crested penguins, p. 189–269. *In* B. Stonehouse [ED.], Biology of the penguins. University Park Press, Baltimore, MD.

The Condor 106:395–400

CAN LANCHESTER'S LAWS HELP EXPLAIN INTERSPECIFIC DOMINANCE IN BIRDS?

ERIN L. SHELLEY, MAILE Y. U. TANAKA, ANNA R. RATNATHICAM AND DANIEL T. BLUMSTEIN[1]
Department of Organismic Biology, Ecology, and Evolution, University of California, 621 Young Drive South, Los Angeles, CA 90095-1606

Abstract. We studied the applicability of Lanchester's laws of combat to explain interspecific dominance in birds. We focused on 10 species of Australian birds in the arid zone of New South Wales that foraged at an established locust trap. Consistent with the ''linear law,'' larger species usually dominated smaller species in one-on-one encounters. We found no support for the ''N-square law,'' which predicted that large numbers of smaller species could dominate larger species when more abundant. Further analysis of the most abundant species revealed that it was less likely to visit the locust trap when larger, more dominant heterospecifics were present. Body size, and not numerical superiority, seems to be an important determinant in interspecific foraging decisions in birds.

Key words: body size, foraging behavior, group size, interspecific competition, Lanchester's laws.

¿Puede la Ley de Lanchester Ayudar a Explicar la Dominancia Interespecífica en Aves?

Resumen. Hemos estudiado la aplicabilidad de las leyes del combate de Lanchester en explicar la domi-

---

Manuscript received 31 July 2003; accepted 8 January 2004.

[1] Corresponding author: E-mail: marmots@ucla.edu

nancia interespecífica en aves. Hemos focalizado este estudio en 10 especies de aves australianas de la zona árida de New South Wales, las cuales se alimentaron en trampas de insectos establecidas para tal fin. Consistente con la ‘‘ley lineal,’’ las especies de mayor tamaño usualmente dominaron a las especies más pequeñas en los encuentros uno a uno. No encontramos evidencia que apoye la ‘‘ley cuadrática,’’ la cual predice que un gran número de especies de pequeño tamaño podrían dominar a especies de tamaño mayor cuando las primeras son más abundantes. Posteriores análisis sobre la especie más abundantes revelaron que la probabilidad de visita a las trampas de insectos es menor cuando individuos heteroespecíficos más grandes y más dominantes están presentes. El tamaño corporal, y no la superioridad numérica, parece ser un importante factor en las decisiones de forrajeo en las aves.

Competition for resources within multispecies systems leads to the establishment of dominance hierarchies in which certain species outcompete others (Wallace and Temple 1987, Travaini et al. 1998, Sandlin 2000). In some cases, body size is the primary factor that determines interspecific rank (Kohda 1991, Daily and Ehrlich 1994, Bassett 1995, McGlynn 2000). However, in other instances, the relative number of individuals, independent of body size or behavior, may affect interspecific dominance (Basset 1997, Burger and Gochfeld 1984, Creel 2001, Chapman and Kramer 1996, McGlynn 2000).

The study of human warfare has led to the development of many different military strategies. In 1916, F. W. Lanchester published his theory of combat, which included two mathematical models which have become known as the ‘‘linear law’’ and the ‘‘N-square law’’ (Lanchester 1916). The linear law predicts that in one-on-one combat, the stronger (i.e., larger) individual will win. The N-square law predicts that larger-numbered groups can overcome smaller-numbered groups, with differences in individual body size being of little or no importance. Aside from military applications, small businesses have used Lanchester's strategies to take over markets dominated by larger business (e.g., Yano 1995), a scenario which is at least superficially much like animals competing for access to a limited resource. Recently, biologists have begun to test the applicability of these laws to a variety of animal species engaged in mortal combat. In 1993, Franks and Partridge were the first to show that Lanchester's models could explain the outcome of interactions among slave-making and army ants. Additional studies of interspecific competition among ants (McGlynn 1999, 2000) provide further support for the linear and N-square laws. Intraspecific interactions among ants (Whitehouse and Jaffe 1996), as well as between chimpanzee groups (Wilson et al. 2002), also follow the predictions Lanchester set forth. In these studies, larger individuals dominated smaller individuals in one-on-one lethal combat (Lanchester's linear law), and greater numbers of individuals dominated fewer numbers regardless of individual body size (Lanchester's N-square law).

We observed the behavior of birds foraging for insects at a locust trap in the arid zone of southeastern Australia. We studied interspecific interactions to determine the effect of (1) species type, (2) body size, and (3) abundance on interspecific dominance rank. In doing so, we evaluated Lanchester's law's ability to explain nonfatal aggression and dominance in this assemblage. Although the interactions between these species are not immediately lethal, the ephemeral and patchy nature of resources in the arid zone increase the importance of locating and obtaining food. Should interspecific interactions interfere with an individual's ability to obtain food, we can envision a large fitness cost.

METHODS

We observed birds foraging at an insect light trap set up by the Australian Plague Locust Commission for monitoring and researching plague locusts on the Fowler's Gap, New South Wales sheep station (31°5′S, 142°42′E). This locust trap, though technically an artificial food source for birds in the area, was in operation from 1976–1988, and 1994 to present. The trap consisted of a 3.0-m-diameter circular metal tub positioned 0.6 m above the ground and filled with 0.15 m of water. Trees and brush were present nearby. We positioned ourselves on a platform 22.3 m from the locust trap. Directly above the center of the tub, a bright light was turned on nightly. Insects, most commonly moths (Order Lepidoptera), were drawn to and disoriented by the light, whereupon they fell into the water and collected on the surface. Additionally, a large number of water insects such as water-boatmen and backswimmers (Hemiptera) and diving beetles (Coleoptera) inhabited the trap. Although the relative abundance of insects in the trap seemed to vary each morning, a variety of insects were present each day. All observed bird species foraged on these insects on multiple occasions, although not all were exclusively insectivorous (e.g., honeyeaters).

During 53 hr of morning observations between 21 April and 3 May 2001, we continuously recorded every dominant–subordinate interspecific interaction that occurred at the locust trap as a win or a loss. At the time of the interaction, the recorder noted the species of the winner and loser, the time of the interaction, and the number of other individuals of each species present at the trap. Presence was predefined as being perched atop or inside the main tub of the trap or the light canister, flying in the immediate airspace, (within 0.3 vertical m of the surface of the trap), or sitting atop a small post connected to one edge of the tub. Dominant-subordinate interactions consisted of pecking at, chasing, supplanting, or any other interactions in which the subordinate individual of one species moved away as a direct result of the dominant individual of a different species' actions. We took care to avoid recording what appeared to be coincidental, simultaneous departures from the locust trap, as well as departures that were potentially attributable to external disturbances.

In order to ascertain which species were likely to interact, and to calculate the overall rate of species visitation, we also took an instantaneous census of the

TABLE 1. Body size and mass hierarchy for insectivorous birds foraging at a locust trap in New South Wales, Australia. Body sizes are midpoints of ranges reported in Pizzey and Knight (2001). Average body masses are from Geffen and Yom-Tov (2000), except for Yellow-throated Miner and White-plumed Honeyeater (Higgins et al. 2001), Spiny-cheeked Honeyeater (Casotti and Richardson 1992), and Singing Honeyeater (Wooler et al. 1985).

Species	Body size (cm)	Body mass (g)
Australian Raven (*Corvus coronoides*)	50.0	674.5
Australian Magpie (*Gymnorhina tibicen*)	41.0	322.8
Apostlebird (*Struthidea cinerea*)	31.0	130.0
Magpie-lark (*Grallina cyanoleuca*)	28.0	80.0
Yellow-throated Miner (*Manorina flavigula*)	26.3	55.0
Spiny-cheeked Honeyeater (*Acanthagenys rufogularis*)	24.0	44.0
Willie Wagtail (*Rhypidura leucophrys*)	20.5	19.0
Restless Flycatcher (*Myiagra inquieta*)	18.5	15.0
Singing Honeyeater (*Lichenostomus virescens*)	20.0	19.0
White-plumed Honeyeater (*Lichenostomus penicillatus*)	16.0	18.5

number of each species present at the trap every 2 min. From the preliminary observations, we determined that a 2-min interval gave the most reasonable overview of the dynamics of bird visitation to the trap. In addition, at the beginning of every hour, the current weather conditions and temperature were recorded.

We standardized the census data by dividing the 6-hr observation window into three 2-hr periods (06:00–08:00, 08:01–10:00, 10:01–12:00) based upon natural divisions in a plot of species abundance over time. Then, for these three time intervals, we divided the number of birds of each species by the total number of observation points to obtain the rate of visitation of each species for each interval. From this, we were able to see what species were rarely or never present at the same time, exclude them, and develop a subhierarchy for each period. Ten avian species (Table 1; scientific names therein) visited the trap during our period of observation and were used for our statistical analyses. These 10 species were all observed foraging on dead insects in the trap on multiple occasions. We removed a single interaction where a Restless Flycatcher very aggressively mobbed an Australian Raven because mobbing is not a typical foraging behavior.

STATISICAL ANALYSES

To test the applicability of Lanchester's linear law to this group of birds, we compared whether the dominance patterns exhibited at the food source matched the size hierarchy we created by comparing body size (cm) and mass (g) of the species. To quantify dominance at the trap, we input the win-loss data into the program Peck Order (Hailman 1994) to create an overall hierarchy spanning the entire observation period. To determine whether body size explained significant variation in dominance ranking, we calculated Spearman rank correlations of rank versus the midpoint of the body length and rank versus average mass. Throughout, we interpret $P < 0.05$ as significant.

We calculated subhierarchies during each of the three census periods and excluded uncommon species until we obtained a linear hierarchy (Landau's $h = 1.0$; Lehner 1996). For period 1, we first excluded Singing Honeyeater because they were never present during that period, and then excluded Australian Ravens, Spiny-cheeked Honeyeaters, and White-plumed Honeyeaters because certain dyadic encounters with these species did not occur. To create a linear hierarchy in period 2, we excluded Australian Ravens because they were not present during that period, and then Spiny-cheeked Honeyeaters, Singing Honeyeaters, and White-plumed Honeyeaters. To create a linear hierarchy in Period 3, we excluded Australian Ravens because they were never present, and then Spiny-cheeked Honeyeaters, Yellow-throated Miners, Apostlebirds, and Australian Magpies.

In addition, because Willie Wagtails were present more often than any other species and were also present throughout the entire observational period, we were able to use a contingency table analysis to determine whether the time Willie Wagtails spent at the feeder was influenced by the presence or absence of other birds.

To test the applicability of Lanchester's N-square law, we determined whether the presence or number of potential competitors influenced the outcome of an encounter. We fitted logistic regressions using StatView 5.1 (SAS Institute 1999) to estimate the variation explained by group size on the likelihood that an individual of a species would win or lose an interaction with another species. Species-pairs were selected based on the number of observations.

RESULTS

LINEAR LAW

Our overall hierarchy, compiled from the win-loss data for the 10 species feeding on the locust trap, was not strictly linear (Table 2). Although not all of the 10 species had the same likelihood of being seen at the same times at the trap, causing certain dyadic encounters to be either missing or tied in our data set, the overall best-fit dominance hierarchy followed the body-size hierarchy (Table 1).

When we focused on birds regularly present at the same time, dominance rank was positively correlated with body size. For both period 1 and period 2, the hierarchy was, from most dominant to most subordi-

TABLE 2. Interspecific dominance matrix for 10 bird species foraging at a locust trap in New South Wales, Australia. Species are arranged by body size. Winners are listed down the left column; losers are listed across the upper row. Values within the matrix represent the number of occurrences of each win-loss dyad. Not all possible dyadic interactions occurred; the matrix reflects the best-fit hierarchy.

	Losers									
Winners	Aust. Raven	Aust. Magpie	Apostle-bird	Magpie-lark	Y-thrtd. Miner	Sp-ch. Honey-eater	Willie Wagtail	Fly-catcher	Singing Honey-eater	Wh-pl. Honey-eater
Australian Raven	—	6	7	2	0	0	0	0	0	0
Australian Magpie	0	—	28	18	15	1	12	4	0	0
Apostlebird	0	1	—	22	11	0	24	5	0	0
Magpie-lark	0	0	8	—	11	6	45	27	1	6
Yellow-throated Miner	0	0	0	0	—	1	5	1	0	0
Spiny-cheeked Honeyeater	0	0	0	0	0	—	4	1	0	1
Willie Wagtail	0	0	1	0	1	0	—	5	8	2
Restless Flycatcher	0	0	0	1	0	0	4	—	3	5
Singing Honeyeater	0	0	0	0	0	0	3	0	—	7
White-plumed Honeyeater	0	0	0	0	0	0	1	0	3	—

nate, Australian Magpies, Apostlebirds, Magpie-larks, Yellow-throated Miners, Willie Wagtails, Restless Flycatchers (Table 3). For period 3, the hierarchy was Magpie-larks, Willie Wagtails, Restless Flycatchers, Singing Honeyeaters (Table 4). All three of these hierarchies were linear with a Landau's $h = 1$. The midpoints of species body length ($r_s = 0.99$, $P < 0.001$) and average body mass ($r_s = 0.95$, $P < 0.001$) were both highly correlated with rank.

The presence of Willie Wagtails was significantly affected by the presence or absence of other species at the locust trap ($\chi^2_1 = 6.1$, $P = 0.01$). Out of 1733 censuses, Willie Wagtails were present during 220. Of these, Willie Wagtails were present at 154 censuses when other species dominant to Willie Wagtails were absent, but were present at only 66 censuses when other species dominant to Willie Wagtails were present. Of the 1513 censuses at which Willie Wagtails were absent, there were 1173 censuses where species dominant to Willie Wagtails were absent as well and 340 censuses where species dominant to Willie Wagtails were present. Willie Wagtails were more likely to be present at the locust trap in the absence of other more dominant birds.

N-SQUARE LAW

Of the 10 logistic regressions, only the Apostlebirds versus all others visiting the feeder showed any significant association between group size and dominance ($P < 0.001$, Table 5). This relationship was, however, negative: as Apostlebird numbers increased, their likelihood of dominating other species decreased.

DISCUSSION

Body size in this particular group of Australian insectivorous birds was positively correlated with the interspecific dominance relationships we observed at Fowler's Gap. The species that dominated more often were those that had a larger overall body size. This supports Lanchester's linear law in that larger species will dominate smaller species in one-on-one interactions.

Further support for the linear law is seen in our analysis of how the presence or absence of Willie Wagtails was influenced by other species. Willie Wagtails were significantly less likely to be at the locust trap when an individual of a larger, more dominant species was present. This suggests that the different bird species might have used the presence and size of other species

TABLE 3. The unique linear hierarchy of species foraging at a locust trap in New South Wales, Australia, during periods 1 (06:00–08:00) and 2 (08:01–10:00). Species are arranged by body size. The species compositions and dominance rankings were the same for these two periods; therefore we combined these numbers into a single matrix. Landau's $h = 1$.

	Losers					
Winners	Magpie	Apostlebird	Magpie-lark	Y-thrtd. Miner	Willie Wagtail	Flycatcher
Australian Magpie	—	28	18	15	12	4
Apostlebird	1	—	22	11	24	5
Magpie-lark	0	8	—	11	45	27
Yellow-throated Miner	0	0	0	—	5	1
Willie Wagtail	0	1	0	1	—	5
Restless Flycatcher	0	0	1	0	4	—

TABLE 4. The unique linear hierarchy of species foraging at a locust trap in New South Wales, Australia, during period 3 (10:01–12:00). Species are arranged by body size. Landau's $h = 1$.

	Losers				
Winners	Magpie-lark	Willie Wagtail	Restless Flycatcher	Sp-ch. Honeyeater	Wh-pl. Honeyeater
Magpie-lark	—	45	27	1	6
Willie Wagtail	0	—	5	8	2
Restless Flycatcher	1	4	—	3	5
Spiny-cheeked Honeyeater	0	3	0	—	7
White-plumed Honeyeater	0	1	0	3	—

present at the locust trap when deciding whether to land and forage (Daily and Ehrlich 1994). These patterns of interspecific social interactions or avoidance can influence both the instantaneous and long-term distributions of birds in a given area. Thus, pairwise dominance relationships may explain the development of different ecological niches, as well as resource partitioning (Fisler 1977, Nagamitsu and Inoue 1997).

However, we found no support for Lanchester's N-square law with our data. Group size was not a significant factor in influencing interspecific dominance interactions among the 10 bird species that fed at the locust trap. Of the 10 logistic regressions we ran, only one was significant. For some of the pairings, the lack of significance may result from a paucity of data. The negative relationship in the one significant regression is further evidence against Lanchester's N-square law. The N-square law also may not apply to these birds due to the lesser degree of cooperation seen in flocks or gatherings of birds as compared to humans, chimpanzees, or ants.

The birds foraging at the locust trap were concentrated around an abundant food source. Thus, it is reasonable to assume that the same dominance relationships identified in our study are likely to apply at concentrated food patches throughout the arid zone.

In conclusion, while it seems that both of Lanchester's laws have great explanatory value for potentially fatal combat among ants and chimpanzees, the N-square law has limited ability to explain the nonfatal interspecific dominance hierarchies in at least one group of Australian insectivorous birds. These specific findings may have applicability to a much broader understanding of behavioral interactions among species inhabiting a common habitat and sharing some or all of the same resources.

Research protocols were approved by the University of New South Wales Animal Care and Ethics Committee (permit # 02/08). Partial support of the project came from grants by the UCLA Office of Instructional Improvement, the Department of Organismic Biology, Ecology and Evolution, and the Lida Scott Brown Ornithology Trust. We thank the staff of the Fowlers Gap Station for logistical support, David Croft for assistance obtaining permits, and Claudia Cecchi, Janice Daniel, Peter Nonacs, and Aviva Liebert for additional help. We also thank Paul Walker and the Australian Plague Locust Commission for the use of their locust trap as well as providing us with background information. Comments by David Dobkin and two anonymous reviewers helped us tighten and clarify our message.

TABLE 5. Summary of the logistic regression models that explained the probability that a given species would win an encounter given the group size of its competitor. Group sizes are means ± SD. Full common names appear in Table 1.

Species 1				Competitor			
Species	Group size	No. of wins	No. of losses	Species	Group size	P	R^2
Apostlebird	6.3 ± 3.3	1	28	Austr. Magpie	1.6 ± 0.5	0.15	0.44
Austr. Magpie	1.7 ± 0.5	18	0	Magpie-lark	1.1 ± 0.3		
Magpie-lark	1.3 ± 0.5	8	22	Apostlebird	3.6 ± 1.8	0.97	0.002
Apostlebird	4.6 ± 2.9	63	44	all species[a]	1.9 ± 0.9	<0.001	0.10
Austr. Raven	1.5 ± 0.5	15	0	all species[a]	4.6 ± 3.2		
Austr. Magpie	1.5 ± 0.5	78	7	all species[a]	3.9 ± 3.0	0.27	0.03
Magpie-lark	1.3 ± 0.5	104	43	all species[a]	2.7 ± 2.0	0.06	0.02
Sp-ch. Honeyeater	1.2 ± 0.5	10	15	all species[a]	1.8 ± 1.3	0.20	0.05
Wh-pl. Honeyeater	1.9 ± 1.4	4	21	all species[a]	1.9 ± 0.9	0.39	0.03
Y-thrtd. Miner	1.9 ± 1.2	7	38	all species[a]	2.8 ± 2.7	0.12	0.06

[a] All other species present during species 1's interactions.

LITERATURE CITED

BASSET, A. 1995. Body size-related coexistence: an approach through allometric constraints on home-range use. Ecology 76:1027–1035.

BASSET, A. 1997. Mechanisms relating biomass concentration in individuals to interspecific resource competition. Oikos 78:31–36.

BURGER, J., AND M. GOCHFELD. 1984. The effects of relative numbers on aggressive interactions and foraging efficiency in gulls: the cost of being outnumbered. Bird Behaviour 5:81–89.

CASOTTI, G., AND N. C. RICHARDSON. 1992. A stereological analysis of kidney structure of honeyeater birds (Meliphagidae) inhabiting either arid or wet environments. Journal of Anatomy 180:281–288.

CHAPMAN, M. R., AND D. L. KRAMER. 1996. Guarded resources: the effect of intruder number on the tactics and success of defenders and intruders. Animal Behaviour 52:83–94.

CREEL, S. 2001. Four factors modifying the effect of competition on carnivore population dynamics as illustrated by African wild dogs. Conservation Biology 15:271–274.

DAILY, G. C., AND P. R. EHRLICH. 1994. Influence of social status on individual foraging and community structure in a bird guild. Oecologia 100:153–165.

FISLER, G. F. 1977. Interspecific hierarchy at an artificial food source. Animal Behaviour 25:240–244.

FRANKS, N. R., AND L. W. PARTRIDGE. 1993. Lanchester battles and the evolution of combat in ants. Animal Behaviour 45:197–199.

GEFFEN, E., AND Y. YOM-TOV. 2000. Are incubation and fledgling periods longer in the tropics? Journal of Animal Ecology 69:59–73.

HAILMAN, J. P. 1994. Peck Order 1.03. Department of Zoology, University of Wisconsin, Madison, WI.

HIGGINS, P. J., J. M. PETER, AND W. K. STEELE [EDS.]. 2001. Handbook of Australian, New Zealand, and Antarctic birds. Vol. 5. Tyrant-flycatchers to Chats. Oxford University Press, Melbourne, Australia.

KOHDA, M. 1991. Intra- and interspecific social organization among three herbivorous cichlid fishes in Lake Tanganyika. Japanese Journal of Ichthyology 38:147–164.

LANCHESTER, F. W. 1916. Aircraft in warfare: the dawn of the fourth arm. Constable, London, UK.

LEHNER, P. N. 1996. Handbook of ethological methods. 2nd ed. Cambridge University Press, Cambridge, UK.

MCGLYNN, T. P. 1999. Non-native ants are smaller than related native ants. American Naturalist 154:690–697.

MCGLYNN, T. P. 2000. Do Lanchester's laws of combat describe competition in ants? Behavioral Ecology 11:686–690.

NAGAMITSU, T., AND T. INOUE. 1997. Aggressive foraging of social bees as a mechanism of floral resource partitioning in an Asian tropical rainforest. Oecologia 110:432–439.

PIZZEY, G., AND F. KNIGHT. 2001. The field guide to the birds of Australia. Angus and Robertson, Sydney, Australia.

SANDLIN, E. A. 2000. Foraging information affects the nature of competitive interactions. Oikos 91:18–28.

SAS INSTITUTE. 1999. StatView 5.1. SAS Institute Inc., Cary, NC.

TRAVAINI, A., J. A. DONAZAR, A. RODRIGUEZ, O. CEBALLOS, M. FUNES, M. DELIBES, AND F. HIRALDO. 1998. Use of European hare (*Lepus europeus*) carcasses by an avian scavenging assemblage in Patagonia. Journal of Zoology, London 246:175–181.

WALLACE, M. P., AND S. A. TEMPLE. 1987. Competitive interactions within and between species in a guild of avian scavengers. Auk 104:290–295.

WHITEHOUSE, M. E. A., AND K. JAFFE. 1996. Ant wars: combat strategies, territory and nest defense in the leaf-cutting ant *Atta laevigata*. Animal Behaviour 51:1207–1217.

WILSON, M. L., N. F. BRITTON, AND N. R. FRANKS. 2002. Chimpanzees and the mathematics of battle. Proceedings of the Royal Society of London Series B 269:1107–1112.

WOOLER, R. D., D. A. SAUNDERS, J. S. BRADLEY, AND C. P. DEREBEIRA. 1985. Geographical variation in size of an Australian honeyeater (*Meliphaga virescens*) (Aves: Meliphagidae): an example of Bergmann's rule. Biological Journal of the Linnean Society 25:355–364.

YANO, S. 1995. New Lanchester strategy. Vol. 1. Lanchester Press Inc., Sunnyvale, CA.

The Condor 106:401–404

PARENTAGE IN AN OKLAHOMA POPULATION OF LOGGERHEAD SHRIKES ASSESSED USING NUCLEAR MICROSATELLITES

MATTHEW A. ETTERSON[1]
Conservation Biology Program, University of Minnesota, 100 Ecology Building, 1987 Upper Buford Circle,
St. Paul, MN 55108

Abstract. I used six nuclear microsatellites to assess rates of intraspecific brood parasitism and extra-pair paternity in relationship to conspecific density in 218 offspring from 44 broods of Loggerhead Shrikes (*Lanius ludovicianus*). I also estimated statistical power associated with these markers for each parentage test and suggest a method for adjusting power estimates when individuals are incompletely genotyped. No offspring were the result of intraspecific brood parasitism. Eight offspring from five families (4% of all offspring; 14% of families) were sired by extra-pair fertilization. Average exclusionary power was 0.94 when adjusted to account for incomplete genotyping. Assuming a 1% genotyping error rate, this power drops to 0.91. This is the first genetic assessment of parentage in a wild population of Loggerhead Shrikes.

Key words: extra-pair fertilization, Lanius ludovicianus, *Loggerhead Shrike, parentage exclusion, power.*

Parentesco en una Población de Oklahoma de *Lanius ludovicianus* Evaluado Usando Microsatélites Nucleares

Resumen. Utilicé seis microsatélites nucleares para evaluar las tasas de parasitismo intra-específico de la nidada y paternidad extra-pareja con relación a la densidad de individuos coespecíficos en 218 crías provenientes de 44 nidadas de *Lanius ludovicianus*. También estimé el poder estadístico asociado con estos marcadores para cada prueba de paternidad y sugiero un método para ajustar las estimaciones de poder cuando el genotipo de los individuos no ha sido determinado completamente. Ninguna cría fue el resultado de parasitismo intra-específico de la nidada. Ocho crías provenientes de cinco familias (4% de todas las crías; 14% de las familias) fueron engendradas por medio de fertilizaciones extra-pareja. El poder de exclusión promedio fue de 0.94 cuando fue ajustado para tener en cuenta los genotipos incompletos. Suponiendo que la tasa de error de evaluación genotípica es del 1%, este poder desciende a 0.91. Esta es la primera evaluación genética de parentesco en una población silvestre de *L. ludovicianus*.

Loggerhead Shrikes (*Lanius ludovicianus*) settle in relatively dense territorial clusters (Cade and Woods 1997, Pruitt 2000, Etterson 2000, 2003). Woods (1995: 154) reported ''spatial clumping'' in the distribution of Loggerhead Shrikes nesting in sagebrush habitats of southwestern Idaho and discussed the potential roles of nest predation and the need to find suitable mates as causes for aggregation. Etterson (2003) found that naïve shrikes nesting in southwest Oklahoma were more likely to settle near conspecifics than were individuals with previous experience in the study area. In an unpublished 1990 report to the Indiana Department of Natural Resources, K. Burton and D. Whitehead found 20 of 117 (17%) nest attempts by Loggerhead Shrikes in Indiana in 1988 and 1989 in a single township (93 km^2). Only 13% of these 117 attempts were isolated from conspecifics by more than 5 km. Pruitt (2000) cited unpublished reports of territorial aggregation in Montana and New York.

Recent research in avian mating systems has suggested that the pursuit of extra-pair mating strategies may lead to aggregation and the evolution of coloniality in territorial birds (Wagner 1993, Hoi and Hoi-Leitner 1997). Westneat and Sherman (1997) found positive correlations between extra-pair fertilization (EPF) rates and conspecific density in eight of 11 studies. Rates of intraspecific brood parasitism have also been shown to correlate with density in at least three bird species including the Eared Grebe (*Podiceps nigricollis*; Hill et al. 1997), Wood Duck (*Aix sponsa*; Semel et al. 1988), and Common Moorhen (*Gallinula chloropus*; Ueda et al. 1993).

The objective of this study was to assess rates of intraspecific brood parasitism and EPF in Loggerhead Shrikes in relation to conspecific density in order to evaluate the potential for extra-pair mating strategies to influence conspecific density in this species.

METHODS

I collected tissue from 44 broods (218 offspring) of shrikes breeding in Comanche County, Oklahoma (34°N, 98°W), during the 1998 and 1999 breeding seasons. For 31 broods (156 offspring) I sampled both parents. For an additional five broods (23 offspring) I sampled only the putative father and for another eight

---

Manuscript received 3 February 2003; accepted 20 November 2003.

[1] Present address: U.S. Environmental Protection Agency, Mid-Continent Ecology Division, 6201 Congdon Boulevard, Duluth, MN 55804. E-mail: etterson.matthew@epa.gov

broods (39 offspring) I sampled only the putative mother. I trapped adults using modified potter traps (Craig 1997) and mist nets, and banded each with a United States Fish and Wildlife Service aluminum band and a unique combination of three plastic color bands. I took one rectrix and two contour feathers from each adult and stored them at −20°C. I sampled nestlings at 8 days using the same protocol.

I extracted DNA from the basal 4–5 mm of the rachis of feathers using the Qiagen DNA Mini Kit (Qiagen, Valencia, California) with the standard protocol modified as follows. I digested the feather tissue for 24–36 hr in lysis buffer and added a second (20 μL) aliquot of Proteinase K to ensure the complete digestion of feather tissue. At the final step, I passed the eluate back through the microfilter (for adult feather tissue only) to increase the concentration of DNA.

I took primers for six microsatellite loci from Mundy et al. (1997). Four of these loci (LS1, LS2, LS3, and LS4; Mundy and Woodruff 1996) were originally developed from Loggerhead Shrike tissue. One locus each was developed from Florida Scrub-Jay (*Aphelocoma coerulescens*) and Long-tailed Manakin (*Chiroxiphia linearis*; SJR4 and LTMR7 respectively, MacDonald and Potts, unpubl. data). I labeled all primers with one of three fluorescent dyes (6-FAM, HEX, TET). I optimized PCR using a MasterAmp PCR optimization kit (Epicentre Technologies, Madison, Wisconsin) and I performed all reactions on Thermolyne Amplitron II Thermal Cyclers (Barnstead International, Dubuque, Iowa) using touchdown PCR (Hecker and Roux 1996) to increase yield and reduce nonspecific priming. I visualized fragments on an ABI 310 Genetic Analyzer (PE Applied Biosystems, Foster City, California). I initially typed fragments using Genotyper 3.0 software (PE Applied Biosystems 1999), and then verified all assignments visually.

STATISTICAL ANALYSES

I calculated observed heterozygosity for each locus as the frequency of adults that were heterozygous at that locus. I estimated expected heterozygosity as $1 - \Sigma_i p^2_i$, where p_i is the frequency of allele *i*. The presence of null alleles could result in an apparent mismatch between parent-offspring genotypes and result in an overestimate of EPF rates. Null alleles will also result in more apparently homozygous individuals than would be expected under Hardy-Weinberg conditions. To determine whether null alleles were likely among the individuals I sampled, I used a recent update of the software program GENEPOP (Version 3.3; Raymond and Rousset 1995) to test for heterozygote deficiency, a one-sided test of departure from Hardy-Weinberg equilibrium. I also performed a second test for null alleles using CERVUS (Marshall et al. 1998). Finally, I used GENEPOP to test for linkage disequilibrium among loci.

PARENTAGE ANALYSIS

For each offspring tested I excluded an attending parent as a true parent when the offspring genotype could not have arisen from the parent based on Mendelian inheritance patterns. To increase power of paternity tests I also compared paternal genotypes to offspring genotypes contingent upon the presumed maternal genotype. This was not necessary to do for maternity tests (i.e., to test for intraspecific brood parasitism) because no offspring failed to share at least one allele at each locus with its presumed mother (see results below). For offspring for which I had sampled only the presumed father ($n = 23$), I tested for cases in which the offspring and presumed father did not share alleles at one or more loci.

I calculated single-locus exclusion power using equations described in Chakraborty et al. (1988), but modified to allow for incomplete genotyping as follows: If π_i is the proportion of individuals typed at locus *i*, and P_E is the calculated exclusionary power at that locus, then the functional exclusionary power at that locus is

$$P'_E = \pi_i \times P_E$$

which gives a revised estimate (β'_i) of the probability of a Type II error:

$$\beta'_i = 1 - P'_E = 1 - \pi_i \times P_E$$

I estimated expected multilocus exclusionary power using equations in Bruford et al. (1992).

For each offspring I also used CERVUS (Marshall et al. 1998) to determine the most likely father from among all genotyped males (including the attending male) nesting concurrently and within 5 km of the nest in which the offspring hatched. I scored an offspring as having been sired by EPF when both exclusion and CERVUS indicated the offspring had been sired by EPF, in other words, when the offspring could not have inherited its alleles from the attending male *and* another genotyped male was scored as being a more likely sire than the attending male. To investigate the relationship between EPF and local density I performed a logistic regression with EPF as the response variable and distance to nearest neighbor as the independent variable using SAS 8.0 (SAS Institute 1999). I calculated distance to nearest neighbor as the linear distance between adjacent nests. I also report the probability of exclusion (here calculated as one minus the probability of nonexclusion) as estimated by CERVUS.

RESULTS

Both GENEPOP and CERVUS detected significant departures from Hardy-Weinberg equilibrium at LS1 ($P < 0.02$ and $P < 0.01$, respectively). Using algorithms from Summers and Amos (1997) CERVUS estimated null allele frequency at LS1 to be 0.03. Using GENEPOP I detected no evidence of linkage disequilibrium among pairwise comparisons of LS1, LS2, LS3, LS4, and SJR4. No comparisons with LTMR7 were possible because the large number of genotypes at this locus resulted in expected values too small to conform to chi-square assumptions.

Multilocus exclusion power ranged from 0.63 to 0.99 and averaged 0.94 (Table 1). Expected multilocus exclusionary power was 0.94. Both observed and expected exclusionary power for each locus are given in Table 1. These estimates always agreed to within 4 percentage points. The average multilocus probability of exclusion as calculated by CERVUS (with a 1% genotyping error rate) was 0.91.

TABLE 1. Number of alleles, heterozygosity, and exclusionary power at six microsatellite loci used for paternity exclusion in Loggerhead Shrikes.

Locus[a]	Alleles	Heterozygosity		Exclusionary power (multilocus)[b]		Proportion of individuals typed (adults/juveniles)
		Observed	Expected	Average	Expected	
LS4	4	0.29	0.35	0.15	0.18	0.97/1.0
LS2	3	0.44	0.47	0.24 (0.35)	0.21 (0.35)	0.98/1.0
SJR4	6	0.38	0.40	0.25 (0.52)	0.22 (0.50)	1.0/1.0
LS3	4	0.39	0.49	0.23 (0.63)	0.23 (0.61)	0.99/1.0
LS1	6	0.72	0.64	0.37 (0.77)	0.41 (0.77)	1.0/1.0
LTMR7	14	0.83	0.90	0.73 (0.94)	0.74 (0.94)	0.92/1.0

[a] Loci are in ascending order by exclusionary power.

[b] Multilocus exclusionary power calculated with all preceding loci in table.

Among 195 offspring from 39 families (all families for which I had sampled the putative mother), all shared at least one allele at each locus with their mother. Among 179 offspring from 36 families for which I had sampled the putative father, eight offspring from five families were both excluded from being sired by the attending male and were successfully assigned to another male within 5 km. EPF occurred in 4% of offspring from 14% of broods. When an EPF occurred it was not typically assigned to the nearest neighbor, except in two cases in which only one other male was genotyped within 5 km. Logistic regression showed a slightly positive (slope parameter <0.001), though nonsignificant, relationship between presence of an EPF offspring and distance to nearest neighbor ($\chi^2 = 0.2$, $P = 0.66$).

DISCUSSION

Exclusionary power using these six markers was good, even with the relatively low degree of variation at most of the loci. The rate of EPF discovered here in Loggerhead Shrikes (4%) is similar to rates reported for other shrike species. Using multilocus DNA fingerprinting, Yamagishi et al. (1992) found that 10 of 99 (10%) Bull-headed Shrike (*Lanius bucephalus*) nestlings were sired by EPF. Fornasari et al. (1994) used the same technique to discover that 1 of 19 (5%) nestlings of Red-backed Shrikes (*Lanius collurio*) were sired by EPF. In a behavioral study of Northern Shrikes (*Lanius excubitor*) in Poland, Lorek (1995) observed 23 of 83 (28%) copulations were extra-pair. However, no biochemical data were collected to determine the associated EPF rate, which, given the difficulty of observing extra-pair copulations, may be substantially higher than EPF rates reported for other shrike species.

These results reinforce behavioral data that suggest Loggerhead Shrikes are primarily monogamous. There is only one report of polygyny in Loggerhead Shrikes (Yosef 1992), suggesting that either females are unwilling to accept polygynous matings, or that males can rarely monopolize the resources necessary to provide for more than one brood on a territory. However, females have been reported to remate once their first mate assumes full responsibility for parental care (Haas and Sloane 1989), a practice termed serial polyandry. Polygyny appears to be more common in the closely related Northern Shrike (Yosef 1992, Probst 2001), though no molecular assessment of paternity in Northern Shrikes has been published. The absence of intraspecific brood parasitism, the low overall population EPF rate, and the lack of evidence for a relationship between extra-pair paternity and density in Loggerhead Shrikes strongly argue against the hypothesis that the pursuit of extra-pair fertilization is a cause for aggregation in this species.

This manuscript benefited greatly from comments by E. Clotfelter and an anonymous reviewer. Microsatellite analyses were done in the Laboratory of Molecular Systematics at the University of Minnesota under the supervision of R. Zink. R. Blackwell-Rago, K. Johnson, K. Omland, and S. Sheffer provided valuable advice on laboratory techniques. Wayne Potts generously provided unpublished primer sequences. Funding was provided by the Dayton Wilkie Natural History Fund, a Doctoral Dissertation Grant from the University of Minnesota, a Frank M. Chapman award from the American Museum of Natural History, and a Student Research Grant from the Animal Behavior Society. J. Tyler provided support in initiating this work. I gratefully acknowledge the logistical and administrative support provided by T. Hodgkins, K. McCurdy, and G. Wampler of the Natural Resources and Enforcement Branch, Directorate of Public Safety, Fort Sill Military Reservation, while conducting the fieldwork associated with this research.

LITERATURE CITED

BRUFORD, M., W. O. HANOTTE, J. F. BROOKFIELD, AND T. BURKE. 1992. Single-locus and multilocus DNA fingerprinting, p. 225–269. *In* A. R. Hoelzel [ED.], Molecular genetic analysis of populations: a practical approach. IRL Press, Oxford, UK.

CADE, T. J., AND C. P. WOODS. 1997. Changes in the distribution and abundance of the Loggerhead Shrike. Conservation Biology 11:21–31.

CHAKRABORTY, R., T. R. MEAGHER, AND P. E. SMOUSE. 1988. Parentage analysis with genetic markers in natural populations. I. The expected proportion of offspring with unambiguous paternity. Genetics 118:527–536.

CRAIG, S. H. 1997. What goes around. . . gets caught!!: an improved trap for shrikes. North American Bird Bander 22:124–125.

Etterson, M. 2000. Monte Carlo simulation tests for non-randomness in the spatial distribution of breeding shrikes. Ring 22:173–179.

Etterson, M. 2003. Conspecific attraction in Loggerhead Shrikes: implications for habitat conservation and reintroduction. Biological Conservation 114:199–205.

Fornasari, L., L. Bottoni, N. Sacchi, and R. Massa. 1994. Home range overlapping and socio-sexual relationships in the Red-backed Shrike *Lanius collurio*. Ethology Ecology & Evolution 6:169–177.

Haas, C. A., and S. Sloane. 1989. Low return rates of migratory Loggerhead Shrikes: winter mortality or low site fidelity. Wilson Bulletin 101:458–460.

Hecker, K. H., and K. H. Roux. 1996. High and low annealing temperatures increase both specificity and yield in touchdown and stepdown PCR. BioTechniques 20:478–485.

Hill, W., K. J. Jones, C. L. Hardenbergh, and M. Browne. 1997. Nest distance mediates the costs of coloniality in Eared Grebes. Colonial Waterbirds 20:470–477.

Hoi, H., and M. Hoi-Leitner. 1997. An alternative route to coloniality in the Bearded Tit: females pursue extrapair fertilizations. Behavioral Ecology 8:113–119.

Lorek, G. 1995. Copulation behavior, mixed reproductive strategy, and mate guarding in the Great Grey Shrike. Proceedings of the Western Foundation for Vertebrate Zoology 6:218–227.

Marshall, T. C., J. Kruuk, and J. M. Pemberton. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. Molecular Ecology 7:639–655.

Mundy, N. I., C. S. Winchell, T. Burr, and D. S. Woodruff. 1997. Microsatellite variation and microevolution in the critically endangered San Clemente Loggerhead Shrike (*Lanius ludovicianus mearnsi*). Proceedings of the Royal Society of London Series B 264:869–875.

Mundy, N. I., and D. S. Woodruff. 1996. Polymorphic microsatellite markers in the Loggerhead Shrike. Molecular Ecology 5:811–813.

PE Applied Biosystems. 1999. Genotyper 3.0 users manual. PE Applied Biosystems, Foster City, CA.

Probst, R. 2001. Successful bigamy in the Great Grey Shrike *Lanius e. excubitor*. Ornis Fennica 78:93–96.

Pruitt, L. 2000. Loggerhead Shrike status assessment. U.S. Fish and Wildlife Service. Fort Snelling, MN.

Raymond, M., and F. Rousset. 1995. GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. Journal of Heredity 86: 248–249.

SAS Institute. 1999. SAS/STAT user's guide. Version 8. SAS Institute Inc., Cary, NC.

Semel, B., P. W. Sherman, and S. M. Beyers. 1988. Effects of brood parasitism and nest-box placement on Wood Duck breeding ecology. Condor 90:920–930.

Summers, K., and W. Amos. 1997. Behavioral, ecological and molecular genetic analyses of reproductive strategies in the Amazonian dart-poison frog, *Dendrobates ventrimaculatus*. Behavioral Ecology 8:260–267.

Ueda, K., H. Uchida, and T. Matsuda. 1993. Egg-dumping by the Moorhen, *Gallinula chloropus*, in Japan. Japanese Journal of Ornithology 42:21–25.

Wagner, R. H. 1993. The pursuit of extrapair copulations by female birds: a new hypothesis of colony formation. Journal of Theoretical Biology 163:333–346.

Westneat, D., and P. W. Sherman. 1997. Density and extrapair fertilization in birds: a comparative analysis. Behavioral Ecology and Sociobiology 41: 205–215.

Woods, C. 1995. Status of Loggerhead Shrikes in the sagebrush habitat of southwestern Idaho. Proceedings of the Western Foundation for Vertebrate Zoology 6:150–154.

Yamagishi, S., I. Nishiumi, and C. Shimoda. 1992. Extrapair fertilization in monogamous Bull-headed Shrikes revealed by DNA fingerprinting. Auk 109:711–721.

Yosef, R. 1992. Behavior of polygynous and monogamous Loggerhead Shrikes and a comparison with Northern Shrikes. Wilson Bulletin 104:747–749.

The Condor 106:405–410

EGG DISCRIMINATION IN THE YELLOWHAMMER

PETR PROCHÁZKA[1,2] AND MARCEL HONZA[1,3]
[1]*Institute of Vertebrate Biology, Academy of Sciences of the Czech Republic, Květná 8,*
CZ-60365 Brno, Czech Republic
[2]*Department of Zoology, Faculty of Science, Charles University, Viničná 7,*
CZ-12844 Prague, Czech Republic

Abstract. In a coevolutionary arms race between a brood parasite and its host, both species evolve adaptations and counteradaptations, such as egg mimicry and egg discrimination. The Yellowhammer (*Emberiza citrinella*) is a minor host of the Common Cuckoo (*Cuculus canorus*) in Europe. We studied egg discrimination in the Yellowhammer in the Czech Republic where it is parasitized only occasionally. To investigate host responses to parasitic eggs, we added either a nonmimetic (blue) or a mimetic (conspecific) egg to 50 nests. The hosts rejected nonmimetic eggs at a higher rate (92%) than mimetic eggs (32%). Neither intraclutch variation nor contrast between mimetic and host eggs had a significant effect on rejection behavior. There is no evidence for intraspecific brood parasitism in this species. The ability to reject mimetic eggs has therefore most likely evolved as an adaptation against interspecific brood parasitism and may be the reason why the Yellowhammer is parasitized only occasionally.

Key words: brood parasitism, cuckoo, egg ejection, egg recognition, Emberiza citrinella, *Yellowhammer.*

Discriminación de Huevos en *Emberiza citrinella*

Resumen. En una carrera armamentista co-evolutiva entre un ave parásita y su hospedador es previsible que ambas especies desarrollen adaptaciones y contraadaptaciones tales como el ovomimetismo y la ovodiscriminación. *Emberiza citrinella* es un huésped menor de *Cuculus canorus* en Europa. Estudiamos la capacidad discriminatoria de los huevos, por parte de *Emberiza citrinella,* en la República Checa, donde la especie es parasitada sólo ocasionalmente. Con objeto de investigar la respuesta del hospedador a los huevos parásitos, añadimos un huevo no mimético (azul) o uno mimético (coespecífico) a 50 nidos. El hospedador rechazó los huevos no miméticos en una proporción más elevada (92%) que los miméticos (32%). Ni la variación de la apariencia del huevo dentro de la puesta, ni el contraste entre los huevos miméticos y los del hospedador, parecen tener algún efecto significativo en el comportamiento de rechazo. No hay evidencias de la existencia de parasitismo intraespecífico en esta especie. Por tanto, la habilidad de *Emberiza citrinella* para rechazar huevos miméticos probablemente ha evolucionado como una adaptación contra el parasitismo interespecífico y esta puede ser la razón de por qué la especie es parasitada sólo de manera ocasional.

Brood parasitism of the Common Cuckoo (*Cuculus canorus*) considerably reduces the reproductive success of its hosts (Øien et al. 1998) and consequently has led to the development of host defenses such as recognition and rejection of the parasite's egg (Davies and Brooke 1988). These, in turn, have selected for counteradaptations, such as egg mimicry in the parasite. This can set in motion a coevolutionary arms race between the host and the brood parasite, resulting in more and more intricate adaptations and counteradaptations (Dawkins and Krebs 1979).

The Common Cuckoo is an obligate brood parasite that lays its eggs in nests of at least 125 species of small passerines (Moksnes and Røskaft 1995). Each female cuckoo lays a particular egg type that matches eggs of a host species (Jourdain 1925). These host-specific races represent genetically differentiated female lineages (Gibbs et al. 2000).

In the present study we investigate egg discrimination in a minor host of the cuckoo, the Yellowhammer (*Emberiza citrinella*). Although the species is a widespread and common passerine in Europe (Biber 1997) and can be regarded as a suitable cuckoo host, it is parasitized only occasionally (Makatsch 1955). Of a total of 11 870 Common Cuckoo eggs stored in European museum collections, 2% were laid in Yellowhammer nests (Moksnes and Røskaft 1995). Of these, only eight were the *Emberiza* egg morph. In their analyses of Czech museum egg collections, Honza et al. (2001) found only nine cuckoo eggs collected from Yellowhammer nests, among a total of 736 parasitized clutches (1%).

Little is known about the egg rejection ability of the Yellowhammer. Experiments conducted by Moksnes et al. (1991) showed that the species rejects nonmimetic eggs but did not test the limits of the species' discrimination and, because they used hard plastic eggs, could not determine accurately whether real eggs would be rejected.

Manuscript received 29 May 2003; accepted 26 December 2003.

[3] Corresponding author. E-mail: honza@brno.cas.cz

Since the Yellowhammer is not at present parasitized regularly, we hypothesized that this species is a rejecter that is ahead of the Common Cuckoo in their coevolutionary arms race. In this study we examined this by experimental brood parasitism. As a first step, we tested whether the species rejects nonmimetic eggs. Then we investigated whether Yellowhammers recognize mimetic conspecific eggs, which would support our hypothesis that the species has evolved good discrimination ability from exposure to heavier parasitism in the past.

METHODS

The study was carried out in farmland near Dukovany (49°05′N, 16°11′E) and Veverské Knínice (49°14′N, 16°24′E), Czech Republic, in 2001–2002. We did not record any cases of interspecific brood parasitism in the investigated species at either site. Since no site-related differences in responses toward either nonmimetic or mimetic eggs were found, data from the two localities were pooled.

All suitable habitats were systematically searched for nests. Eggs were measured to the nearest 0.1 mm using vernier calipers. Eggs found during laying were numbered with waterproof ink according to their order; those found later were floated to estimate their approximate laying date (Hays and Lecroy 1971). All host and parasitic eggs were marked with ink to allow for individual identification.

As a first step, we tested whether the species rejects nonmimetic eggs. We used real eggs from abandoned Yellowhammer or Red-backed Shrike (*Lanius collurio*) clutches, and painted them light blue to represent the Redstart (*Phoenicurus phoenicurus*) cuckoo-egg morph found in the nearby village of Oslavany by Čapek (1910). To test whether Yellowhammers discriminate against mimetic eggs, we used alien conspecific eggs. We placed only one egg in each experimental nest. Average measurements of experimental eggs (20.9 × 16.1 mm, $n = 48$) were somewhat smaller than the average of real Common Cuckoo eggs throughout its European breeding range (22.7 × 16.3 mm, Makatsch 1976). Measurements of the experimental eggs (length: 19.3–23.2 mm, breadth: 15.3–17.4 mm) were however within the range of real Common Cuckoo eggs (length: 19.7–27.1 mm, breadth: 14.7–18.9 mm; Makatsch 1976).

To test for the effect of nest stage, we introduced the parasitic eggs in either of the following periods: (1) end of egg laying, usually after the fourth egg was laid; (2) early incubation (1–5 days); or (3) late incubation (6–10 days). Host eggs were not removed when the experimental egg was put into the nest, because this has been shown to have no influence on host rejection (Rothstein 1975, Davies and Brooke 1988, Moksnes and Røskaft 1989, Lawes and Kirkman 1996, but see Lyon 2003 for evidence of American Coots [*Fulica americana*] counting eggs). The whole clutch, including the introduced egg, was photographed in a standardized manner (gray background, color scale) using a Canon EOS 500 camera and Kodak 200 ISO color film. The nests were visited every day for the next 5 days to ascertain host reaction. If the hosts did not remove the parasitic egg (ejection) or the nest was not abandoned (desertion) during this period, the egg was considered to have been accepted. All nests depredated within the 5-day period were excluded from the analyses. Besides the experimental nests, 26 additional clutches were used as a control group. These nests were inspected and the eggs handled in the same way as the experimental nests, except that no parasitic egg was placed into them.

To avoid pseudoreplication due to possibly testing a second or replacement clutch of the same bird, we did not carry out our experiments repeatedly in the same Yellowhammer territory. This was justified by the fact that females renest close to their first nest (Hasse 1963).

Intraclutch variability and contrast between mimetic and host eggs were estimated from the photos by six persons unaware of the results of the experiment. The intraclutch variation in egg color and marking pattern was measured on a scale from one to five (Øien et al. 1995): (1) no variation, all the eggs were similar; (2) at least one egg differed slightly from the others; (3) at least one egg showed marked differences from the others; (4) at least one egg differed dramatically from the others; and (5) all the eggs were different from one another. The contrast in egg color and marking pattern between the mimetic and host eggs was scored on a scale from one to three (Braa et al. 1992): (1) no contrast between host and mimetic egg, the alien egg being indistinguishable from the host eggs; (2) medium contrast between host and mimetic eggs, with the alien egg distinguishable from the host eggs, but only moderate difference; and (3) high contrast between host and mimetic eggs, with the alien egg easily distinguishable from the host eggs. For contrast and intraclutch variability comparisons, the mean of the assessments of the test persons was used. These observers' scores were tested for ''reliability,'' i.e., whether the variance between each person in ranking the same set of eggs differed significantly. There were no significant differences in scoring between the six observers in contrast (Kruskal-Wallis $H_{5,204} = 7.9$, $P = 0.16$) nor in intraclutch variation of egg appearance (Kruskal-Wallis $H_{5,204} = 8.9$, $P = 0.11$), suggesting that each subject scored the eggs in a similar manner. For the statistical analyses we used STATISTICA 6.0 (StatSoft 2001). Means are presented ± SD.

RESULTS

In total, 50 Yellowhammer nests were used for the experiments. Of these, 13 were parasitized with nonmimetic eggs and 37 with mimetic eggs (Table 1). The rejection rate was significantly higher in experimental nests than in the control group (experimental nests pooled: Yates corrected $\chi^2_1 = 13.2$, $P < 0.001$). Both the nonmimetic and mimetic treatments showed higher ejection rates than the control treatment (Yates corrected $\chi^2_1 = 28.4$, $P < 0.001$ and $\chi^2_1 = 7.4$, $P < 0.01$, respectively). This clearly indicates that ejection was a discriminatory response to the introduced eggs. Only one case of nest desertion was recorded in each treatment and in the control group. Desertion was thus not an obvious rejection response to our experimental brood parasitism.

TABLE 1. Yellowhammer rejection responses to a brood parasitism experiment. Each Yellowhammer nest was parasitized with one real egg, either painted blue (nonmimetic) or unaltered (mimetic). Control nests were handled in the same manner, but received no eggs.

			Rejected		
Treatment	*n*	Accepted	Ejected	Deserted	Total
Mimetic	37	25	11	1	12
Nonmimetic	13	1	11	1	12
Control	26	25	0	1	1

Both nonmimetic and mimetic eggs were ejected selectively. We recorded no partial egg losses in the control group, suggesting that no recognition errors (hosts ejecting their own eggs in the absence of parasitism) occurred. Similarly, no rejection costs (measured as the number of host eggs which disappeared from experimentally parasitized clutches) were detected in either experimental treatment.

We found no significant differences in the number of rejections and acceptances of either mimetic ($\chi^2_2 = 0.7$, $P = 0.98$) or nonmimetic eggs with respect to laying date ($\chi^2_2 = 1.1$, $P = 0.95$; Table 2). There was no difference in rejection rate among nests parasitized during laying, early incubation, and late incubation in either mimetic ($\chi^2_2 = 3.0$, $P = 0.81$) or nonmimetic treatments ($\chi^2_2 = 2.4$, $P = 0.79$). Rejection rate was higher in the nonmimetic treatment than in the mimetic treatment (Yates corrected $\chi^2_1 = 11.5$, $P < 0.001$; nest stages pooled). No significant difference in time until ejection between nonmimetic (mean 1.0 ± 0.0 days, $n = 11$) and mimetic eggs (mean = 1.4 ± 0.5 days, $n = 11$; Mann-Whitney *U*-test: $z = -1.4$, $P = 0.15$) was found.

TABLE 2. Response of Yellowhammers to experimental brood parasitism over the course of the breeding season. Date of egg laying is the date the first egg in each nest was laid.

	Date of egg laying		
	14 April– 10 May	11 May– 6 June	7 June– 3 July
Mimetic			
Accept	7	12	6
Reject	4	4	4
Nonmimetic			
Accept	1	0	0
Reject	5	2	4

Mean intraclutch variation in egg appearance among acceptors and rejecters of mimetic eggs was 1.7 ± 0.4 ($n = 23$) and 1.9 ± 0.5 ($n = 11$), respectively (Mann-Whitney *U*-test: $z = -1.2$, $P = 0.25$). Mean contrast between mimetic and host eggs among acceptors and rejecters was 2.2 ± 0.6 ($n = 23$) and 2.6 ± 0.6 ($n = 11$), respectively (Mann-Whitney *U*-test: $z = -1.5$, $P = 0.13$). Two logistic regressions were carried out to determine the effect of contrast and intraclutch variation (independent variables) on rejection vs. acceptance (dependent variable). Intraclutch variation in egg appearance had no significant effect on rejection behavior ($\chi^2_1 = 1.6$, $P = 0.21$). Moreover, rejection was not significantly affected by the contrast between mimetic and host eggs ($\chi^2_1 = 2.8$, $P = 0.09$).

DISCUSSION

The fact that only one (8%) of 13 nonmimetic eggs was accepted in our study clearly shows that Yellowhammers are strong rejecters of eggs unlike their own. More interestingly, we demonstrated that the species

TABLE 3. Comparison of rejection rates of host species experimentally parasitized with mimetic (conspecific) and nonmimetic eggs.

	Frequency of rejection (%)		
Host species	Mimetic eggs (*n*)	Nonmimetic eggs (*n*)	Source
Australian Reed Warbler *Acrocephalus australis*	35 (37)	82 (11)[a]	Welbergen et al. (2001)
Common Whitethroat *Sylvia communis*	54 (13)	100 (21)	Procházka and Honza (2003)
Blackcap *Sylvia atricapilla*	37 (35)	96 (23)	Honza et al., unpubl. data
Brambling *Fringilla montifringilla*	52 (25)	90 (31)[a]	Braa et al. (1992)
Chaffinch *Fringilla coelebs*	54 (24)	69 (16)[a]	Braa et al. (1992)
Yellowhammer *Emberiza citrinella*	32 (37)	92 (13)	this study
Reed Bunting *Emberiza schoeniclus*	38 (8)	91 (11)[a]	Moksnes and Røskaft (1992), Moksnes et al. (1990)

[a] Model eggs used.

also rejects conspecific eggs. Rejection rate of conspecific eggs by Yellowhammers in this study (32%) is similar to that found in other species (Table 3).

Conspecific brood parasitism may be a source of selection for Yellowhammer egg recognition. However, the species does not show any of the common features of conspecific parasites in passerines (Petrie and Møller 1991). Although we monitored the nests daily during egg laying and early incubation, we did not record any cases of intraspecific parasitism. This finding is supported by a DNA analysis by Sundberg and Dixon (1996), who reported no intraspecific parasitism in the species. In addition, Yom-Tov (2001) did not list the species in a recent review of intraspecific brood parasitism. In light of the above facts, we believe that the rejection of conspecific eggs in the species has most likely evolved as an adaptation against interspecific brood parasitism.

Acceptance was the most common response when facing mimetic eggs, whereas ejection was the most common response to nonmimetic eggs. Desertion was a very scarce type of egg rejection and its frequency in parasitized nests was approximately the same in the unparasitized control group. This very low desertion rate contrasts with the results of Moksnes et al. (1991), who recorded desertion in three (38%) of eight nests. This difference may be caused by the use of hard model eggs in the latter study. The Yellowhammer has a small grasp index (a measure of the bill's ability to hold an egg; Moksnes et al. 1991), so it is probably not able to eject cuckoo-sized eggs by grasp-ejection (see also Martín-Vivaldi et al. 2002).

Sixteen (47%) experimental conspecific eggs contrasted markedly with the host's eggs so that they appeared nonmimetic, at least to humans (contrast score >2.5 on the scale used). Quite surprisingly, the hosts accepted eight of these eggs. According to signal detection theory, as applied by Davies et al. (1996) to quantify costs and benefits of acceptance versus rejection in parasitized and unparasitized Reed Warbler (*Acrocephalus scirpaceus*) nests, Yellowhammers should accept mimetic cuckoo eggs at low levels of parasitism, and reject them when the probability of parasitism is high. Although we did not record any cases of cuckoo parasitism during our study, Yellowhammers rejected 32% of conspecific eggs. This ability to recognize introduced eggs may have been facilitated by the interclutch variability in eggshell coloration. However, contrast between the mimetic and host eggs did not differ significantly between acceptors and rejecters, as has been demonstrated in several other species (Jackson 1998, Lahti and Lahti 2002, Stokke et al. 2002). We suggest that acceptors could have been first-year breeders who did not know the appearance of their own eggs, as has been shown for the Great Reed Warbler (*Acrocephalus arundinaceus*) by Lotem et al. (1992). The response of birds may also depend on the visual system of the species (Cherry and Bennett 2001): eggs that appear nonmimetic to humans might be perceived by the hosts as mimetic. Alternatively, our sample sizes may have been too small to obtain significant results.

During their experiments with nonmimetic model cuckoo eggs, Moksnes et al. (1991) found that in all eight nests the introduced eggs were rejected. Of these, three were abandoned, in one nest the model egg was ejected, and in four nests so-called unselective ejections occurred: at least one Yellowhammer egg disappeared, probably due to ejection costs during puncture-ejection of the model cuckoo egg. We did not record any such rejection costs. This finding accords with results of Martín-Vivaldi et al. (2002), who showed that species with a smaller grasp index suffered higher costs when rejecting hard artificial eggs, but not when rejecting real eggs.

We detected no recognition errors. The cost of recognition errors should help explain the ‘‘equilibrium hypothesis’’ (Rothstein 1982, Davies and Brooke 1989, Lotem et al. 1992, 1995) that the adaptive value of rejection is determined by the costs of recognition errors and the probability of being parasitized. Because Yellowhammers reject mimetic eggs in the absence of cuckoo parasitism at our study site, we suggest that the species may have been a more frequent host in the past (Čapek 1910), but it evolved such a strong rejection capability that the cuckoo abandoned this species as a host, and the Yellowhammer cuckoo gens was eventually outcompeted by other gentes. Davies and Brooke (1989) hypothesized that host species freed from parasitism should slowly revert to accepting nonmimetic eggs, whereas Rothstein (2001) suggested that ex-hosts may show long-term retention of egg recognition in the absence of parasitism. Our study reveals that the Yellowhammer has retained its good discrimination ability and this fact may prevent the cuckoo from reusing the host.

We thank students from Charles University in Prague for assessing the scores of egg appearance, Javier R. Álvarez for his Spanish translation of the abstract and Lubomír Kerndl for his hospitality. Comments from Michael I. Cherry, Arnon Lotem, and an anonymous reviewer greatly improved earlier versions of the manuscript. The study was supported by the Grant Agency of Charles University (grant no. B-BIO-124/2001 to PP) and by the Grant Agency of the Czech Republic (grant no. A6093203 to MH).

LITERATURE CITED

BIBER, O. 1997. *Emberiza citrinella*—Yellowhammer, p. 746–747. *In* W. J. M. Hagemeijer and M. J. Blair [EDS.], The EBCC atlas of European breeding birds: their distribution and abundance. T & A D Poyser, London.

BRAA, A. T., A. MOKSNES, AND E. RØSKAFT. 1992. Adaptations of Bramblings and Chaffinches towards parasitism by the Common Cuckoo. Animal Behaviour 43:67–78.

ČAPEK, W. 1910. Einiges über die Fortpflanzungsgeschichte des Kuckucks aus Mähren. Berichte des 5. Internationalen Ornithologischen Kongress Berlin:579–582.

CHERRY, M. I., AND A. T. D. BENNETT. 2001. Egg colour matching in an African cuckoo, as revealed by ultraviolet-visible reflectance spectrophotometry. Proceedings of the Royal Society of London Series B 268:565–571.

Davies, N. B., and M. de L. Brooke. 1988. Cuckoos versus Reed Warblers: adaptations and counter-adaptations. Animal Behaviour 36:262–284.

Davies, N. B., and M. de L. Brooke. 1989. An experimental study of co-evolution between the Cuckoo, *Cuculus canorus* and its hosts. II. Host egg markings, chick discrimination and general discussion. Journal of Animal Ecology 58:225–236.

Davies, N. B., M. de L. Brooke, and A. Kacelnik. 1996. Recognition errors and probability of parasitism determine whether Reed Warblers should accept or reject mimetic Cuckoo eggs. Proceedings of the Royal Society of London Series B 263: 925–931.

Dawkins, R., and J. R. Krebs. 1979. Arms races between and within species. Proceedings of the Royal Society of London Series B 205:489–511.

Gibbs, H. L., M. D. Sorenson, K. Marchetti, M. de L. Brooke, N. B. Davies, and H. Nakamura. 2000. Genetic evidence for female host-specific races of the Common Cuckoo. Nature 407:183–186.

Hasse, H. 1963. Die Goldammer (*Emberiza citrinella*). Ziemsen, Wittenberg-Lutherstadt, Germany.

Hays, H., and M. LeCroy. 1971. Field criteria for determining incubation stage in eggs of the Common Tern. Wilson Bulletin 83:425–429.

Honza, M., A. Moksnes, E. Røskaft, and B. G. Stokke. 2001. How are different Common Cuckoo *Cuculus canorus* morphs maintained? An evaluation of different hypotheses. Ardea 89:341–352.

Jackson, W. M. 1998. Egg discrimination and egg-color variability in the Northern Masked Weaver: the importance of conspecific versus interspecific parasitism, p. 407–418. *In* S. I. Rothstein and S. K. Robinson [eds.], Parasitic birds and their hosts: studies in coevolution. Oxford University Press, New York.

Jourdain, F. C. R. 1925. A study of parasitism in the cuckoos. Proceedings of the Zoological Society of London 1925:639–667.

Lahti, D. C., and A. R. Lahti. 2002. How precise is egg discrimination in weaverbirds? Animal Behaviour 63:1135–1142.

Lawes, M. J., and S. Kirkman. 1996. Egg recognition and interspecific brood parasitism rates in Red Bishops (Aves: Ploceidae). Animal Behaviour 52: 553–563.

Lotem, A., H. Nakamura, and A. Zahavi. 1992. Rejection of cuckoo eggs in relation to host age: a possible evolutionary equilibrium. Behavioral Ecology 3:128–132.

Lotem, A., H. Nakamura, and A. Zahavi. 1995. Constraints on egg discrimination and cuckoo–host co-evolution. Animal Behaviour 49:1185–1209.

Lyon, B. E. 2003. Egg recognition and counting reduce costs of avian conspecific brood parasitism. Nature 422:495–499.

Makatsch, W. 1955. Der Brutparasitismus in der Vogelwelt. Neumann Verlag, Radebeul, Germany.

Makatsch, W. 1976. Die Eier der Vögel Europas. Vol. 2. Neumann Verlag, Radebeul, Germany.

Martín-Vivaldi, M., M. Soler, and A. P. Møller. 2002. Unrealistically high costs of rejecting artificial model eggs in Cuckoo *Cuculus canorus* hosts. Journal of Avian Biology 33:295–301.

Moksnes, A., and E. Røskaft. 1989. Adaptations of Meadow Pipits to parasitism by the Common Cuckoo. Behavioral Ecology and Sociobiology 24:25–30.

Moksnes, A., and E. Røskaft. 1992. Responses of some rare Cuckoo hosts to mimetic model Cuckoo eggs and to foreign conspecific eggs. Ornis Scandinavica 23:17–23.

Moksnes, A., and E. Røskaft. 1995. Egg-morphs and host preference in the Common Cuckoo (*Cuculus canorus*): an analysis of cuckoo and host eggs from European museum collections. Journal of Zoology, London 236:625–648.

Moksnes, A., E. Røskaft, and A. T. Braa. 1991. Rejection behavior by Common Cuckoo hosts towards artificial brood parasite eggs. Auk 108:348–354.

Moksnes, A., E. Røskaft, A. T. Braa, L. Korsnes, H. M. Lampe, and H. C. Pedersen. 1990. Behavioural responses of potential hosts towards artificial cuckoo eggs and dummies. Behaviour 116: 64–85.

Øien, I. J., A. Moksnes, and E. Røskaft. 1995. Evolution of variation in egg color and marking pattern in European passerines: adaptations in a coevolutionary arms race with the Cuckoo, *Cuculus canorus*. Behavioral Ecology 6:166–174.

Øien, I. J., A. Moksnes, E. Røskaft, and M. Honza. 1998. Cost of Cuckoo *Cuculus canorus* parasitism to Reed Warblers *Acrocephalus scirpaceus*. Journal of Avian Biology 29:209–215.

Petrie, M., and A. P. Møller. 1991. Laying eggs in others' nests: intraspecific brood parasitism in birds. Trends in Ecology & Evolution 6:315–320.

Procházka, P., and M. Honza. 2003. Do Common Whitethroats (*Sylvia communis*) discriminate against alien eggs? Journal für Ornithologie 144: 354–363.

Rothstein, S. I. 1975. An experimental and teleonomic investigation of avian brood parasitism. Condor 77:250–271.

Rothstein, S. I. 1982. Successes and failures in avian and nestling recognition with comments on the utility of optimality reasoning. American Zoologist 21:547–560.

Rothstein, S. I. 2001. Relic behaviours, coevolution and the retention versus loss of host defences after episodes of avian brood parasitism. Animal Behaviour 61:95–107.

StatSoft. 2001. STATISTICA (data analysis software system). Version 6. StatSoft Inc., Tulsa, OK.

Stokke, B. G., M. Honza, A. Moksnes, E. Røskaft, and G. Rudolfsen. 2002. Costs associated with recognition and rejection of parasitic eggs in two European passerines. Behaviour 139:629–644.

Sundberg, J., and A. Dixon. 1996. Old, colourful male Yellowhammers, *Emberiza citrinella*, benefit from extra-pair copulations. Animal Behaviour 52:113–122.

WELBERGEN, J., J. KOMDEUR, R. KATS, AND M. BERG. 2001. Egg discrimination in the Australian Reed Warbler (*Acrocephalus australis*): rejection response toward model and conspecific eggs depending on timing and mode of artificial parasitism. Behavioral Ecology 12:8–15.

YOM-TOV, Y. 2001. An updated list and some comments on the occurrence of intraspecific nest parasitism in birds. Ibis 143:133–143.

The Condor 106:410–415

SPATIOTEMPORAL PREDICTABILITY OF SCHOOLING AND NONSCHOOLING PREY OF PIGEON GUILLEMOTS

MICHAEL A. LITZOW[1], JOHN F. PIATT, ALISA A. ABOOKIRE, SUZANN G. SPECKMAN, MAYUMI L. ARIMITSU AND JARED D. FIGURSKI
Alaska Science Center, U.S. Geological Survey, 1011 East Tudor Road, Anchorage, AK 99503

Abstract. Low spatiotemporal variability in the abundance of nonschooling prey might allow Pigeon Guillemots (*Cepphus columba*) to maintain the high chick provisioning rates that are characteristic of the species. We tested predictions of this hypothesis with data collected with beach seines and scuba and hydroacoustic surveys in Kachemak Bay, Alaska, during 1996–1999. Coefficients of variability were 20–211% greater for schooling than nonschooling prey on day, seasonal, and km scales. However, the proportion of schooling prey in chick diets explained relatively little variability in Pigeon Guillemot meal delivery rates at the scale of hours ($r^2 = 0.07$) and weeks ($r^2 = 0.19$). Behavioral adaptations such as flexible time budgets likely ameliorate the negative effects of high resource variability, but we propose that these adaptations are only effective when schooling prey are available at distances well below the maximum foraging range of the species.

Key words: Cepphus, *demersal, foraging, pelagic, provisioning, quality–variability trade-off, seabirds.*

Previsibilidad Espacio-Temporal de Presas que Forman y No Forman Cardúmenes de *Cepphus columba*

Resumen. La baja variabilidad espacio-temporal en la abundancia de presas que no forman cardúmenes podría permitir que *Cepphus columba* mantenga las altas tasas de aprovisionamiento de los pichones que caracterizan a esta especie. Evaluamos las predicciones de esta hipótesis con datos colectados mediante redes barredoras de playa y buceo y muestreos hidro-acústicos en la Bahía Kachemak, Alaska, durante 1996–1999. Los coeficientes de variabilidad fueron 20–211% mayores para las presas que forman cardúmenes que para las que no forman cardúmenes a las escalas diaria, estacional y de km. Sin embargo, la proporción de presas que forman cardúmenes en la dieta de los pichones explicó relativamente poca variabilidad en las tasas de entrega de alimento de *C. columba* a la escala de horas ($r^2 = 0.07$) y semanas ($r^2 = 0.19$). Las adaptaciones de comportamiento como presupuestos de tiempo flexibles probablemente corrigen los efectos negativos de la alta variación de recursos, pero proponemos que estas adaptaciones son sólo efectivas cuando las presas que forman cardúmenes están disponibles a distancias bien por debajo del rango máximo de forrajeo de la especie.

Cepphus guillemots are the only auks (Alcidae) that raise two chicks to near-adult weight in the nest (Sealy 1973). *Cepphus* guillemots also have shorter foraging ranges than other auks (typically <10 km), and feed on a higher proportion of demersal fishes and benthic invertebrates than other members of the family (Gaston and Jones 1998). These prey contain less lipid than the pelagic fishes and crustaceans that dominate the diets of most auks, and are therefore lower in energy density (kJ g^{-1}; Norrbin and Båmstedt 1984, Anthony et al. 2000). The higher energy density of pelagic prey results in increased chick growth rates and reproductive success for Pigeon Guillemots (*Cepphus columba*) that feed their chicks these prey (Golet et al. 2000, Litzow et al. 2002). However, in spite of these benefits of pelagic prey, *Cepphus* guillemots often feed chicks mostly demersal fishes, even when pelagic prey are apparently abundant (Cairns 1987, Golet et al. 2000,

---

Manuscript received 4 April 2003; accepted 9 October 2003.

[1] Present address: Kodiak Fisheries Research Center, 301 Research Ct., Kodiak, AK 99615. E-mail: mike_litzow@yahoo.com

Litzow et al. 2000). The answer to this paradox may lie in differences in dispersion of demersal prey, which are typically nonschooling, and pelagic prey, which are exclusively schooling. Kuletz (1983) and Cairns (1987) proposed that nonschooling fishes are spatially and temporally more predictable than schooling fishes, and that this predictability offsets the disadvantage of lower energy density by allowing *Cepphus* guillemots to maintain the high provisioning rates necessary to raise two chicks to near-adult weight. This ''quality–variability trade-off'' hypothesis fits with the general view that distributions of schooling fishes and crustaceans are spatially and temporally more heterogeneous than those of nonschooling taxa (Valiela 1995), and the recognition that high variability of schooling prey is an important constraint on seabird foraging success (Lack 1968, Ashmole 1971). Schooling prey are more variable than nonschooling prey on interannual time scales, both in the environment (Litzow and Piatt 2003) and in Pigeon Guillemot diets (Golet et al. 2000). However, we are not aware of previous studies that have compared variability in abundance of the two prey groups at scales (days, weeks, and km) that match the temporal and spatial scales of *Cepphus* foraging during chick rearing. Such a comparison may shed light on factors shaping the foraging ecology and life history of seabirds feeding on these two prey types.

In this paper we compare the spatial and temporal variability of schooling and nonschooling prey of Pigeon Guillemots at these finer scales, using data on prey abundance that were collected in Kachemak Bay, Alaska, during 1996–1999 with beach seines, scuba transects, and hydroacoustic surveys. We also use data from all-day watches of Pigeon Guillemot chick provisioning to relate the proportion of schooling prey in the diet to variability in meal delivery rates. Our objectives were to test two predictions of the quality–variability trade-off hypothesis: (1) schooling prey species are spatially and temporally more variable in abundance than nonschooling prey species; and (2) meal delivery rates are more variable when schooling prey dominate diets.

METHODS

Kachemak Bay (59°35′N, 151°19′W) is located on the east shore of lower Cook Inlet, Alaska. Pigeon Guillemots nest in approximately 30 small colonies of 2–15 nests each and in numerous solitary sites on the south shore of Kachemak Bay, and approximately 500–600 adults are present in the area during the nesting season. Chick diets at some colonies are dominated by a pelagic schooling fish, Pacific sand lance (*Ammodytes hexapterus*), while diets at other colonies are dominated by a variety of nonschooling demersal fishes and hermit crabs (*Pagurus* spp.; Litzow et al. 1998, 2000).

We used catch per unit effort (with units of number of fish set^{-1}) data from beach seines to measure seasonal and km-scale variability in prey abundance (see Abookire et al. 2000, Litzow et al. 2000 for detailed methods). We fished with a 44-m-long net at 11 stations every 2 weeks during June, July, and August of 1996–1999 ($n = 231$ sets). Stations were separated by 1.5–16 km over 44 km of shoreline (straight-line distance), and sets were made within one hour of spring low tides. Beach seines sample the shallow ($\leq$5 m) nearshore waters where Pigeon Guillemots in the study area mostly forage (Litzow et al., unpubl. data). Fish were identified to species, except for snake pricklebacks (*Lumpenus sagitta*) and slender eelblennys (*L. fabricii*), which could not be reliably distinguished in the field. We were only interested in studying fishes that were important prey for guillemots and that were caught often enough in beach seines to generate accurate abundance estimates. We therefore limited our analysis to taxa with catch per unit effort $\geq$1 fish set^{-1} and those documented as major prey of Pigeon Guillemots in Alaska (i.e., $\geq$1% of meals in a colony-year; Golet et al. 2000, Litzow et al. 2000).

We used repeated scuba and hydroacoustic surveys to measure among-day variability in prey abundance during July 1999. Scuba and hydroacoustic transects were set in areas where radio-tagged Pigeon Guillemots had been observed foraging on nonschooling fishes and sand lance, respectively (Litzow and Piatt 2003). All surveys were conducted within 1 hr of low tide. Scuba transects were 60–100 m long and took place in 5–11 m of water. Transect depth was held constant $\pm$1 m. We counted all demersal fishes and hermit crabs in a 2-m swath along the transect and identified prey to the lowest possible taxonomic level. Nonschooling prey abundance was defined as the number of prey items in taxonomic groups consumed by Pigeon Guillemots (Arctic shanny [*Stichaeus punctatus*], flatfish [Pleuronectidae], gunnels [Pholidae], pricklebacks [*Lumpenus* spp.], rockfish [*Sebastes* spp.], ronquils [*Bathymaster signatus* and *Ronquilus jordani*], sculpins [Cottidae], and hermit crabs). Three transects (separated by 0.5 to 11 km) were each surveyed two to three times at intervals of 1–2 days ($n = 7$ total replicates).

Hydroacoustic surveys were conducted from an 11-m boat. Six transects were each surveyed on 3 consecutive days ($n = 18$ total replicates). Transects were 100 m long, ran perpendicular to the shore beginning in 3-m-deep water, and were separated by >200 m. Hydroacoustic data were collected with a single-beam 120-kHz Biosonics DT4000 transducer with a 6° beam angle (Biosonics, Inc., Seattle, Washington). Data were analyzed with Echoview (Sonar Data Proprietary Ltd. 2000). Species composition could not be determined during our hydroacoustic surveys, so we used relative acoustic biomass (mean backscattering m^{-2}), and did not attempt to estimate actual biomass using species-specific target strengths. We calculated relative acoustic biomass with binned cells (5 m × 1 min blocks) with an integration threshold of -68 dB and bottom blanking at -1 m, and values were averaged for each transect. Midwater trawls in Kachemak Bay indicate that the pelagic fish community is dominated by sand lance, with an order of magnitude less Pacific herring (*Clupea pallasi*), capelin (*Mallotus villosus*), juvenile walleye pollock (*Theragra chalcogramma*), and juvenile Pacific cod (*Gadus macrocephalus*; Robards et al. 1999; Abookire et al., unpubl. data), so we assumed that sand lance comprised the majority of acoustic biomass during our surveys.

We collected Pigeon Guillemot delivery rate data in July and August during 1996–1999 at six guillemot colonies in Kachemak Bay. We observed breeding Pigeon Guillemots from anchored boats (using binoculars) or from blinds (using telescopes) during all-day watches (06:00–22:00 AST). We watched two to five nests during each watch, and typically could not identify individual mates, so we use the nest as our sample unit ($n = 64$ nests). We recorded the time of each delivery, and identified each meal to the lowest possible taxonomic level. A subset of nests were accessible so that we could determine brood size and chick age, and we observed these more than once in a year so that we could calculate seasonal variability in delivery rate ($n = 22$). The mean range of dates for nests watched more than once was 13.5 ± 5.6 [SD] days.

STATISTICAL ANALYSES

Among-day variability in abundance for schooling and nonschooling prey was defined as the coefficient of variability (CV) in abundance among replicates at individual hydroacoustic and scuba transects, respectively. Seasonal variability for both prey types was defined as CV among bimonthly sampling periods at individual beach seine sites, and grand means of annual values from individual sites were used in analysis. Km-scale variability was defined as the annual mean CV among sites. For analysis of seasonal and km-scale variability we used individual taxa nested within prey type (schooling or nonschooling) as our sample unit. We treated CV values for the 11 stations as subsamples of seasonal-scale variability for each prey species by including site as an independent factor in a general linear model (GLM; Zar 1999). For analysis of km-scale variability we treated annual mean values of CV among seine stations as subsamples by including year as a factor. We also compared abundance between prey groups by comparing catch per unit effort in GLM with site, species(prey type), and prey type as factors. Catch per unit effort data were log ($x + 1$) transformed for this analysis to meet assumptions of homoscedasticity.

We calculated hour-scale variability in delivery rate (meals hr^{-1}) as SD in delivery rate among hours within individual watches for individual nests. To avoid pseudoreplication we used average SD values when individual nests were watched more than once in a year. Seasonal-scale variability was calculated as SD in delivery rate among days for nests that were watched more than once in a year. Delivery rates are affected by changes in nestling demand (brood size and chick age; Drent 1965). We controlled for variability in brood size by calculating per capita delivery rates (meals $chick^{-1}$ hr^{-1}). We controlled for variability in chick age in GLM by including SD in chick age among individual provisioning watches, as well as the mean proportion of schooling prey in the diet, as independent variables, and SD in delivery rate as the dependent variable. We used partial r^2 values in order to assess the contribution to variability in delivery rates due to each of these independent factors. Proportional data were arcsine transformed to meet assumptions of normality, and type-III sums of squares were used for all GLM analysis (SAS Institute 2000). We set $\alpha = 0.05$. Means are presented ± SE, and seine CV values are least-squares means from GLM.

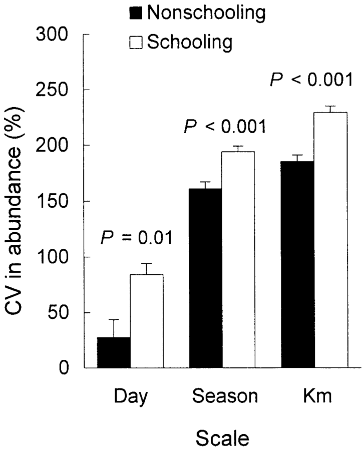

FIGURE 1. Spatiotemporal variability of schooling and nonschooling prey of Pigeon Guillemots in Kachemak Bay, Alaska. Variability is expressed as mean + SE of the coefficient of variation. Day-scale data are from scuba (nonschooling fishes and hermit crabs; $n = 7$ total replicates of 3 transects) and hydroacoustic transects (schooling fishes; $n = 18$ total replicates of 6 transects). Seasonal and km-scale data are from beach seines ($n = 231$ total sets at 11 locations).

RESULTS

Beach seine catches were dominated by three schooling Pigeon Guillemot prey taxa (sand lance, Pacific herring, and Pacific cod) and three nonschooling prey taxa (great sculpin [*Myoxocephalus polyacanthocephalus*], rock sole [*Lepidopsetta bilineatus*], and *Lumpenus* pricklebacks). Together these taxa made up 96% of the 232 224 fish caught in seines. *Lumpenus* pricklebacks, sculpins, and hermit crabs made up 94% of the 573 prey items observed on scuba transects. Among-day CV of schooling prey on hydroacoustic surveys (84 ± 10%) was 211% greater than that of nonschooling prey on scuba transects (27 ± 16%; $t_4 = 3.1$, $P = 0.01$; Fig. 1). Seasonal CV of beach seine catch per unit effort (Fig. 1) was 20% greater for schooling prey (194 ± 5%) than for nonschooling prey (161 ± 6%; $F_{15,48} = 3.8$, $P < 0.001$, Table 1). Km-scale CV in beach seine catch (Fig. 1) was 24% greater for schooling prey (229 ± 6%) than for nonschooling prey (185 ± 6%; $F_{8,15} = 17.3$, $P < 0.001$, Table 1). Mean catch per unit effort was also 40 times greater for schooling fishes (317 ± 206 fish set^{-1}) than for nonschooling fishes (8 ± 5 fish set^{-1}; $F_{15,50} = 6.9$, $P < 0.001$, Table 1).

We detected a weak, significant relationship between the proportion of schooling prey in the diet and hour-scale variability in meal delivery rates (linear regression, $n = 64$ nests, $r^2 = 0.07$, $P = 0.01$; Fig. 2a). Variability in delivery rate was also higher at the seasonal scale (Fig. 2b) when schooling prey dominated

TABLE 1. Comparisons of variability and abundance between Pigeon Guillemot prey types (schooling and nonschooling), and the effect of the proportion of schooling prey on seasonal variability in meal delivery rates at Pigeon Guillemot nests: GLM results. Seine catch is measured as catch per unit effort (number of fish set^{-1}).

Response variable	df	MS	*F*	*P*
Seasonal CV in seine catch				
Site	10	1706	1.8	0.09
Species (Prey type)	4	4799	5.0	<0.01
Prey type	1	16 627	17.4	<0.001
Error	48	958		
Km-scale CV in seine catch				
Year	3	1918	4.4	0.02
Species (Prey type)	4	10 679	24.5	<0.001
Prey type	1	11 870	27.3	<0.001
Error	15	436		
Mean seine catch				
Site	10	1.0	2.7	0.01
Species (Prey type)	4	3.7	10.0	<0.001
Prey type	1	13.2	35.7	<0.001
Error	50	0.4		
Seasonal SD in delivery rate				
SD in chick age	1	0.03	2.1	0.16
Proportion schooling prey in diet	1	0.06	4.6	0.05
Error	19	0.01		

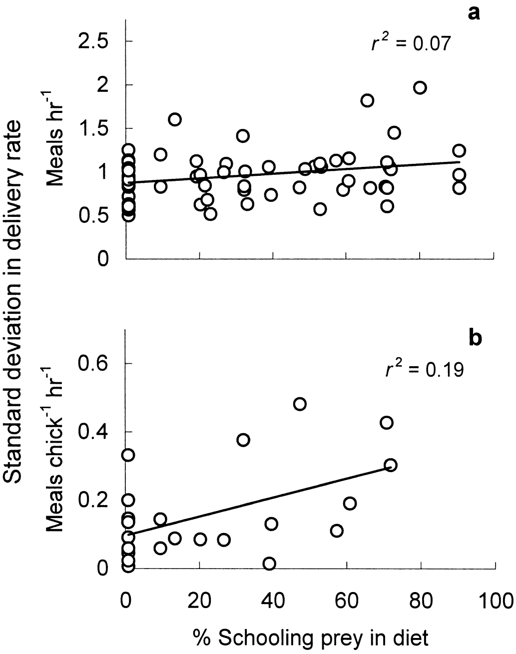

FIGURE 2. Variability in Pigeon Guillemot meal delivery rates in relation to the proportion of schooling prey in the diet at the scale of (a) hours and (b) season. Each dot represents a single nest-year. Twenty dots lie on the *y*-axis in the top panel, nine in the bottom panel. Percentages of schooling prey were arcsine transformed prior to analysis.

the diet (n = 22 nests, $F_{2,19}$ = 4.8, P = 0.02, partial r^2 [SD in chick age] = 0.10, partial r^2 [proportion of schooling prey in diet] = 0.19; Table 1).

DISCUSSION

Our results support the prediction of the quality–variability trade-off hypothesis that nonschooling prey are less variable than schooling prey at multiple spatial and temporal scales. Many species of auks, cormorants, and penguins prey on both nonschooling (mostly demersal) and schooling (mostly pelagic) prey, so this result may have broad implications for many pursuit-diving seabirds (Tremblay and Cherel 2000). Differences between the two prey types were most striking at the seasonal and km scales, as intensive beach seine sampling provided high statistical power for these comparisons. Although sampling effort was limited for both scuba and hydroacoustic surveys, we were also able to detect a large difference between prey types in day-scale variability.

Our results also support the prediction that provisioning with schooling prey will result in increased variability in meal delivery rates. However, diet composition accounted for only 7% of variability in delivery rates at the hour scale, and 19% at the seasonal scale (when nestling demand was controlled for). The proportion of schooling prey in the diet explained 21% of variability among individual nests in mean energy provisioning rates (kJ hr^{-1}), even when nestling demand was not taken into account (Litzow et al. 2002). Diets of lipid-rich schooling prey also increased chick growth rates and reproductive success, and chick survival and reproductive success were less variable for parents that provisioned with schooling prey (Golet et al. 2000, Litzow et al. 2002). The increases in variability in delivery rate that we observed in the current study seem inadequate to explain selection of nonschooling prey, given the known advantages of schooling prey. If variability in prey abundance only weakly affects variability in delivery rates, and has no apparent negative effects on reproductive success, why are nonschooling fishes typically the dominant items in *Cepphus* chick diets?

Pigeon Guillemots react to variability in prey abundance with prey switching and flexible foraging effort (Litzow et al. 2000, Litzow and Piatt 2003), and these behavioral buffers likely reduce the effect that high variability in schooling prey abundance has on variability in meal delivery rates. However, km-scale patterns of prey utilization and availability in Kachemak Bay suggest that these behavioral adaptations may allow Pigeon Guillemots to buffer against high variability only when schooling prey are available close to the colony. Sand lance comprise 67–73% of chick diets at three colonies that are <0.5 km from an area that supports the highest density of sand lance in Kachemak Bay (Abookire et al. 2000, Litzow et al. 2000). In contrast, diets are 15% and 0% sand lance at two colonies that are 4 km and 10 km, respectively, from the same sand-lance-rich area (Litzow et al. 2000). We hypothesize that *Cepphus* guillemots are able to buffer against high short-term variability in schooling prey abundance only when these prey are available very close to the colony (within ~ 1 km). Successful foraging on variable schooling prey apparently requires a buffer of discretionary time that can be allocated to foraging when prey availability is low (Litzow and Piatt 2003). Because Pigeon Guillemots make so many foraging trips during peak chick demand (10–15 trips day^{-1} parent^{-1}, Litzow et al., unpubl. data), such discretionary time is likely not available to individuals foraging at maximal ranges.

Finally, schooling prey abundance (mean beach seine catch per unit effort) in this study was more than an order of magnitude greater than that of nonschooling prey. This high abundance may help Pigeon Guillemots to buffer against temporal variability in abundance, and may make schooling prey less susceptible to depletion around the colony (''Ashmole's halo''; Ashmole 1963), as has been demonstrated for the nonschooling prey of Double-crested Cormorants (*Phalacrocorax auritus*; Birt et al. 1987).

Our thanks to the many people who assisted with fieldwork: April Benson, Dave Black, Bryan Duggan, Jennifer Litzow, Jeff Moy, Cynthia Restrepo, Pam Seiser, Becka Seymour, Brian Smith, Kim Trust, and Sadie Wright. Special thanks to Martin Robards for leading beach seine sampling in 1996–1997. Bradford Keitt, Greg Snedgen, and Tom Van Pelt helped with logistics. We thank Alex Prichard and Dan Roby for their many contributions to guillemot research in Kachemak Bay, and two anonymous reviewers for helpful criticism. Funding was provided by the *Exxon Valdez* Oil Spill Trustee Council and the U.S. Minerals Management Service.

LITERATURE CITED

ABOOKIRE, A. A., J. F. PIATT, AND M. D. ROBARDS. 2000. Nearshore fish distributions in an Alaskan estuary in relation to stratification, temperature, and salinity. Estuarine, Coastal and Shelf Science 51:45–59.

ANTHONY, J. A., D. D. ROBY, AND K. R. TURCO. 2000. Lipid content and energy density of forage fishes from the northern Gulf of Alaska. Journal of Experimental Marine Biology and Ecology 248:53–78.

ASHMOLE, N. P. 1963. The regulation of numbers of tropical oceanic birds. Ibis 103:458–473.

ASHMOLE, N. P. 1971. Seabird ecology and the marine environment, p. 223–286. *In* D. S. Farner and J. R. King [EDS.], Avian biology. Vol. 1. Academic Press, New York.

BIRT, V. L., T. P. BIRT, D. GOULET, D. K. CAIRNS, AND W. A. MONTEVECCHI. 1987. Ashmole's halo: direct evidence for prey depletion by a seabird. Marine Ecology Progress Series 40:205–208.

CAIRNS, D. K. 1987. The ecology and energetics of chick provisioning by Black Guillemots. Condor 89:627–635.

DRENT, R. H. 1965. Breeding biology of the Pigeon Guillemot, *Cepphus columba*. Ardea 53:99–160.

GASTON, A. J., AND I. L. JONES. 1998. The auks. Oxford University Press, New York.

GOLET, G. H., K. J. KULETZ, D. D. ROBY, AND D. B. IRONS. 2000. Adult prey choice affects chick growth and reproductive success in Pigeon Guillemots. Auk 117:82–91.

KULETZ, K. J. 1983. Mechanisms and consequences of foraging behavior in a population of breeding Pigeon Guillemots. M.Sc. thesis, University of California, Irvine, CA.

LACK, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

LITZOW, M. A., AND J. F. PIATT. 2003. Variance in prey abundance influences time budgets of breeding seabirds: evidence from Pigeon Guillemots *Cepphus columba*. Journal of Avian Biology 34:54–64.

LITZOW, M. A., J. F. PIATT, A. A. ABOOKIRE, A. K. PRICHARD, AND M. D. ROBARDS. 2000. Monitoring temporal and spatial variability in sandeel (*Ammodytes hexapterus*) abundance with Pigeon Guillemot (*Cepphus columba*) diets. ICES Journal of Marine Science 57:976–986.

LITZOW, M. A., J. F. PIATT, AND J. D. FIGURSKI. 1998. Hermit crabs in the diet of Pigeon Guillemots in Kachemak Bay, Alaska. Colonial Waterbirds 21: 242–244.

LITZOW, M. A., J. F. PIATT, A. K. PRICHARD, AND D. D. ROBY. 2002. Response of Pigeon Guillemots to variable abundance of high-lipid and low-lipid prey. Oecologia 132:286–295.

NORRBIN, F., AND U. BÅMSTEDT. 1984. Energy contents in benthic and planktonic invertebrates of Kosterfjorden, Sweden. A comparison of energetic strategies in marine organism groups. Ophelia 23: 47–64.

ROBARDS, M. D., J. F. PIATT, A. B. KETTLE, AND A. A.

ABOOKIRE. 1999. Temporal and geographic variation in fish communities of lower Cook Inlet, Alaska. Fishery Bulletin 97:962–977.

SAS INSTITUTE. 2000. SAS/STAT user's guide, version 8.1. SAS Institute Inc., Cary, NC.

SEALY, S. G. 1973. Adaptive significance of post-hatching developmental patterns and growth rates in the Alcidae. Ornis Scandinavica 4:113–121.

SONAR DATA PROPRIETARY LTD. 2000. Echoview v. 2.1. Hobart, Tasmania.

TREMBLAY, Y., AND Y. CHEREL. 2000. Benthic and pelagic dives: a new foraging behaviour in Rockhopper Penguins. Marine Ecology Progress Series 204:257–267.

VALIELA, I. 1995. Marine ecological processes. Springer, New York.

ZAR, J. H. 1999. Biostatistical analysis. Simon and Schuster, Upper Saddle River, NJ.

The Condor 106:415–419

RAPTOR PREDATION ON WINTERING DUNLINS IN RELATION TO THE TIDAL CYCLE

DICK DEKKER[1,3] AND RON YDENBERG[2]
[1]3819-112 A Street, Edmonton, AB T6J 1K4, Canada
[2]Department of Biological Sciences, Simon Fraser University, Burnaby, BC V5A 1S6, Canada

Abstract. At Boundary Bay, British Columbia, Canada, Peregrine Falcons (*Falco peregrinus*) captured 94 Dunlins (*Calidris alpina*) in 652 hunts. The two main hunting methods were open attacks on flying Dunlins (62%) and stealth attacks on roosting or foraging Dunlins (35%). Peregrines hunted throughout the day, yet the kill rate per observation hour dropped 1–2 hr before high tide and peaked 1–2 hr after high tide. The drop in kill rate coincided with the departure of the mass of Dunlins for over-ocean flights lasting 2–4 hr. The peak in kill rate occurred just after the tide began to ebb and the Dunlins returned to forage in the shore zone. The hypothesis that closeness to shoreline vegetation is dangerous for Dunlins is supported by three converging lines of evidence: (1) the high success rate (44%) of peregrine hunts over the shore zone compared to the rate (11%) over tide flats and ocean; (2) the high kill rate per observation hour at high tide; and (3) the positive correlation of kill rate with the height of the tides. Seven of 13 Dunlins killed by Merlins (*Falco columbarius*) and all five Dunlins killed by Northern Harriers (*Circus cyaneus*) were also captured in the shore zone.

Key words: Calidris alpina, *Dunlin,* Falco peregrinus, *Peregrine Falcon, raptor predation, tidal cycle.*

Depredación de *Calidris alpina* por Rapaces durante el Período Invernal con Relación al Ciclo de la Marea

Resumen. En la Bahía Boundary, Columbia Británica, Canadá, halcones *Falco peregrinus* capturaron 94 ejemplares de *Calidris alpina* en 652 horas. Los dos métodos principales de caza fueron ataques abiertos sobre individuos que estaban volando (62%) y ataques encubiertos sobre individuos que estaban posados o forrajeando (35%). *F. peregrinus* cazó a lo largo del día, pero la tasa de matanza por hora de observación disminuyó 1–2 hr antes de la pleamar y alcanzó un máximo 1–2 hr después de la pleamar. La caída en la tasa de matanza coincidió con la partida en masa de *C. alpina* para realizar vuelos sobre el océano que duraron 2–4 hr. El pico en la tasa de matanza ocurrió justo después de que la marea comenzó a menguar y de que los individuos de *C. alpina* regresaron a forrajear a la zona de playa. La hipótesis de que la cercanía de la vegetación a la línea de playa es peligrosa para *C. alpina* es apoyada por tres líneas convergentes de evidencia: (1) la alta tasa de éxito (44%) de las cacerías de *F. peregrinus* sobre la zona de playa comparada con la tasa (11%) de las cacerías sobre los planos de la marea y el océano; (2) la alta tasa de matanza por hora de observación durante la pleamar; y (3) la correlación positiva de la tasa de matanza con la altura de las mareas. Siete de 13 individuos de *C. alpina* cazados por *F. columbarius* y todos 5 individuos de *C. alpina* cazados por *Circus cyaneus* también fueron atrapados en la zona de playa.

Predation risk has been implicated by many researchers as an important determinant in the feeding behavior of a wide variety of prey species (Lima et al. 1985, Milinski 1986). According to theory, avian prey species balance predation risk with foraging needs. For instance, in a trade-off between relative safety from predators and optimal caloric gain, forest passerines tend to forage close to the protective cover of trees and bushes, whereas open-country birds stay well

---

Manuscript received 29 May 2003; accepted 12 November 2003.

[3] E-mail: tj_dick_dekker@hotmail.com

away from vegetation that could conceal raptors (Valone and Lima 1987, Lima 1988). In estuarine habitats, shorebirds frequent open expanses of mudflats which allow for the timely discovery of approaching raptors. Raptors that hunt shorebirds, such as the Peregrine Falcon (*Falco peregrinus*) and the Merlin (*Falco columbarius*), commonly use stealth methods to take their prey by surprise (Page and Whitacre 1975, Dekker 1980, 1988, Palmer 1988, Cresswell 1996, White et al. 2002). If rising tides inundate the mudflats and force the shorebirds close to the vegetated high-tide line, most leave and fly to roosting sites in adjacent country. In some locations, shorebirds roost in habitats they do not normally frequent, such as agricultural lands (Butler 1994) or wave-swept beaches (Buchanan 1996). On the northwest Pacific coast of North America, and probably elsewhere in its extensive wintering range, Dunlin flocks fly out over the ocean and remain in flight for 2–4 hr until the tide turns. This behavior was interpreted as a possible antipredator strategy by Brennan et al. (1985) and first documented as such by Dekker (1998). Hotker (2000) saw the same phenomenon on the north coast of Germany and termed it ''airborne roosting.'' Staying in flight over the water far offshore makes sense if roosting sites close to the high-tide mark are dangerous. Ydenberg et al. (2002) found that the choice of stopover sites by migrating Western Sandpipers (*Calidris mauri*) in British Columbia, Canada, could best be explained by a hypothesis that sandpipers are more vulnerable to raptor predation on small feeding sites than on wide expanses of open mudflats.

In this article, we examine a large data set of observed hunts and kills by Peregrine Falcons to test the hypothesis that proximity to shoreline vegetation is dangerous for Dunlins, and that Dunlins tend to avoid risk when they are satiated, but are more willing to take risk when hungry. As additional evidence for that hypothesis, we also report on Dunlin kills by Merlins (*Falco columbarius*) and Northern Harriers (*Circus cyaneus*).

METHODS

The study area was at Boundary Bay, on the southern edge of the Fraser River estuary (49°05′N, 123°00′W) in British Columbia, Canada. The bay is 16 km across and the intertidal zone is roughly 4 km wide at the lowest ebb. The tidal rhythm includes two flood tides, one usually higher than the other, per 24-hr period. During winter the highest tides almost always occur during daylight hours and inundate all intertidal mudflats and most of the narrow strip of saltmarsh, which is covered with low vegetation. A dyke protects low-lying agricultural fields inland. Boundary Bay is a major stopover for migratory waterbirds and a wintering location for circa 50 000 Dunlins and 1000 Black-bellied Plovers (*Pluvialis squatarola*). Birds of prey are common (Butler and Campbell 1987). In winter, the bay is hunted over by at least six peregrines and one or more Merlins (Dekker 2003).

Between early November and early February, 1994–2003, DD spent part or all of 151 days (940 hr) in the study area, walking the dyke or sitting in a parked vehicle. Flocks of Dunlins were monitored for alarm behavior such as sudden flushing. Hunting raptors were also discovered by frequently scanning the area through 8× wide-angle binoculars. Perched peregrines and Merlins were often kept under surveillance for periods of up to 2 hr in the hope of seeing them hunt. We use the term ''hunt'' to mean a completed attack of which the outcome was known. A hunt could include one or more passes or swoops at the same Dunlin. An attack on a flock and subsequent pursuit of a single Dunlin fleeing that flock were counted as one hunt. However, if the falcon abandoned the pursuit and again attacked the same or a different flock, it was tallied as another hunt. This definition of a hunt was also used by Dekker (1980, 1988, 2003) and is the equivalent of the term ''attack'' as formulated by Cresswell (1996). In this paper, both terms are used interchangeably.

Field data were recorded in diary form and entered into an annotated table of hunts and kills, divided over three zones. Zone 1 represented the saltmarsh shore including a 5–10 m strip of wrack and sparsely vegetated mud beyond the ragged marsh edge. To investigate whether peregrine hunting success was influenced by distance from shore, we arbitrarily split the intertidal zone in two: zone 2 extended roughly 0.5 km from the saltmarsh; zone 3 lay beyond zone 2. Depending on the tide height, zones 2 and 3 could consist of mudflats and ocean. Although a hunt or pursuit might cross over from one zone into the next, the position of the prey at the start of the attack defined the zone in which the hunt was considered to have taken place. In a few borderline cases, the choice amounted to a judgment call or best guess. Details on Peregrine Falcon characteristics and hunting methods, and Dunlin behavior when avoiding raptors were given in Dekker (2003).

We recorded the zone (1, 2, or 3) in which each hunt took place and the time until or since the nearest high tide. From this summary, we derived the kill rate per observation hour in relation to the time of day (intervals of 1 hr) and the time of the nearest high tide, based on the tide tables published for Point Atkinson, British Columbia. In a separate data analysis, RY compared the kill rate to the height of the tide (grouped into 40-cm intervals) at the time of the kill, using the algorithm available at XTide (Flater 1998). The result was tested for significance by standard regression procedures. The peregrine hunting success rate over the shore zone (zone 1) was compared statistically to zones 2 and 3 by a *G*-test of independence (Sokal and Rohlf 1981).

No attempt was made to record the number of Dunlins present in the attack zone when hunts and kills took place. Large numbers of Dunlins do not necessarily translate into a high kill rate. On the contrary, singletons or small, isolated flocks of prey were reported to be more vulnerable to stealth attacks by peregrines than large or multiple flocks spaced out over a wide area (Dekker 1980, 1998, Thiollay 1982).

RESULTS

A total of 652 peregrine hunts directed at Dunlins was observed. Of these, 94 ended in kills. Hunts and kills took place throughout daylight hours at average rates

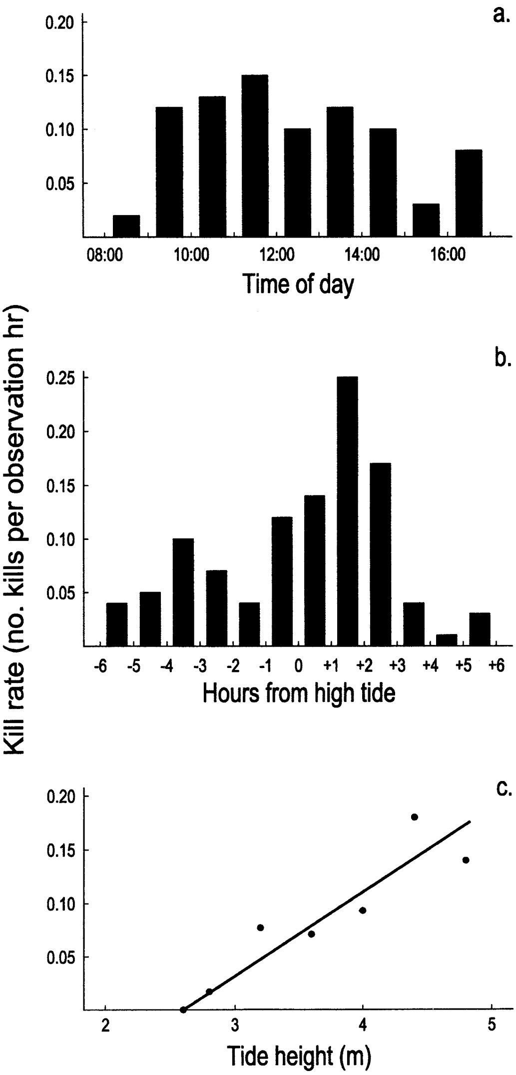

FIGURE 1. Temporal and tidal patterns of Peregrine Falcon predation on Dunlins wintering at Boundary Bay, British Columbia, Canada. (a) Kill rate (no. captures per observation hr) in relation to the time of day. Number of kills and observation time (hr) in the successive intervals were 1/49, 11/95, 15/117, 19/128, 13/136, 15/126, 13/127, 3/110, 4/52. (b) Kill rate relative to the crest of the nearest high tide. Number of kills and observation time (hr) in the successive intervals were 2/49, 3/55, 6/62, 5/75, 4/87, 12/100, 13/106, 25/104, 18/90, 3/79, 1/69, 2/58. (c) Correlation between kill rate and height of the tide. The regression equation is $\textit{kill rate} = 0.068 \times \textit{tide height}$ (m) $- 0.16$ ($r^2 = 0.86$, $F^{1.5} = 29.8$, $P < 0.001$). Number of kills and observation time (hr) for the successive points were 0/25, 1/58, 8/104, 16/224, 26/279, 36/199, 7/50.

TABLE 1. Success rates of Peregrine Falcons hunting Dunlins at Boundary Bay, British Columbia, Canada. Zone 1 represents the ocean shore–saltmarsh edge; zone 2 extends 0.5 km beyond zone 1; zone 3 begins 0.5 km from the saltmarsh. Depending on tide height, zones 2 and 3 could consist of mudflats and ocean.

Zone	No. hunts	No. kills	Success rate (%)
Zone 1	75	33	44
Zone 2	299	33	11
Zone 3	278	28	10
Total	652	94	14

of 0.69 hunts per hr and 0.10 kills per hr. The kill rate per observation hour was quite consistent throughout the day except for declines in early morning (08:00–09:00) and late afternoon (15:00–16:00; Fig. 1a).

The kill rate showed a strong association with the tidal cycle, rising with the flooding tide and falling with the ebbing tide (Fig. 1b). The kill rate peaked 1–2 hr after high tide. The only anomaly in this pattern was a marked low in kill rate beginning 2 hr before high tide. The rate during this 1-hr interval was nearly one-half of the previous interval and one-third of the next. The kill rates also showed a strong and significant linear relation with the height of the tide, rising steadily to 0.14–0.18 kills per hr at tide heights over 4.2 m (Fig. 1c).

The success rate of hunts differed substantially between zones and apparently as a function of the type of attack. In zone 1 all attacks were aimed at Dunlins roosting or feeding near the saltmarsh, and peregrines always attacked using stealth, approaching very low (<1 m) over the shoreline vegetation or rushing up over the dyke. Surprise could be near complete, resulting in the capture of a Dunlin the moment the flock flushed in alarm. In zone 1, peregrines had a success rate of 44% (33 kills in 75 hunts; Table 1). If a stealth hunt in this zone was not immediately successful, peregrines rarely gave chase.

The success rate of all hunts in zone 2 was nearly the same as in zone 3 (11% vs. 10%). Combined, the success rate of stealth hunts in these two zones was 14% (21 kills in 154 hunts), significantly lower than in zone 1 ($G = 14.2$, $P < 0.001$). Most (70%) hunts in zones 2 and 3 did not use stealth, but were open attacks on Dunlins in flight or of birds that had flushed well ahead of the falcon. These open attacks on flying Dunlins had a success rate of 9% (37 kills in 406 hunts). The success rate of all peregrine attacks over zones 2 and 3 (11%) was significantly lower than all hunts over zone 1 (44%; $G = 29.4$, $P < 0.001$).

Other raptors also attacked Dunlins. Harriers frequently attempted to approach roosting Dunlins by stealth. Of an estimated 300 harrier attacks only five were successful and all of these took place in zone 1. Probably reflecting the low risk posed by harriers, Dunlins showed minimal avoidance response. If flushed by harriers, the Dunlins returned to the same place as soon as the raptor had passed by. Merlins were far less common than harriers, but more adept hunters of Dunlins; 7 of 23 stealth attacks on flocks roosting in zone 1 were successful (30%). Merlins also hunted over zones 2 and 3, using stealth as the initial strategy in 28 attacks on flocks. After the stealth approach failed, six captures were made by persistent pursuit of single Dunlins that had left the flock (21%).

Attacks by Merlins and peregrines always caused Dunlin flocks to move to another location or to begin their over-ocean flights, which generally started 1–2 hr before the rising tide inundated all mudflat habitat.

DISCUSSION

The hypothesis that raptor predation risk for small shorebirds increases with closeness to vegetation is supported in this study by three converging lines of evidence: (1) the high success rate of peregrines hunting over the saltmarsh zone; (2) the relatively high kill rate per observation hour when Dunlins are in the saltmarsh zone; and (3) the positive correlation of kill rate with the height of the rising tide. The results of this study also lend additional support for the hypothesis that the over-ocean flocking of Dunlins during high winter tides is an antipredator strategy (Dekker 1998, Hotker 2000). Flying far from shore, at varying altitudes depending on weather conditions, the Dunlins are safe from the most dangerous type of raptor attack: a stealth approach concealed behind vegetation.

The overall percentage of stealth hunts by peregrines in this study (35%) is nearly equivalent to the 36% reported in 233 shorebird hunts on the coast of Scotland (Cresswell 1996). By contrast, the percentage of stealth flights in 569 shorebird hunts recorded at a large marshy lake in Alberta was 77% (Dekker 1988). The explanation for these dissimilar values is that the habitat in these two areas was quite different. At the lake, reedy shorelines created suitable cover for stealth hunts. Open attacks on flying shorebirds were uncommon at the lake except when drought had caused the shallows to recede well away from shore (Dekker 1991, 1999). By the same token, the high proportion of open hunts at Boundary Bay (62%) reflected the lack of opportunities for surprise over zones 2 and 3. Once the Dunlins were >10 m from the saltmarsh (the boundary between zones 1 and 2), the distance from shore had no significant bearing on the hunting success rate of peregrines (i.e., kill rates for zones 2 and 3 were nearly equivalent).

While peregrines evidently hunt and capture prey throughout the day, the fact that they killed much less often just before and much more often just after high tide cannot be related to habitat. If that were so, the kill rate per observation hour 1–2 hr before and 1–2 hr after high tide should be the same, which is clearly not the case. The most plausible reason for the observed difference is related to the behavior of the Dunlins. Well before the cresting tide, often when the floodwaters are still >50 m from the saltmarsh, the great majority of Dunlins depart on their over-ocean flights, while others fly inland especially during or after heavy rain. The drop in kill rate during this period reflects the decreased vulnerability of the birds during over-ocean flights. (The kill rate at inland roosting sites outside the study area was not recorded.)

The peak in kill rate immediately after high tide is probably due to the Dunlins' need to compensate for energy expended during 2–4 hr of over-ocean flying. Returning Dunlins are likely to be hungry, more intent on foraging and less vigilant than at other times during the tidal cycle. Consequently, the trade-off temporarily shifts toward increased risk.

A second and complementary reason for the high kill rate just after high tide is that some peregrines, particularly the adults, spend most of the day perching and may not start hunting until flocks of Dunlins begin to congregate near the saltmarsh. Adult peregrines are significantly more successful in the use of stealth than juveniles. Only 25% of all hunts were by adults, yet they accounted for 47% of kills (Dekker 2003).

PREY SELECTION

Based on the examination of prey remains, a relatively high percentage of shorebirds caught by raptors are known to be juveniles (Kus et al. 1984, Whitfield 1985, Warnock 1994). The mechanics of age-related prey selection seem simple if we assume that juveniles are on the outsides of flocks, either on the ground or in flight (Ydenberg and Prins 1984, Ruiz et al. 1989, Newton 1998). In this study, at least 69% of captured Dunlins were taken by peregrines directly from the outside or tail end of flocks (Dekker 2003). Furthermore, the percentage of juveniles may be high in small, isolated flocks that render themselves vulnerable to stealth attacks during the high tide. Such risky behavior includes (1) late departure on over-ocean flocking flights; (2) persistence in roosting or foraging along the high-tide line; (3) early return to shore after over-ocean flocking; and (4) a switch to inland roosts or feeding sites. The proportion of juveniles in flocks in such high-risk situations, and their physical condition compared to conspecifics that flock over the ocean, might present an interesting avenue for further research.

This study was privately financed by DD. During the last year, travel expenses were partially reimbursed by the Centre for Wildlife Ecology at Simon Fraser University, British Columbia. Accommodation in 2000–2003 was provided by D. Leach. Occasional co-observers were I. Dekker, D. Hancock, R. Swanston, and P. Thomas. G. Court did the *G*-tests. I. Gordon assisted with the data analysis for Figure 1c. R. Dekker prepared the graphs. Referees J. Buchanan and R. Butler made helpful comments on the first draft of this paper.

LITERATURE CITED

BRENNAN, L. A., J. B. BUCHANAN, S. G. HERMAN, AND T. M. JOHNSON. 1985. Interhabitat movements of wintering Dunlins in western Washington. Murrelet 66:11–16.

BUCHANAN, J. 1996. A comparison of behavior and success rates of Merlins and Peregrine Falcons when hunting Dunlins in two coastal habitats. Journal of Raptor Research 30:93–98.

BUTLER, R. W. 1994. Distribution and abundance of Western Sandpipers, Dunlins, and Black-bellied Plovers in the Fraser River estuary, p. 18–23. *In*

R. W. Butler and K. Vermeer [EDS.], The abundance and distribution of estuarine birds in the Strait of Georgia, British Columbia. Canadian Wildlife Service Occasional Paper No. 83, Ottawa, ON, Canada.

BUTLER, R. W., AND R. W. CAMPBELL. 1987. The birds of the Fraser River delta: populations, ecology and international significance. Canadian Wildlife Service Occasional Paper No. 65, Ottawa, ON, Canada.

CRESSWELL, W. 1996. Surprise as a winter hunting strategy in Sparrowhawks, Peregrines, and Merlins. Ibis 138:684–692.

DEKKER, D. 1980. Hunting success rates, foraging habits, and prey selection of Peregrine Falcons migrating through central Alberta. Canadian Field-Naturalist 94:371–382.

DEKKER, D. 1988. Peregrine Falcon and Merlin predation on small shorebirds and passerines in Alberta. Canadian Journal of Zoology 66:925–928.

DEKKER, D. 1991. Prairie water: wildlife at Beaverhills Lake, Alberta. University of Alberta Press, Edmonton, AB, Canada.

DEKKER, D. 1998. Over-ocean flocking by Dunlins (*Calidris alpina*) and the effect of raptor predation at Boundary Bay, British Columbia. Canadian Field-Naturalist 112:694–697.

DEKKER, D. 1999. Bolt from the blue—wild peregrines on the hunt. Hancock House Publishing, Surrey, BC, Canada.

DEKKER, D. 2003. Peregrine Falcon predation on Dunlins and ducks and kleptoparasitic interference from Bald Eagles wintering in British Columbia. Journal of Raptor Research 37:91–97.

FLATER, D. [ONLINE]. 1998. Xtide: harmonic tide clock and tide predictor. <http://www.flaterco.com/xtide/> (1 December 2003).

HOTKER, H. 2000. When do Dunlins spend high tide in flight? Waterbirds 23:482–485.

KUS, B. E., P. ASHMAN, G. W. PAGE, AND L. E. STENZEL. 1984. Age-related mortality in a wintering population of Dunlin. Auk 101:69–73.

LIMA, S. L. 1988. Vigilance and diet selection: a simple example in the Dark-eyed Junco. Canadian Journal of Zoology 66:593–596.

LIMA, S. L., T. L. VALONE, AND T. CARACO. 1985. Foraging efficiency—predation risk trade-off in the grey squirrel. Animal Behavior 33:155–165.

MILINSKI, M. 1986. Constraints placed by predators on feeding behaviour, p. 236–252. *In* T. L. Pitcher [ED.], The behaviour of teleost fishes. Croom Helm Ltd., London.

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

PAGE, G., AND D. F. WHITACRE. 1975. Raptor predation on wintering shorebirds. Condor 77:73–83.

PALMER, R. S. 1988. Handbook of North American birds. Vol. 5. Diurnal raptors, part 2. Yale University Press, New Haven, CT.

RUIZ, G. M., P. G. CONNORS, S. E. GRIFFIN, AND F. A. PITELKA. 1989. Structure of a wintering Dunlin population. Condor 91:562–570.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. Freeman and Co., New York.

THIOLLAY, J. M. 1982. Les ressources alimentaires facteur limitant la reproduction d'une population insulaire de Faucun Pelerins (*Falco peregrinus brookei*). Alauda 50:16–44.

VALONE, T. J., AND S. L. LIMA. 1987. Carrying food items to cover for consumption: the behavior of ten bird species feeding under the risk of predation. Oecologia 71:286–294.

WARNOCK, N. D. 1994. Biotic and abiotic factors affecting the distribution and abundance of a wintering population of Dunlin. Ph.D. dissertation, University of California, Berkeley, CA.

WHITE, C. M., N. J. CLUM, T. J. CADE, AND W. G. HUNT. 2002. Peregrine Falcon (*Falco peregrinus*). *In* A. Poole and F. Gill [EDS.], The birds of North America, No. 660. The Birds of North America, Inc., Philadelphia, PA.

WHITFIELD, D. P. 1985. Raptor predation on wintering waders in southeast Scotland. Ibis 127:544–558.

YDENBERG, R. C., R. W. BUTLER, D. B. LANK, C. G. GUGLIELMO, M. LEMON, AND N. WOLF. 2002. Trade-offs, condition dependence and stopover site selection by migrating sandpipers. Journal of Avian Biology 33:47–55.

YDENBERG, R. C., AND H. H. T. PRINS. 1984. Why do birds roost communally?, p. 123–239. *In* P. R. Evans, J. D. Goss-Custard, and W. G. Hale [EDS.], Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge, UK.

The Condor 106:420–423

NORTHERN HAWK OWLS AND RECENT BURNS: DOES BURN AGE MATTER?

KEVIN C. HANNAH[1,3] AND JEFF S. HOYT[2,4]
[1]*Department of Renewable Resources, University of Alberta, Edmonton, AB T6G 2H1, Canada*
[2]*Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada*

Abstract. The Northern Hawk Owl (*Surnia ulula*) remains one of the least-studied birds in North America. Although hawk owls use burned forest, reports of this association have been primarily anecdotal and outside the breeding season. We present the first comparison of hawk owl relative abundance between burned and unburned conifer-dominated boreal forest in North America. Hawk owls were detected only in postfire forest and were not detected in nearby unburned coniferous forest. There was a significant negative exponential relationship between hawk owl abundance and burn age, suggesting that burns were only suitable up to 8 years postfire. A conservative estimate of a peak in breeding density was three nests per 100 km^2 for a 2-year-postfire forest. Wildfire and newly burned forests may be an important feature for hawk owls in the Nearctic boreal forest. This raises the question whether management of this species through improved forestry techniques is a sufficient conservation measure.

Key words: breeding, burned forest, clearcut logging, fire, Northern Hawk Owl, Surnia ulula.

Surnia ulula y Fuegos Recientes: ¿Es la Edad de la Quema Importante?

Resumen. El búho *Surnia ulula* es una de las aves de Norte América que ha sido menos estudiada. Aunque estos búhos utilizan bosques quemados, los reportes de esta asociación han sido principalmente anecdóticos y han tenido lugar fuera de la época reproductiva. En este estudio presentamos la primera comparación de la abundancia relativa de *S. ulula* entre ambientes quemados y no quemados en bosques boreales de Norte América dominados por coníferas. Los búhos fueron detectados únicamente en bosques quemados y no se encontraron en bosques de coníferas cercanos que no habían sido quemados. Existió una relación exponencial negativa significativa entre la abundancia de *S. ulula* y la edad de las quemas, lo que sugiere que los bosques quemados sólo fueron adecuados para la especie hasta ocho años después del fuego. Una estimación conservadora del pico en la densidad reproductiva fue de tres nidos por 100 km^2 para un bosque luego de dos años de ser quemado. Los fuegos naturales y los bosques recientemente quemados podrían ser importantes para *S. ulula* en los bosques boreales Neárticos. Esto lleva a considerar si el manejo de esta especie a través de técnicas forestales mejoradas es una medida de conservación suficiente.

The Northern Hawk Owl (*Surnia ulula*) is one of the least-studied birds in North America (Duncan and Duncan 1998). To date, only two studies have focused on the breeding biology of this species in the Nearctic boreal forest (Kertell 1986, Rohner et al. 1995). Being nomadic, hawk owls concentrate and breed in areas of temporarily high microtine rodent abundance (Mikkola 1983), with no apparent differentiation between habitats (Cramp 1985). Several authors have suggested that hawk owls may be attracted to recently burned forests (Lane and Duncan 1987, Duncan and Harris 1997, Hobson and Schieck 1999, Duncan and Duncan 1998), though evidence has been primarily anecdotal. Densities of microtine rodents, such as voles, are known to increase following fire (Simon et al. 1998), most likely in response to increased seed availability postfire (Carleton and MacLellan 1994). Fires may benefit hawk owls by increasing the number of potential nest cavities, increasing small-mammal habitat, and providing more open habitat for hunting (Mindell 1983, Peck and James 1983, Jones 1987). While conducting playback surveys for Black-backed Woodpeckers (*Picoides arcticus*) and American Three-toed Woodpeckers (*P. dorsalis*) in east-central Alberta, we were surprised to find relatively large numbers of hawk owls in recently burned forests.

The purpose of our study was to determine the habitat relationships of Northern Hawk Owls in the boreal forest of east-central Alberta. We compare Northern Hawk Owl habitat occupancy of recently burned, mature, and old-growth conifer-dominated stands. Secondly, we examine hawk owl occupancy of different-aged postfire forests to determine how long after a fire the forest remains suitable habitat for hawk owls. Finally, we describe hawk owl nest trees and provide estimates of breeding density and nest success.

METHODS

The study area and design follow that outlined by Hoyt and Hannon (2002). Hawk owl surveys were conducted in the boreal forest of east-central Alberta during spring and summer of 1997 and 1998. In 1997 we

---

Manuscript received 18 April 2003; accepted 24 November 2003.

[3] Present address: Alaska Bird Observatory, P.O. Box 80505, Fairbanks, AK 99708. E-mail: khannah@alaskabird.org

[4] Present address: Biodiversity Branch, Ministry of Water, Land and Air Protection, Government of British Columbia, Victoria, BC V8W 9M4, Canada.

FIGURE 1. The relationship between burn age and hawk owl detection rate (owls hr^{-1}) in recent burns. Values for burn age are log-transformed, representing burns 3, 4, 8, 8, 16, and 17 years following fire.

sampled hawk owl occupancy in coniferous forests dominated by white spruce (*Picea glauca*), black spruce (*Picea mariana*), or jack pine (*Pinus banksiana*) of three seral stages; 2-year-old burn, mature (<110 years) and old (>110 years). Conifer-dominated forests contained <50% trembling aspen (*Populus tremuloides*). The burned forest site was located in a single 135 000-ha stand-replacing burn that occurred in April 1995, near Mariana Lake (55°05′N, 111°55′W). Mature and old forest sites were located within 50 km of the burn (Hoyt and Hannon 2002).

Our results in 1997 led us to suspect that hawk owls were selecting burned conifer-dominated forest over old and mature conifer-dominated unburned forest. In 1998, we conducted hawk owl surveys in six additional burns (3, 4, 8, 8, 16, and 17 years since fire) to determine how long postfire forests remain suitable for hawk owls. The 3-year-old burn was the Mariana Lake burn. The majority of the burned trees remained standing in the 3-, 4-, and 8-year-postfire forests, and regenerating trees and shrubs were generally less than 1 m tall. Fallen trees were more prevalent in the 16- and 17-year-postfire forests, and tree regeneration was generally between 1 and 3 m (JSH, unpubl. data). All burns were greater than 2000 ha (2160–135 000 ha).

Surveys for hawk owls were conducted from 8–23 April 1997. Surveys were conducted on foot and on all-terrain vehicles. Hawk owls were detected either by visual observation of perched or hunting birds, or by following and locating calling birds. Hawk-owl sampling effort was evenly distributed both temporally and spatially among conifer-dominated forest types. Totals of 26.6, 27.9 and 27.5 hr were spent surveying in recently burned, mature and old forests respectively. In 1998, in each of the six fires, between 8.8 and 10.4 hr (mean 9.6 ± 0.2 hr) were spent surveying from 3–24 April 1998 using the same method.

Individuals located on surveys early in the season were monitored throughout the season to determine their pairing or nesting status. We defined a confirmed nest as a territorial pair with at least one juvenile present and a probable nest as a territorial pair where nesting success could not be confirmed.

STATISTICAL ANALYSES

The recently burned forests surveyed in 1998 did not represent a continuous range of ages; therefore we log transformed our independent variable (burn age). The relationship between hawk owl relative abundance and burn age was examined graphically by constructing a scatterplot and choosing the curve of best fit to illustrate the relationship. Curve estimation and regression analysis was performed using SPSS 11.0 (SPSS 2001). Unless otherwise noted, all values reported are means ± SE.

RESULTS

In 1997, a total of 15 hawk owls were detected at a rate of 0.4 owls hr^{-1} in the 2-year-postfire forest. No hawk owls were detected in either mature or old unburned, conifer-dominated forest within 50 km of the Mariana Lake fire in 1997. In 1998, hawk-owls were detected in the 3-, 4-, and one of the 8-year-postfire forests. The detection rate was highest in the 3-year-postfire forest, with a total of seven owls detected at a rate of 0.7 owls hr^{-1}, followed by the 4- and 8-year-postfire forests with one owl detected in each at a rate of 0.1 owls hr^{-1}. In 1998, no hawk owls were detected in the second 8-year-postfire forest, or in the 16- and 17-year-postfire forests. The relationship between hawk owl relative abundance and burn age was best fit by a negative exponential curve (Fig. 1; $r = 0.67$, $F_{1,4} = 8.0$, $P = 0.05$), whereby hawk owl occupancy of postfire forest was greatest in recent burns, declining rapidly in burned forests up to 8 years postfire.

A total of five confirmed nests (four in 1997, one in 1998) and four probable nests (two in 1997, two in 1998) were observed. All confirmed and probable nests were in forest burns ≤4 years old. Of the four confirmed nesting hawk owls in 1997, we were able to describe three nest trees. In all cases hawk owls used natural cavities in large-diameter (>30-cm diameter at breast height) trees. Two nests were located in trembling aspen and one in white spruce. Natural cavities were created where a limb of the tree had been burned into the sapwood creating a large (10–20 cm) hollow, lateral opening in the trunk of the tree. All nests were situated between 4 and 10 m above the ground in moderate to heavily burned aspen-dominated stands close to an aspen–black spruce ecotone. Fledglings were observed at four locations in late May and June (three in 1997, one in 1998). Fledgling numbers varied from three to five young, with an average of 4.0 ± 0.6 young per nest. All three nests were located within the same township (10 × 10 km), so we made a conservative estimate of peak nesting density at 3 nests per 100 km^2 in 1997. Only one nest was located in 1998, so we were unable to estimate breeding density.

DISCUSSION

Previous studies have suggested that hawk owls are attracted to recently burned forests, but there has been little quantitative evidence of this, especially during the breeding season. In this study we detected hawk owls in postfire forests, with no hawk owls detected in unburned conifer-dominated forest. Recently burned forests may provide more snags for perching and nesting, increased microtine abundance and availability (because of the forest's openness; Jones 1987, Duncan and Duncan 1998).

In Norway, hawk owls preferentially use clearcuts in the spring. The snow may melt sooner in these areas, thereby providing access to microtine rodents sooner than in forested areas (Nybo and Sonerud 1990). Although we did not conduct any formal surveys in clearcuts, we observed no hawk owls in recent clearcuts (1 to 6 years postcut) in areas immediately north and west of the Mariana Lake burn site during 1997 and 1998. Furthermore, in >1000 hr of bird surveys conducted between February and July in clearcuts near Calling Lake, Alberta (55°15′N, 113°19′W, approximately 320 km west of our study site), there has never been a confirmed hawk owl sighting (F. Schmiegelow, unpubl. data). Data on responses of prey populations to clearcut logging versus natural fire remain unclear (Bendell 1974). Clearcuts do not contain the same abundance of potential nest sites and hunting perches as postfire forests, especially given low snag retention rates (<10%) following harvest in this part of Alberta. With a trend toward reduced rotation ages and more homogeneous forest stands, current forestry practices may prove to be unfavorable to hawk owl populations (Duncan and Harris 1997, Duncan and Duncan 1998).

In the early stages of postfire succession, the accessibility of prey would be high, but over time, access to microtine prey would greatly decline when regenerating vegetation increased in height and density, thereby potentially limiting hawk owl abundance. Duncan and Harris (1997) suggested that hawk owl accessibility to prey may be limited after 20 years of regeneration. In addition to reduced prey accessibility, prey abundance may also decline as older postfire forests continue to regenerate. The lack of hawk owls in burns older than 8 years in this study suggests that accessibility or availability may be reduced even earlier in our region.

In recently burned forest, the aspen–black spruce edge may represent crucial nesting habitat where high burn severity makes natural cavities available. As fire burns through black spruce forest it increases in intensity and severity. Upon reaching the edge of an aspen-dominated stand, trees on the edge of the stand are severely burned before the fire loses intensity (Rowe and Scotter 1973). Sonerud (1997) suggested that the loss of old trees and suitable cavities for nesting may locally limit hawk owl breeding opportunities in Fennoscandia. However, several authors suggest that hawk owls select breeding territories in response to prey abundance rather than habitat requirements (Pullianen 1978, Lane and Duncan 1987). Given our limited knowledge of this species in North America, it is difficult to ascertain whether nest sites or prey availability may be more limiting to hawk owl populations.

In recent years there has been a trend toward increased fire suppression and intensified salvage logging in the boreal region. These practices may be reducing high-quality habitat for populations of birds adapted to habitats shaped largely by wildfire (Welsh 1993). In particular, Black-backed and American Three-toed Woodpeckers are strongly associated with recent postfire habitat (Hutto 1995, Hobson and Scheick 1999, Hoyt and Hannon 2002). While this study is limited by minimal replication and small sample sizes, our results strongly suggest that in conifer-dominated forests of the western boreal forest, burned forest is important breeding habitat for hawk owls.

Further research is needed to quantitatively assess the significance of burned and unburned forests to hawk owls in the North American boreal region. More work on limiting factors, especially the relative influence of prey abundance and nest-site availability, would be beneficial. Wildfire and newly burned forests may be an important feature for hawk owls in the Nearctic boreal forest. This raises the question whether management of this species through improved forestry techniques is a sufficient conservation measure.

We thank E. Chernoff, L. Tomyn, and K. Sabourin for assistance in the field, F. K. A. Schmiegelow for providing unpublished data, and S. J. Hannon for facilitating this study by supporting JSH's M.Sc. thesis research. C. Rohner, J. Marks, H. Powell, and D. Dobkin provided helpful comments on earlier versions of this manuscript. This research was supported by Wildlife Habitat Canada; Challenge Grants in Biodiversity, Department of Biological Sciences, University of Alberta; the Alberta Conservation Association; Alberta Sports, Parks, Recreation and Wildlife Foundation; the Canadian Circumpolar Institute; and the Sustainable Forest Management Network. JSH was supported by a Post-Graduate Scholarship from the National Sciences Engineering Research Council of Canada and by a Walter H. Johns Scholarship from the University of Alberta.

LITERATURE CITED

BENDELL, J. F. 1974. Effects of fire on birds and mammals, p. 73–138. *In* T. T. Kozlowski and C. E. Ahlgren [EDS.], Fire and ecosystems. Academic Press, New York.

CARLETON, T. J., AND P. MACLELLAN. 1994. Woody vegetation responses to fire versus clear-cut logging: a comparative survey in the central Canadian boreal forest. Ecoscience 1:141–152.

CRAMP, S. [ED.]. 1985. Handbook of the birds of Europe, the Middle East and North Africa. Vol. 4. Oxford University Press, Oxford, UK.

DUNCAN, J. R., AND P. A. DUNCAN. 1998. Northern Hawk Owl (*Surnia ulula*). *In* A. Poole and F. Gill [EDS.], The birds of North America, No. 356. The Birds of North America, Inc., Philadelphia, PA.

DUNCAN, P. A., AND W. C. HARRIS. 1997. Northern Hawk Owls (*S. u. caparoch*) and forest management in North America: a review. Journal of Raptor Research 31:187–190.

HOBSON, K. A., AND J. SCHIECK. 1999. Changes in bird communities in boreal mixedwood forest: harvest and wildfire effects over 30 yrs. Ecological Applications 9:849–863.

HOYT, J. S., AND S. J. HANNON. 2002. Habitat associations of Black-backed and Three-toed Woodpeckers in the boreal forest of Alberta. Canadian Journal of Forest Research 32:1881–1888.

HUTTO, R. L. 1995. Composition of bird communities following stand replacement fires in northern

Rocky Mountain (U.S.A.) conifer forests. Conservation Biology 9:1041–1058.

JONES, E. T. 1987. Observations of the Northern Hawk Owl in Alberta, p. 149–151. *In* R. W. Nero, R. J. Clark, R. J. Knapton, and R. H. Hamre [EDS.], Biology and conservation of northern forest owls: symposium proceedings. USDA Forest Service General Technical Report RM-142.

KERTELL, K. 1986. Reproductive biology of Hawk Owls *Surnia ulula* in Denali National Park, Alaska. Journal of Raptor Research 20:91–101.

LANE, P. A., AND J. R. DUNCAN. 1987. Observations of Northern Hawk-Owls nesting in Roseau County. Loon 59:165–174.

MIKKOLA, H. 1983. Owls of Europe. Buteo Books, Vermillion, SD.

MINDELL, D. P. 1983. Nesting raptors in southwestern Alaska: status, distribution and aspects of biology. USDI Bureau of Land Management, Alaska State Office, Alaska Technical Report 8, Anchorage, AK.

NYBO, J. O., AND G. A. SONERUD. 1990. Seasonal changes in diet of Hawk Owls *Surnia ulula*: importance of snow cover. Ornis Fennica 67:45–51.

PECK, G. K., AND R. D. JAMES. 1983. Breeding birds of Ontario. Nidiology and distribution. Vol. 1: nonpasserines. Life Sciences Miscellaneous Publication, Royal Ontario Museum, Toronto, ON, Canada.

PULLIANEN, E. 1978. Nesting of the Hawk Owl, *Surnia ulula*, and Short-eared Owl, *Asio flammeus*, and the food consumed by owls on the island of Ulkokrunni in the Bothnian Bay in 1977. Aquilo Serie Zoologica 18:17–22.

ROHNER, C., J. N. M. SMITH, J. STROMAN, M. JOYCE, F. I. DOYLE, AND R. BOONSTRA. 1995. Northern Hawk-Owls in the Nearctic boreal forest: prey selection and population consequences of multiple prey cycles. Condor 97:208–220.

ROWE, J. S., AND G. W. SCOTTER. 1973. Fire in the boreal forest. Quaternary Research 3:444–464.

SIMON, N. N. P., F. E. SCHWAB, E. M. BAGGS, AND G. I. M. COWAN. 1998. Distribution of small mammals along successional and mature forest types in western Labrador. Canadian Field Naturalist 112:441–445.

SONERUD, G. A. 1997. Hawk owls in Fennoscandia: population fluctuations, effects of modern forestry, and recommendations on improving foraging habitats. Journal of Raptor Research 31:167–174.

SPSS. 2001. SPSS base 11.0 user's guide. SPSS Inc., Chicago.

WELSH, D. A. 1993. Birds and boreal forests in Ontario, p. 40–47. *In* H. Kunkhe [ED.], Birds in the boreal forest. Forestry Canada Northwest Region, Northern Forestry Center, Edmonton, AB, Canada.

The Condor 106:423–429

DIET OF THE NESTLING TREE SWALLOW

JEAN M. MENGELKOCH[1], GERALD J. NIEMI[1,3] AND RONALD R. REGAL[2]

[1]*Department of Biology and Natural Resources Research Institute, University of Minnesota, Duluth, MN 55812*

[2]*Department of Mathematics and Statistics, University of Minnesota, Duluth, MN 55812*

Abstract. Dietary samples from nestling Tree Swallows (*Tachycineta bicolor*) in northwestern Minnesota were compared to invertebrate availability as measured by aerial tow nets. The majority of the biomass in the nestlings' diet was adult insects with larval stages of aquatic origin, while absolute numbers of insects of both aquatic and terrestrial origin were similar. Orders of invertebrates in the diet and available were similar in number but not in biomass. Diet showed little variation by time of day, date of sampling or the age of the nestling. The mean number of odonates in the nestling Tree Swallows' diet increased exponentially as the percentage of open water and open water + cattail marsh increased within a 400-m foraging radius.

Key words: diet, foraging, insect sampling, Tachycineta bicolor, *Tree Swallow.*

Dieta de los Pichones de *Tachycineta bicolor*

Resumen. Se compararon muestras dietarias de pichones de la golondrina *Tachycineta bicolor* tomadas en el noroeste de Minnesota con la disponibilidad de invertebrados medida con redes aéreas. La mayor parte de la biomasa en la dieta de los pichones correspondió a insectos adultos con estadíos larvales de origen acuático, mientras que los números absolutos de insectos

---

Manuscript received 18 April 2003; accepted 13 November 2003.

[3] Corresponding author. E-mail: gniemi@nrri.umn.edu

de origen acuático y no acuático fueron similares. Los órdenes de invertebrados presentes en la dieta y disponibles en el ambiente fueron similares en números pero no en biomasa. La dieta mostró poca variación entre horas del día, fechas de muestreo o edad de los pichones. El número promedio de odonatos en la dieta de los pichones de *T. bicolor* aumentó exponencialmente a medida que se incrementó el porcentaje de agua abierta y de agua abierta + pantanos de espadañas dentro de un radio de forrajeo de 400 m.

Tree Swallows (*Tachycineta bicolor*) are widespread across all of North and Central America (Robertson et al. 1992) and are easily attracted to specific areas by nest boxes (Bishop et al. 1995). This makes them popular choices for field studies including innovative work that uses them as bioindicators of contamination in surrounding areas (Robertson et al. 1992, Nichols et al. 1995). Adult Tree Swallows primarily forage within a 400-m radius of the nest (Quinney and Ankney 1985, Dunn and Hannon 1992), and in so doing accumulate contaminants from these localized environments (Ankley et al. 1993, St. Louis et al. 1993, Nichols et al. 1995).

Tree Swallows typically nest near water, where they forage on flying invertebrates with both aquatic and terrestrial larval stages (Holroyd 1972, 1983, Quinney and Ankney 1985, Robertson et al. 1992). Insects accumulate most of their body mass, and hence acquire most contaminants, during the larval stage. Therefore, by studying in detail the insects nestling Tree Swallows eat and the proportions that come from aquatic and terrestrial origins, we can better understand the bioaccumulation and storage of contaminants in the environment.

Nestling Tree Swallows are principally fed aquatic insects (Holroyd 1972, 1983, Quinney and Ankney 1985, Blancher and McNicol 1991, Robertson et al. 1992). While many orders of insects are fed to the nestlings, the majority are dipterans (Holroyd 1983, Quinney and Ankney 1985, Blancher et al. 1987, McCarty and Winkler 1991). Most of the prey are <7 mm in length (Quinney and Ankney 1985, McCarty and Winkler 1991, 1999), but insects >13 mm have represented a significant portion of the total biomass of prey in a few studies (Blancher et al. 1987, McCarty and Winkler 1999). Diet is affected by the surrounding habitat; Quinney and Ankney (1985) found fewer dipterans were fed to nestlings in a dry field compared with those near water.

The objective of this study was to determine the dietary components of nestling Tree Swallows at a finer taxonomic level than has previously been reported. Identification at this level allowed us to distinguish dipterans with aquatic and terrestrial larval stages. We examined: (1) composition and origin of the dietary components; (2) effects of habitat on diet; and (3) variation across diurnal, seasonal, and nestling age effects on the diet.

METHODS

STUDY AREA

The study was conducted in northwestern Minnesota at Agassiz National Wildlife Refuge (24 899 ha). The refuge is located in eastern Marshall County, northeast of Thief River Falls, Minnesota (48°26′N, 96°09′W). Surrounded by agricultural land, the refuge is composed of a mosaic of habitats, including wetland (16 212 ha), shrubland (4049 ha), forest (1662 ha), grassland (1662 ha), and cropland (121 ha).

Five nest box sites distributed throughout the refuge were positioned parallel to waterways entering the refuge from three of the major watersheds of the area and two major wetlands on the refuge. In mid-April 1998, 30–40 nest boxes were placed at least 30 m apart in a single row within a couple of meters of the water at each site. In a few instances a gap much greater than 30 m between nest boxes occurred.

DIET

Nestling dietary samples were collected from 14 June to 16 July 1998. To avoid disrupting a separate study of Tree Swallows and heavy metal contamination, samples were not taken from a site until at least 10 nestlings from separate nest boxes reached 12 days of age. Food samples were collected from 5–15-day-old nestlings between 08:00 and 17:30 CDT using the ligature method (Orians 1966, Willson 1966, Orians and Horn 1969, Bryant and Turner 1982, Yorks 1999). Previous experience suggested that nestlings younger than five days were too small for us to safely and accurately collect samples from them. Tree Swallows will prematurely fledge if disturbed after 16 days of age (Kuerzi 1941, Burtt 1977, DeSteven 1980, Robertson et al. 1992).

Ligatures were 10.2-cm cable ties spray-painted gray to black to blend in with the feathers of the nestling. The ligatures were tightened around the nestlings' necks to prevent swallowing but still allow normal breathing. The ligatures were cut off with small scissors once the food was collected.

Ligatures remained on nestlings for 1–1.5 hr (Orians 1966, Orians and Horn 1969, Johnson et al. 1980, Yorks 1999). Each bolus was removed with forceps and preserved in 70% ethyl alcohol for later identification (Orians 1966, McCarty and Winkler 1991). Boluses generally consisted of a tight ball of insects. Some live insects may have been able to escape, and the ligatures may not have prevented some small insects from being swallowed. The nest was also checked for regurgitated boluses, and any that were found were also included in the analysis. Prior to applying the ligatures, the nest was checked for regurgitated invertebrates, but none were found. Therefore, all the invertebrates collected from either the nestlings or the nest were representative of the invertebrates fed to the nestlings during the sampling period. Boluses collected from all the nestlings in a nest were pooled before counting.

AERIAL SAMPLING

Aerial tow nets that rotate in the wind, as described by Quinney and Ankney (1985), were used to collect aerial insects potentially available to the foraging Tree Swallows. The conical nets were 69 cm long, 38 cm in diameter at the mouth of the net, <6 cm at the rear of the net, and terminated with a sleeve attached to a jar containing 70% ethanol. The center of the nets was positioned about 2 m above the ground (Quinney and

TABLE 1. Habitat composition within 400 m of nest boxes at each of five sites where we studied nestling Tree Swallow diet, Agassiz National Wildlife Refuge, Middle River, Minnesota, in July 1998.

Habitat type	Agassiz Pool ha (%)	Ditch 11 ha (%)	Mud River ha (%)	Parker Pool ha (%)	Thief River ha (%)
Open water	40.0 (36)	3.8 (4)	35.6 (44)	42.1 (15)	49.3 (51)
Cattail marsh	56.5 (51)	26.7 (26)	37.7 (47)	147.5 (53)	46.1 (47)
Open field	12.1 (11)	12.5 (12)		6.4 (2)	
Scrub-shrub		59.0 (57)		12.9 (5)	
Deciduous woods			5.8 (7)	67.4 (24)	
Roads	1.9 (2)	1.2 (1)	1.8 (2)	2.8 (1)	2.2 (2)

Ankney 1985). One net was placed at each of the five sites and was located in the middle of the row of nest boxes and at least 15 m to the side to avoid disrupting the swallows. The nets were open concurrently with the collection of the food samples from the nestlings, from approximately 08:00–17:30 CDT from 14 June–13 July 1998 on alternating days and areas of the refuge. Five of the 23 nets were open until the next morning, but samples did not appear to differ from samples collected during the day. In total, 23 samples were collected.

SAMPLE ANALYSIS

Dietary and tow net samples were examined using an incremental magnification stereomicroscope with a digitizing pad (Micro plan II™, Laboratory Computer Systems, Inc., distributed by Nikon, Melville, New York). With a few exceptions, insects were identified to order using several keys (Borror et al. 1989, Daly et al. 1998). Dipteran larvae occupy extremely diverse habitats, so all dipterans were identified to family to increase the ability to classify larval habitat as aquatic or terrestrial. All families of crane flies were lumped as tipulids, as there was difficulty distinguishing them. Stratiomyids and syrphids were identified to genus, due to their even greater diversity of larval habitat. The majority of hemipterans have terrestrial larval stages, but corixids and saldids are aquatic, so these two families were identified and analyzed as well. To our knowledge, this is one of the finest taxonomic descriptions of the nestling Tree Swallows' diet, and it is the only degree of identification capable of assessing larval habitat of the invertebrates.

The invertebrates were categorized as aquatic, possibly aquatic, terrestrial, or unknown according to the larval stage of their life cycle (Blancher and McNicol 1991). Several references were used to determine the life histories of the invertebrates (Borror et al. 1989, Daly et al. 1998). ''Possibly aquatic'' indicates that a particular taxon includes both aquatic and terrestrial species. Since the primary purpose of this study was to determine the extent to which swallows consumed insects of aquatic origin, it was unnecessary to be more specific than simply ''terrestrial.''

Invertebrate lengths were converted to biomass using previously developed regression models: Sage (1982) for arachnids; Sample et al. (1992) for all insects according to order, and dipterans according to suborder. Samples were split into categories based on the time (morning vs. afternoon) and date (14–24 June, 25 June–5 July, and 6–16 July) of sampling and the nestling age (5–9 days vs. 10–15 days).

HABITAT

Cover types were assessed visually in the field to ascertain the proportion of habitats available at each site to Tree Swallows and their food supply within their 400-m foraging range (Table 1; Quinney and Ankney 1985, Dunn and Hannon 1992, Ankley et al. 1993). Habitat composition was determined for each site rather than for each individual nest box. Even though we were unable to ascertain the actual foraging range of the Tree Swallows at our site, we felt it was a reasonable estimate of their primary foraging area. The total area of habitat estimated for each site differed among sites because the number of nest boxes in each site was not the same and the distances between the boxes were sometimes >30 m.

STATISTICAL ANALYSES

A mixed-model ANOVA (procedure MIXED, SAS Institute 2001) was used to determine if biomass of invertebrates from aquatic, possibly aquatic, and terrestrial larval origins changed with time of day, date, or nestling age. We used a separate mixed model (procedure MIXED, SAS Institute 1996) to ascertain if the biomasses of Diptera and Odonata in the diet were affected by time of day, date, and age of nestling. The mixed model is similar to a general linear model (procedure GLM, SAS Institute 1996) but accounts for both random and fixed effects and minimizes the effects of unequal sample sizes. In this study, site and nest were random effects. The fixed effects were age of nestling, time of day, and date of sampling. All the assumptions of normal distributions and equality of variances were met by these data. Chi-square tests were used to compare the number of insects of each order and size class in the nestling Tree Swallow's diet and in the nets. Least-squares means were determined for the number of Diptera and Odonata in each site and were plotted against the amount of open water, cattail marsh, and open water + cattail marsh. Regression was used to determine the fit of the curves. The alpha level was set at 0.05.

RESULTS

Fifty-six nests were sampled twice, yielding 261 boluses for 283 nestlings. A total of 4670 individual invertebrates was counted, and the invertebrates ranged in length from 0.4–43.0 mm. Boluses contained an

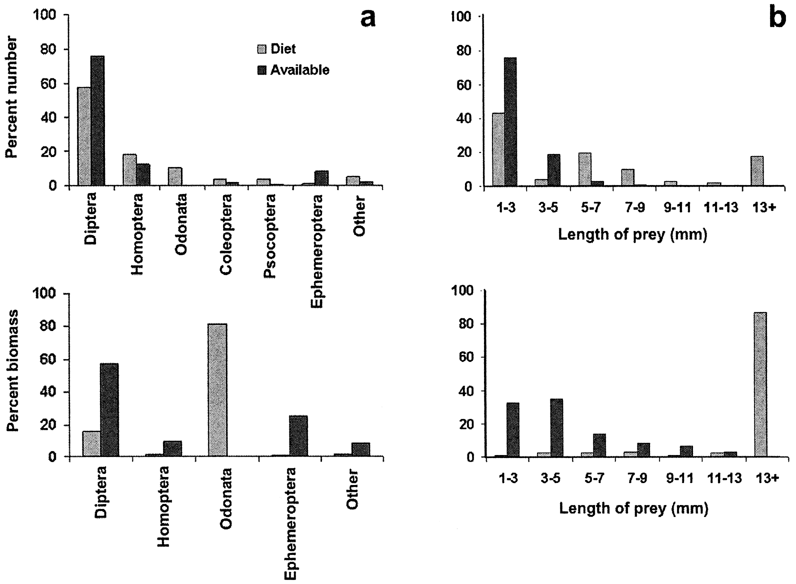

FIGURE 1. Use versus availability of insects found in the diet of nestling Tree Swallows at Agassiz National Wildlife Refuge, Minnesota. Insects were categorized by (a) order and (b) size class, and results are reported in terms of individuals and biomass. Data represent 4670 invertebrates from nestling boluses and 1564 invertebrates from tow nets collected at five sites from June–July 1998.

average of 20.0 ± 3.0 (SE) invertebrates comprising a total of 10 insect orders, plus spiders, and snail shells. Within Diptera, 31 families were represented by at least 10 specimens. Syrphids accounted for 35% of the dipteran biomass, tabanids 18%, chironomids 13%, tipulids 8%, and stratiomyids 4%. Nearly all of the Odonata specimens were suborder Zygoptera, family Coenagrionidae. Snail shells were not included in the analysis, because many of the shells had broken into multiple tiny pieces and would have been difficult to quantify accurately.

Approximately equal numbers of nests from the two nestling age classes (5–9 and 10–15 days) and time of day (08:00–12:00; 12:00–17:30) were used in analysis. Since nests tended to contain more nestlings earlier in the sampling period, over 60% of the samples were taken from 14–24 June and less than 20% were taken from each of the 25 June–5 July and 6–16 July periods.

The 23 tow net samples yielded 1564 invertebrates. Lengths ranged from 0.1–12.4 mm. Eight insect orders plus spiders were collected. Within Diptera, chironomids represented 65% of the total biomass, Sciaridae 7%, Tipulidae 6%, and Culicidae 5%. The vast majority of Ephemeroptera in the nets were exuviae (shed exoskeletons), which were assumed to represent available adults. Fifty-two percent of the samples were collected from 14–24 June, 35% from 25 June–5 July, and 13% from 6–16 July.

The nestlings were fed a smaller proportion of Diptera by number than the nets indicated were available, but more Homoptera and Odonata ($\chi^2_6 = 247\,527$; $P < 0.001$; Fig. 1). Dipterans accounted for the majority of the biomass in the nets (57%), but not in the diet (Odonata 82% and Diptera 16%; Fig. 1). In addition, nestlings were fed larger invertebrates by mass than were caught in the tow nets (Fig. 1). Almost 87% of the biomass in the diet consisted of odonates and dipterans (syrphids and tabanids) >13 mm long; invertebrates of this length were not found in any net samples.

PREY ORIGIN

Similar numbers of aquatic (50%) and terrestrial (44%) invertebrates were fed to the nestling Tree Swallows; however, over twice as many invertebrates of aquatic (68%) larval stages were available as terrestrial (27%). The distribution of numbers of invertebrates from each of the larval habitats differed significantly between the diet and the nets ($\chi^2_3 = 164.5$; $P < 0.001$). Conversely, more insects with aquatic (95%) larval stages were consumed by biomass than were available in the nets (71%), but more biomass of terrestrial invertebrates (25%) was available than was in the diet (4%). Variability in diet between the five sites at Agassiz was minimal. In all the sites, 90–98% of the diet by biomass was aquatic and 2–8% terrestrial.

DIURNAL, SEASONAL, AND NESTLING AGE EFFECTS

Diet composition in terms of the larval habitat of prey was not significantly affected by nestling age (aquatic: $F_{1,32} = 0.60$, $P > 0.40$; terrestrial: $F_{1,32} = 0.62$, $P > 0.40$), time of day (aquatic: $F_{1,32} = 0.52$, $P > 0.40$; terrestrial: $F_{1,32} = 0.53$, $P > 0.40$), or date (aquatic: $F_{2,32} = 0.04$, $P > 0.90$; terrestrial: $F_{2,32} = 0.12$, $P > 0.80$) the sample was taken. In every case 92–96% of the biomass was aquatic and 3–6% was terrestrial. However, there was a significant age × time interaction for invertebrates of terrestrial larval habitats ($F_{1,32} = 4.63$, $P < 0.05$). The least-squares (adjusted) mean

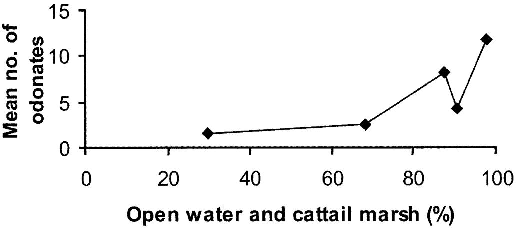

FIGURE 2. Mean number of Odonata in nestling Tree Swallows' diet increased with percentage of open water and cattail marsh within a 400-m radius of five study sites. Data represent 261 boluses collected at Agassiz National Wildlife Refuge in Middle River, Minnesota from June–July 1998.

of percent biomass of terrestrial prey was larger in afternoons than in mornings for nestlings 5–9 days old. In contrast, mean percent biomass of terrestrial invertebrates was larger in the morning than the afternoon for the older nestlings (10–15 days). The biomass of Diptera and Odonata were not affected by age of the nestling (Diptera: $F_{1,28} = 2.46$, $P > 0.10$; Odonata: $F_{1,9} = 0.17$, $P > 0.60$), time of day (Diptera: $F_{1,28} = 0.00$, $P > 0.90$; Odonata: $F_{1,9} = 0.09$, $P > 0.70$), or date (Diptera: $F_{2,28} = 0.82$, $P > 0.40$; Odonata: $F_{2,9} = 0.47$, $P > 0.60$) the sample was taken.

EFFECTS OF HABITAT ON THE DIET

The mean number of dipterans in the nestling Tree Swallows' diets was not related to the percentage of open water ($r^2 = 0.07$, $P > 0.60$), cattail marsh ($r^2 = 0.21$, $P > 0.40$), or open water + cattail marsh ($r^2 = 0.09$, $P > 0.60$) within the foraging radius at each site.

There was no direct relationship between the mean number of Odonates fed to nestling swallows and the percentage cattail marsh within the foraging radius ($r^2 = 0.22$, $P > 0.40$). However, there was an exponential relationship between the mean number of Odonates and the percentage of open water ($r^2 = 0.81$, $P < 0.05$), and open water + cattail marsh ($r^2 = 0.78$, $P < 0.05$), within the foraging radius (Fig. 2).

DISCUSSION

EFFECTS OF HABITAT ON DIET

There was no relationship between the mean number of dipterans in the diet of nestling Tree Swallows and available habitats. This was largely due to the huge diversity of dipterans in the diet. However, odonates have an aquatic larval stage and use both open areas of water with emergent and submergent vegetation for reproduction and dense areas of vegetation for roosting (Needham and Heywood 1929, Bick and Bick 1965). Thus it makes sense that as the percentage of foraging area composed of open water and open water + cattail marsh increased, the mean number of odonates in the diet increased exponentially.

Dipterans and odonates were an important food source for nestling Tree Swallows at Agassiz National Wildlife Refuge. However, odonates have not always been shown to have a significant role in the diet. Odonates numerically composed less than 1% of the diet in Quinney and Ankney's (1985) study of nestling Tree Swallows living near water. Blancher et al. (1987), and McCarty and Winkler (1991) found that ≤5% of the diet was odonates. In fact, among studies of nestling Tree Swallow diet, only McCarty and Winkler (1999) documented odonates as >10% of the nestlings' diet.

The differences in dietary composition might be attributed to varying habitat available to the foraging swallows. Habitat has been infrequently quantified in past studies. McCarty and Winkler (1999) reported that their New York study site of about 22 ha was 67% pond or lake. However, this area could include habitat outside the 400-m foraging radius of the swallows. The diet was composed of approximately 45% Diptera, 20% Odonata, and 15% Hemiptera by mass (McCarty and Winkler 1999). The habitat within the foraging radius of Tree Swallows at Agassiz National Wildlife Refuge was 72% open water and cattail marsh, and encompassed 671 ha. The diet of nestlings at Agassiz NWR was >80% Odonata by mass; they are clearly an important component of the diet.

In addition to habitat availability, biotic and abiotic characteristics of habitat can also influence invertebrate abundance. Blancher and McNicol (1991) found that nestling Tree Swallows were fed more Odonata in acidic wetlands (pH < 5). In addition, fishless wetlands and those with low dissolved oxygen content correlated with a higher percentage of Odonata in the diet. Agassiz waterways have a pH level of 7–9 and all the wetlands have fish (P. Trihey, unpubl. data; J. P. Mattsson, pers. comm.), but the swallows were fed almost five times as many odonates by biomass than swallows in acidic wetlands (>50% without fish) and almost nine times as many as in other wetlands studied by Blancher and McNicol (1991). Therefore, our results suggest that Blancher and McNicol's results are not universal.

DIURNAL, SEASONAL, AND NESTLING AGE EFFECTS

There was an interaction between the age of nestling and time of day for invertebrates consumed of terrestrial larval origins. The source of this interaction was likely related to the small percentage (4%) of biomass in the diet represented by invertebrates of terrestrial larval origins. Although this was a significant interaction, the small percentages present may represent some minor shifts in foraging patterns among the adults but also could be a spurious result.

PROBLEMS WITH AERIAL TOW NETS

Odonata were not well represented in the net samples at Agassiz either by number (<1%) or size (most of the invertebrates ≥13 mm were most likely Odonata). Since the majority of the biomass in Tree Swallow diet was Odonata, their absence in the nets indicates a problem using the nets to adequately quantify insect availability. Suction traps have been shown to capture similar numbers of large insects (Johnson 1950); therefore, they would not be more useful. A more effective means of quantifying insect availability may be a combination of aerial tow nets for the smaller insects and floating emergence traps for emerging aquatic invertebrates, including Odonata (Morgan et al. 1963, McCarty 1997).

PREY ORIGIN

Although similar numbers of invertebrates with aquatic and terrestrial larval habitats were in the diet, >90% of the biomass was invertebrates with aquatic larvae. They are clearly a vital component of the diet of nestling Tree Swallows at Agassiz National Wildlife Refuge. Only one other study has attempted to classify the invertebrates in the diet by their larval habitat. Blancher and McNicol (1991) found that the boluses of nestlings contained slightly more invertebrates of aquatic than terrestrial origin, but only about 65% of the mass was from invertebrates with aquatic origins. The main difference between our results was that odonates contributed to only 10% of the total biomass in the diet in their study.

Because nestling Tree Swallows in aquatic areas are fed more invertebrates with aquatic larvae by biomass (Blancher and McNicol 1991), they would be good bioindicators of contamination in aquatic areas.

Funding for this study was provided by the U.S. Geological Survey and the University of Minnesota. Agassiz National Wildlife Refuge provided housing on the field site. Many thanks to T. Custer for assistance with the development of this study. Thanks to C. Richards for help with the invertebrate aspect of the study and for reviewing the manuscript. Thanks to D. Breneman for verifying the invertebrate reference collection. We would also like to thank K. Schmude for assistance identifying some of the dipterans to genus. This is contribution no. 361 of the Center for Water and the Environment, Natural Resrouces Research Institute, University of Minnesota, Duluth.

LITERATURE CITED

ANKLEY, G. T., G. J. NIEMI, K. B. LODGE, H. J. HARRIS, D. L. BEAVER, D. E. TILLITT, T. R. SCHWARTZ, J. P. GIESY, P. D. JONES, AND C. HAGLEY. 1993. Uptake of planar polychlorinated biphenyls and 2,3,7,8-substituted polychlorinated dibenzofurans and dibenzo-*p*-dioxins by birds nesting in the Lower Fox River/Green Bay, Wisconsin. Archives of Environmental Contaminants and Toxicology 24:332–344.

BICK, G. H., AND J. C. BICK. 1965. Demography and behavior of the damselfly, *Argia apicalis* (Say), (Odonata:Coenagrionidae). Ecology 46:461–472.

BISHOP, C. A., M. D. KOSTER, A. A. CHEK, D. J. T. HUSSELL, AND K. JOCK. 1995. Chlorinated hydrocarbons and mercury in sediments, Red-winged Blackbirds (*Agelaius phoeniceus*) and Tree Swallows (*Tachycineta bicolor*) in the Great Lakes-St. Lawrence River Basin. Environmental Toxicology and Chemistry 14:491–501.

BLANCHER, P. J., C. J. FURLONGER, AND D. K. MCNICOL. 1987. Diet of the nestling Tree Swallow (*Tachycineta bicolor*) near Sudbury, Ontario, summer 1986. Canadian Wildlife Service Technical Report Series Number 31, Ottawa, ON, Canada.

BLANCHER, P. J., AND D. K. MCNICOL. 1991. Tree Swallow diet in relation to wetland acidity. Canada Journal of Zoology 69:2629–2637.

BORROR, D. J., C. A. TRIPLEHORN, AND N. F. JOHNSON. 1989. An introduction to the study of insects. Saunders College Publishing, Philadelphia, PA.

BRYANT, D. M., AND A. K. TURNER. 1982. Central place foraging by swallows (Hirundinidae): the question of load size. Animal Behaviour 30:845–856.

BURTT, E. H. JR. 1977. Some factors in the timing of parent chick recognition in swallows. Animal Behavior 25:231–239.

DALY, H. V., J. T. DOYEN, AND A. H. PURCELL III. 1998. Introduction to insect biology and reproduction. Oxford University Press, Oxford, UK.

DESTEVEN, D. 1980. Clutch size, breeding success and parental survival in the Tree Swallow *Iridoprocne bicolor*. Evolution 34:278–291.

DUNN, P. O., AND S. J. HANNON. 1992. Effects of food abundance and male parental care on reproductive success and monogamy in Tree Swallows. Auk 109:488–499.

HOLROYD, G. L. 1972. Resource use by four avian species of aerial insect feeders. M.Sc. thesis, University of Toronto, Toronto, ON, Canada.

HOLROYD, G. L. 1983. Foraging strategies and food of a swallow guild. Ph.D. dissertation, University of Toronto, Toronto, ON, Canada.

JOHNSON, C. G. 1950. The comparison of suction trap, sticky trap and tow-net for the quantitative sampling of small airborne insects. Annals of Applied Biology 37:268–285.

JOHNSON, E. J., L. B. BEST, AND P. A. HEAGY. 1980. Food sampling biases associated with the ''ligature method.'' Condor 82:186–192.

KUERZI, R. G. 1941. Life history studies of the Tree Swallow. Proceedings of the Linnean Society of New York 52–53:1–52.

MCCARTY, J. P. 1997. Aquatic community characteristics influence the foraging patterns of Tree Swallows. Condor 99:210–213.

MCCARTY, J. P., AND D. W. WINKLER. 1991. Use of an artificial nestling for determining the diet of nestling Tree Swallows. Journal of Field Ornithology 62:211–217.

MCCARTY, J. P., AND D. W. WINKLER. 1999. Foraging ecology and diet selectivity of Tree Swallows feeding nestlings. Condor 101:246–254.

MORGAN, N. C., A. B. WADDELL, AND W. B. HALL. 1963. A comparison of the catches of emerging aquatic insects in floating box and submerged funnel traps. Journal of Animal Ecology 32:203–219.

NEEDHAM, J. C., AND H. B. HEYWOOD. 1929. A handbook of the dragonflies of North America. Charles C. Thomas Publisher, Springfield, IL.

NICHOLS, J. W., C. P. LARSEN, M. E. MCDONALD, G. J. NIEMI, AND G. T. ANKLEY. 1995. Bioenergetics-based model for accumulation of PCBs by nestling Tree Swallows, *Tachycineta bicolor*. Environmental Science and Technology 29:604–612.

ORIANS, G. H. 1966. Food of nestling Yellow-headed Blackbirds, Cariboo Parklands, British Columbia. Condor 68:321–337.

ORIANS, G. H., AND H. S. HORN. 1969. Overlap in foods and foraging of four species of blackbirds in the potholes of central Washington. Ecology 50: 930–938.

QUINNEY, T. E., AND C. D. ANKNEY. 1985. Prey size selection by Tree Swallows. Auk 102:245–250.

ROBERTSON, R. J., B. J. STUTCHBURY, AND R. R. COHEN. 1992. Tree Swallow (*Tachycineta bicolor*). *In* A. Poole, P. Stettenheim, and F. Gill [EDS.], The birds of North America, No. 11. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.

SAGE, R. D. 1982. Wet and dry-weight estimates of insects and spiders based on length. American Midland Naturalist 108:407–411.

SAMPLE, B. E., R. J. COOPER, R. D. GREER, AND R. C. WHITMORE. 1992. Estimation of insect biomass by length and width. American Midland Naturalist 129:234–240.

SAS INSTITUTE. 1996. SAS user's guide, Version 6.12. SAS Institute, Inc., Cary, NC.

SAS INSTITUTE. 2001. SAS user's guide, Version 8.02. SAS Institute, Inc., Cary, NC.

ST. LOUIS, V. L., L. BREEBART, J. C. BARLOW, AND J. F. KLAVERKAMP. 1993. Metal accumulation and mettalothionein concentrations in Tree Swallow nestlings near acidified lakes. Environmental Toxicology and Chemistry 12:1203–1207.

WILLSON, M. F. 1966. Breeding ecology of the Yellow-headed Blackbird. Ecological Monographs 36:51–77.

YORKS, A. L. 1999. Effects of polychlorinated biphenyls (PCBs) on reproduction, physiological processes, and biomarkers in Tree Swallows (*Tachycineta bicolor*). Ph.D. dissertation, University of Maryland, Baltimore, MD.

The Condor 106:429–434

HOW MUCH SUITABLE HABITAT IS LEFT FOR THE LAST KNOWN POPULATION OF THE PALE-HEADED BRUSH-FINCH?

STEFFEN OPPEL[1], H. MARTIN SCHAEFER[2,4], VERONIKA SCHMIDT[2] AND BORIS SCHRÖDER[3]
[1]*Insel Trischen, 25718 Friedrichskoog, Germany*
[2]*Institute for Avian Research, "Vogelwarte Helgoland," An der Vogelwarte 21,*
26386 Wilhelmshaven, Germany
[3]*University of Potsdam, Institute of Geoecology, P.O. Box 601553, 14415 Potsdam, Germany*

Abstract. The Pale-headed Brush-Finch (*Atlapetes pallidiceps*) is threatened with extinction due to loss of habitat. The only remnant population consists of 30–35 pairs and is confined to a single valley in the Andes of southwestern Ecuador. We investigated the habitat types used by this species in order to quantify the amount of available suitable habitat. The species used semiopen habitat types featuring a mosaic of dense scrub 2–4 m tall and grassy patches. Low continuous scrub was also used in larger proportions than on average available; forest and open country were not included in territories. Suitable habitat covered 28% of the area, and 16% was still available for new brush-finch territories. We identified a minimum of seven coherent patches that could support eight further pairs of the species. The valley can thus potentially support 40–50 pairs. The occupied habitat as described here should serve as a guideline in searching for new habitat.

Key words: Atlapetes pallidiceps, *compositional analysis, conservation, Ecuador, habitat selection, Pale-headed Brush-Finch.*

¿Cuánto Hábitat Adecuado Está Disponible para la Ultima Población de *Atlapetes pallidiceps*?

Resumen. *Atlapetes pallidiceps* es una especie endémica a un sólo valle en el suroeste del Ecuador. La especie está en peligro de extincción debido a la pérdida del hábitat. En este estudio analizamos los tipos de hábitat ocupados de *Atlapetes pallidiceps* con la intención de evaluar la cantidad de hábitat adecuado para una expansión de la población. *Atlapetes pallidiceps* ocupó hábitats semi-abiertos con un mosaico de matorral denso (2–4 m de altura) y lugares con vegetación herbácea. La especie también ocupó matorrales bajos continuos, mientras que los territorios no incluyeron bosques ni terrenos abiertos. Los hábitats adecuados cubrieron el 28% del área de estudio, y el 16% estuvo todavía disponible para el establecimiento de territorios nuevos. Identificamos un mínimo de siete parches coherentes que podrían sostener ocho parejas más del *Atlapetes pallidiceps*. Por lo tanto, el área tie-

---

Manuscript received 21 July 2003; accepted 14 January 2004.

[4] Corresponding author. E-mail: martin.schaefer@biologie.uni-freiburg.de

ne el potencial para soportar 40–50 parejas. Sería recomendable aplicar nuestra clasificación de los tipos de hábitat ocupados como guía para la búsqueda de nuevas áreas para este especie.

The Pale-headed Brush-Finch (*Atlapetes pallidiceps*) is a critically endangered endemic bird species of a semiarid valley in the Andes of southwestern Ecuador (Collar et al. 1992, BirdLife International 2000). It was considered extinct for 30 years until a small population of ca. 30 pairs was rediscovered in Yunguilla Valley in 1998 (Agreda et al. 1999, Krabbe 2004). The species appears to have always been confined to a limited geographic and ecological zone, but at present all of its habitat is modified by human land-use (Paynter 1972, Dercon et al. 1998). Habitat loss and degradation are therefore likely to play a prominent role in the decline of the Pale-headed Brush-Finch. A quantitative analysis of the habitat preferences of this species has not been presented so far (Paynter 1972, Ridgely and Greenfield 2001). Hence, data facilitating the identification of further extant populations are still lacking.

A land purchase has secured some habitat for the only remnant population of the Pale-headed Brush-Finch (Agreda et al. 1999), but brood parasitism by Shiny Cowbirds (*Molothrus bonariensis*) remains a threat (Oppel et al. 2004a). Cowbird shooting is being applied to reduce parasitism rates; this technique can enable host populations to grow (Hall and Rothstein 1999, Griffith and Griffith 2000), but has often failed due to the lack of suitable habitat (Whitfield et al. 1999, DeCapita 2000). It is therefore of crucial interest how much suitable habitat is left for the Pale-headed Brush-Finch in the Yunguilla Valley.

In this study, we first determined which habitat types the Pale-headed Brush-Finch occupied, using GIS to analyze used vs. available habitat features. Applying this result as a definition of suitable habitat, we calculated the amount of suitable habitat that is not currently occupied by existing territories. Size and spatial arrangement of unoccupied suitable habitat patches were then examined, in order to determine the number of potential territories providing sufficient habitat for further pairs.

METHODS

STUDY AREA

The Yunguilla Valley is located ca. 50 km southwest of Cuenca in the upper Río Jubones drainage, Province Azuay, Ecuador (3°13′S, 79°16′W). It belongs to a moderately cool area situated in a transitional zone between the arid lower Río Jubones valley and the humid upper reaches of the Andean west slope (Dercon et al. 1998). In this area, stable ecoclimatic conditions likely led to high endemism and a dense human population since the times of the Incas (Fjeldså et al. 1999). Current land uses are mainly corn crops and cattle pastures (Bossuyt et al. 1997, Dercon et al. 1998). The Pale-headed Brush-Finch was rediscovered here in 1998, on two steep slopes (ca. 45°) covering ca. 80 ha and ranging from 1650–2000 m in elevation (Agreda et al. 1999). The area is now protected and largely ungrazed by livestock. A subsequently discovered population on the neighboring hill inhabits an area of approximately equal size that is still grazed by cattle (B. Carlos and F. Sornoza, unpubl. data). Both hills feature semiopen habitats with dense early successional arid scrub consisting mostly of composite and verbenaceous species (e.g., *Steiractinia sodiroi*, N. Krabbe, pers. comm.), interspersed with non-native *Melinis minutiflora* grassland of old or recent pastures. Small stands of *Acacia* sp. and lauraceous trees are found in more humid parts, and fragments of semihumid forest persist on west-facing and southern slopes. Dwarf bamboo (*Chusquea* sp.) forms large patches in small depressions, ravines, and on the western slopes. The study area comprises ca. 150 ha including the reserve and an adjacent slope. It is surrounded by agricultural lands, secondary forest, and human settlements.

TERRITORY AND HABITAT MAPPING

Birds were monitored from dawn to early afternoon every day from late March to mid-June 2002. Territory boundaries were defined by the outermost song perches connected to form a minimum convex polygon (White and Garrott 1990). Habitat features were mapped in June 2002, and units with homogenous vegetation structure were defined by three variables: (1) habitat type (1 = open grassland and crops; 2 = semiopen grassland with single bushes covering $<50\%$; 3 = semiopen grassland with single bushes covering $>50\%$; 4 = low deciduous scrub ≤ 4 m height; 5 = low bamboo scrub ≤ 4 m height; 6 = tall deciduous scrub >4 m height; 7 = tall bamboo scrub >4 m height; 8 = mature forest or woodland; 9 = solitary trees), (2) vegetation density (1 = open; 2 = semiopen; 3 = open scrub with visibility >10 m; 4 = dense scrub with visibility 5–10 m; 5 = dense scrub with visibility <5 m), and height of the woody scrub (1 = 0–2 m; 2 = 2–4 m; 3 = 4–6 m; 4 = >6 m). We created a map from photographs taken from the opposite slopes, because plane topographic maps underestimate the area on steep slopes and were not available in an appropriate scale. The obtained pictures approximate an orthophoto, but may lead to some distortion along the slope. We therefore used only relative measures of use and availability to avoid bias introduced by distorted distance measures.

ANALYTICAL APPROACH

To describe the use of habitat features by the Pale-headed Brush-Finch in the study area, we intersected the map of all territories with the habitat feature map using ArcView GIS software (ESRI 1999, Sandkühler and Schröder 1999, Osborne et al. 2001). This yielded the proportion of every variable category for both the territories (use) and the entire study area (availability). We used compositional analysis (Aebischer et al. 1993) to compare habitat used in territories and habitat available in the study area. This technique overcomes the unit-sum constraint caused by the lack of independence between proportions that sum to 100% (Johnson 1980). In compositional analysis, a log-transformed ratio of one category over a random category from the same variable results in linearly independent data (Aebischer et al. 1993). The log-ratios of utilized habitat proportions are compared with the log-ratios of available habitat proportions, and differences around zero indicate random use of the category. We replaced all

TABLE 1. Percentage (mean ± SD) of habitat types in the study area and within 26 territories of the Pale-headed Brush-Finch in Yunguilla Valley, Ecuador, in 2002.

Habitat types	Study area	Territories
Open grassland, crops	15 ± 8	1 ± 2
Semiopen, single shrubs <50%	20 ± 11	18 ± 18
Semiopen, single shrubs >50%	18 ± 6	32 ± 21
Deciduous scrub ≤4 m tall	9 ± 5	19 ± 19
Bamboo scrub ≤4 m tall	13 ± 5	14 ± 13
Deciduous scrub >4 m tall	14 ± 5	13 ± 22
Bamboo scrub >4 m tall	4 ± 3	2 ± 7
Forest	7 ± 8	0.2 ± 0.8
Solitary trees	0.5 ± 0.5	0.5 ± 0.9

zero values with 0.0001 (Aebischer et al. 1993), and computed a matrix of all log-ratio differences for every habitat category using alternate categories as denominators. Categories were then ranked by adding all log-ratio difference values; the largest positive value representing the most selected, the smallest (largest negative) value the least selected category (Aebischer et al. 1993, Graham 2001, Ratcliffe and Crowe 2001). We tested for deviation from zero of all replication units (brush-finch territories) by using one-sample randomization tests with a significance level of $\alpha = 0.05$ (Manly 1997a). This was performed with RT software (Manly 1997b).

The unoccupied habitat was calculated by subtracting the occupied areas from the study area total. We then defined optimal habitat as those polygons that featured (1) the two most selected habitat types, (2) the most selected vegetation height, and (3) the three most selected density categories. Secondary habitat was defined as the two next best habitat types featuring the same height and density categories as in optimal habitat. Based on these definitions we assigned the values *optimal*, *secondary* (both combined to constitute *suitable*) or *unsuitable* to all habitat polygons. We then calculated the mean proportion of optimal and secondary habitat in occupied territories, and used this value as a threshold to remove polygons of unoccupied suitable habitat that were too small and isolated. Optimal and secondary habitat polygons that were large enough, or adjoined with other suitable polygons to form a sufficiently sized patch, were considered suitable for the establishment of further brush-finch territories. All analyses were carried out for each slope separately, but results represent relative values averaged across the study area as well as total number of potential territories. Results are given as means ± SD.

FIELD VALIDATION

From February through June 2003, territories of Pale-headed Brush-Finches were mapped in a section of Yunguilla Valley, in order to validate predictions derived from habitat classification. We made field observations independent of habitat classification and compared territory distribution in 2003 with predicted habitat suitability derived from the 2002 data set. The percentage of predicted suitable habitat included in new territories was used to assess prediction success. Prediction success was averaged across all new territories and is given as mean percentage ± SD.

RESULTS

Twenty-six territories of the Pale-headed Brush-Finch were detected in the study area in 2002. They did not include habitat types in proportion to habitat abundance ($\chi^2_{18} = 240.4$, $P < 0.001$). Semiopen habitat types covered 50% of all territories, and scrub <4 m tall contributed another 33% to all territory areas (Table 1). Open country and forest remnants comprised less than 2% of territories. The scrub height in territories deviated from random use, with heights of 2–4 m being used more, and scrub <2 m and >4 m used less than available in the study area ($\chi^2_6 = 100.0$, $P < 0.001$). Seventy-three percent of the scrub in territories was 2–4 m high, and another 14% was between 4 and 6 m high. Only 2% of the scrub in territories exceeded 6 m in height. The five density categories had balanced proportions in occupied territories, ranging from 16% (category 5) to 23% (category 2). Only the category ''open'' was used significantly less than available in the study area ($\chi^2_2 = 31.9$, $P < 0.001$).

The ranking matrix obtained from compositional analysis ordered the habitat types in the following sequence: semiopen with >50% bushes > semiopen with <50% bushes and both categories of low scrub > solitary and tall deciduous scrub > tall bamboo scrub, open country, and forest (Table 2). Based on the sum of log-ratio differences, we defined three habitat pools: a selected habitat pool including semiopen and low scrub habitat types, a tolerated habitat pool containing solitary trees and tall deciduous scrub, and an avoided habitat pool comprising tall bamboo, forest, and open country. The selected habitat pool was used to calculate potential habitat still available for brush-finches in the study area.

Analysis of vegetation density yielded only that dense scrub with 5–10 m visibility was used over dense scrub with visibility less than 5 m ($P < 0.05$), but did not differ from other density categories. Definition of suitable habitat was therefore based on the three remaining density categories. Optimal habitat, defined as polygons featuring both semiopen habitat types, scrub height from 2–4 m, and intermediate vegetation densities (categories 2 to 4), covered 16% of the study area. Of the total area of optimal habitat,

TABLE 2. Simplified ranking matrix of Pale-headed Brush-Finch habitat selection in Yunguilla Valley, Ecuador, calculated from proportions of habitat types in 26 territories (Table 1). For each pair of habitat types the ratio of the area in each pair's territory was calculated. Next, the ratio of the area available in the total study area was subtracted, and the mean of this difference over all 26 territories was calculated. Matrix elements represent signs of this mean difference, 0 = no significant deviation from zero; + = $P < 0.05$; ++ = $P < 0.01$ from a one-sample randomization test. Negative values suggest avoidance; positive values suggest selection.

	Habitat type									Sum of differences	Rank
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)		
(1) Open grassland, crops		—	—	—	—	—	0	0	—	–31.5	9
(2) Semiopen, single shrubs <50%			0	0	0	0	++	++	0	12.5	2
(3) Semiopen, single shrubs >50%				0	0	+	++	++	++	22.6	1
(4) Deciduous scrub ≤4 m tall					0	0	++	++	0	10.4	3
(5) Bamboo scrub ≤4 m tall						0	++	++	0	8.5	4
(6) Deciduous scrub >4 m tall							+	++	0	–2.6	6
(7) Bamboo scrub >4 m tall								0	—	–13.9	7
(8) Forest									—	–22.4	8
(9) Solitary trees										0.3	5

47% was occupied by territories in 2002, leaving an area unoccupied that equates to 9% of the study area. Optimal habitat was present in all brush-finch territories and covered on average 36% ± 21%, range (5–85%). Secondary habitat, (polygons featuring low scrub habitat types [categories 4 and 5], scrub height of 2–4 m, and intermediate vegetation densities [categories 2 to 4]), covered 12% of the study area, of which 39% was occupied in 2002. Within brush-finch territories, secondary habitat covered 21 ± 21%, range (0–65%).

Unoccupied suitable habitat covered 16% of the study area. Of this area, 34% of patches were too small (1–73% of territory mean), and isolated between either existing territories or unsuitable habitat (Fig. 1a). The remainder included seven areas with enough optimal and secondary habitat to support eight new territories. Another three areas remained with only secondary habitat, but large enough for at least one territory each, covering 11% of the study area. In sum, at present the area in Yunguilla supports suitable habitat for a minimum of eight, and possibly up to 14 further territories of the Pale-headed Brush-Finch.

In 2003, 21 territories were found in the study area, of which 17 were almost identical to territories of the previous year (Fig. 1). Three of the new territories were established in areas classified as suitable habitat, and one new territory was established in an area with little suitable habitat (Fig. 1b). Classification success was 66 ± 35%, range (15–90%). One more territory was located outside the study area and could therefore not be included in this analysis.

DISCUSSION

The Pale-headed Brush-Finch avoids forests or tall scrub vegetation. It inhabits heterogeneous semiopen scrubland, where patches of scrub with medium height are interspersed with small grassy clearings. Dense continuous scrub adjacent to open areas is present in most territories, and is considered important for nest sites (Oppel et al. 2004b). Territories were established in patches of pure deciduous or bamboo scrub. Approximately 16% of the study area provided suitable but unoccupied habitat for the species in 2002. However, more than one-third of these patches were too small and not directly connected to other suitable habitats, and were thus considered unavailable for territory establishment. Yet, territories might provide the minimum amount of cover and food supply even if they include unsuitable habitat. Some of the patches that we considered to be too small and isolated might thus be combined in a larger than average territory. Thus, our definition of available habitat for at least eight further territories is fairly conservative, as only coherent patches of suitable habitat qualified for new potential territories. We identified three further areas with sufficient secondary habitat to support another three or four pairs. The validation in 2003 indicated that the predictions derived from our habitat classification were accurate and useful. Two territories were established where expected, one new pair settled in suitable habitat that had previously been occupied, and one more pair settled adjacent to the study area.

The Pale-headed Brush-Finch is unobtrusive and difficult to detect. It is therefore possible that some of the areas described as unoccupied in this study are in reality already occupied. On the other hand, factors like predation and cowbird parasitism affecting the reproductive output of the species (Oppel et al. 2004b) might render suitable patches unoccupied. It can, however, be assumed that the study area can support at least 40–50 territories of the Pale-headed Brush-Finch. Reduction in territory size resulting from increasing pressure within an expanding population might elevate the number of pairs that the study area can accommodate. Furthermore, an adjacent slope not surveyed in 2002 held another two pairs in 2003. Since we used distribution data to define suitable habitat, it has to be

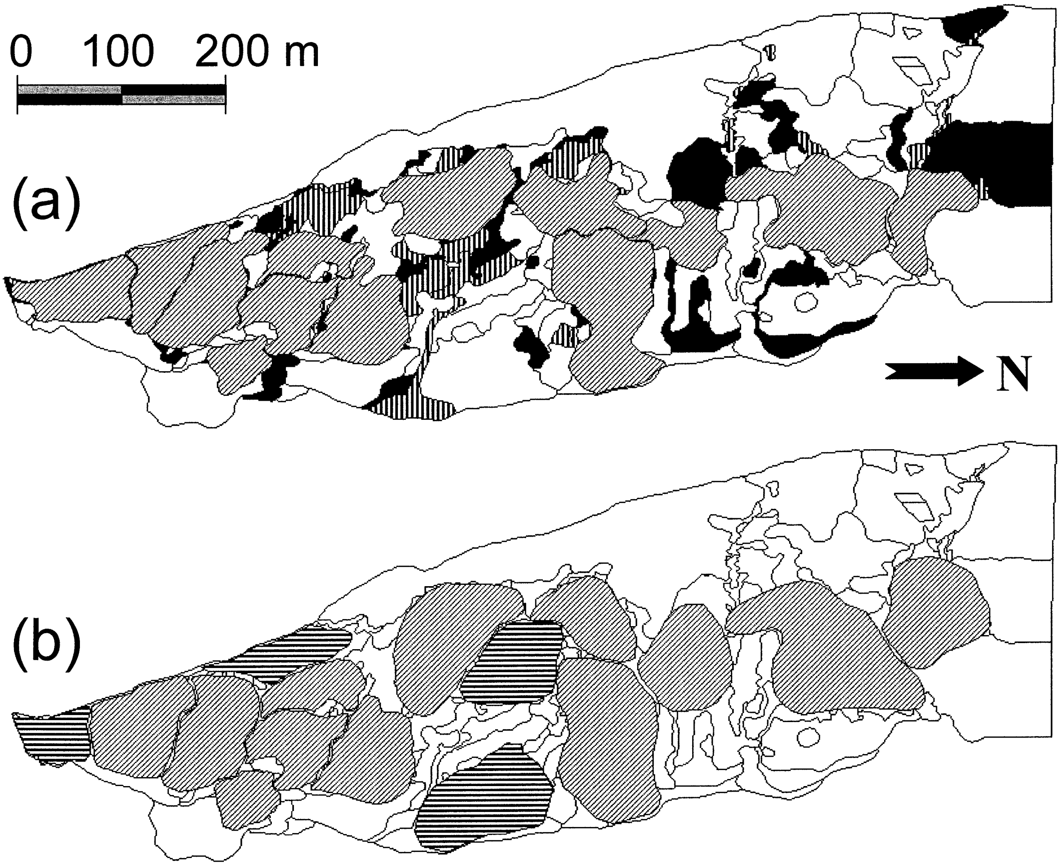

FIGURE 1. Map of the east slope of the Pale-headed Brush-Finch reserve in Yunguilla Valley, Ecuador. An additional 13 pairs were located on further slopes in and outside of the reserve in 2002. (a) Cross-hatched areas are brush-finch territories occupied in 2002, black areas indicate unoccupied ''optimal'' habitat (semiopen habitat with moderately dense scrub), vertically barred areas unoccupied ''secondary'' habitat (low, <4 m tall, moderately dense scrub). Unsuitable forest, tall bamboo, and open country habitat is unshaded. (b) Brush-finch territories found during the 2003 validation survey, divided into old pairs (cross-hatched) and pairs new to the reserve in 2003 (horizontally barred).

cautioned that there is no guarantee that presence of individuals in a certain habitat is related to habitat quality (van Horne 1983, Pulliam 1988, Jones 2001). Cowbird parasitism or interspecific competition by other brush-finch species might reduce the availability of suitable habitat (although the sympatric Stripe-headed Brush-Finch [*Buarremon torquatus*] uses a different microhabitat, Oppel et al. 2004b).

The identification and protection of new areas with suitable habitat seems essential for the conservation of the Pale-headed Brush-Finch to reduce the risks inherent to small populations at a single site. Repeated searches in the 1990s found former localities in the Río Jubones drainage degraded and devoid of the Pale-headed Brush-Finch (Collar et al. 1992, Krabbe 2004). Though suitable habitat is rare, it persists at a few localities (N. Krabbe, pers. comm.), and succession on fallow land might create new suitable habitat. Assessing the species' presence in all suitable areas outside the Yunguilla Valley would thus yield important insight into habitat use, colonization probability, and the ability to cope with cowbird parasitism at a different locality. Our results provide an important tool for this search and also to implement successful land management in the Yunguilla reserve to counteract conversion from scrub into forests.

This study was funded by the German Academic Foreign Exchange Service (DAAD), grant number 332404010, the Royal Society for the Protection of Birds, and the Swedish Club300, and conducted in collaboration with the Institute for Avian Research in Wilhelmshaven, Germany. The research was carried out under permit No. 004-IC-FAU-DBAP/MA of the Ministerio del Ambiente, Ecuador, and supported by Fundacion Jocotoco, the landowner of the study area. J. Heathcote was of great help with field observations, habitat mapping, and data entry. C. Pohl kindly provided the Spanish abstract. F. Bairlein and P. Stoddard improved the manuscript with helpful comments.

LITERATURE CITED

AEBISCHER, N. J., P. A. ROBERTSON, AND R. E. KENWARD. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74: 1313–1323.

AGREDA, A., N. KRABBE, AND O. RODRIGUEZ. 1999. Pale-headed Brushfinch *Atlapetes pallidiceps* is not extinct. Cotinga 11:50–54.

BIRDLIFE INTERNATIONAL. 2000. Threatened birds of the world. Lynx Edicions, Barcelona, and BirdLife International, Cambridge, UK.

BOSSUYT, B., G. DERCON, B. D. BIÈVRE, F. CISNEROS, AND J. DECKERS. 1997. Agro-ecological zoning of the Austro Ecuatoriano. The Land 1:159–170.

COLLAR, N. J., L. P. GONZAGA, N. KRABBE, A. M. NIETO, L. G. NARANJO, T. A. PARKER, AND D. C. WEGE. 1992. Threatened birds of the Americas. International Council for Bird Preservation, Cambridge, UK.

DECAPITA, M. E. 2000. Brown-headed Cowbird control on Kirtland's Warbler nesting areas in Michigan, p. 333–341. *In* J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy [EDS.], Ecology and management of cowbirds and their hosts. University of Texas Press, Austin, TX.

DERCON, G., B. BOSSUYT, B. D. BIÈVRE, F. CISNEROS, AND J. DECKERS. 1998. Zonificacion agroecologica del Austro Ecuatoriano. Promas, Universidad de Cuenca, Cuenca, Ecuador.

ESRI. 1999. Getting to know ArcView GIS. Environmental Systems Research Institute Press, New York.

FJELDSÅ, J., E. LAMBIN, AND B. MERTENS. 1999. Correlation between endemism and local ecoclimatic stability documented by comparing Andean bird distributions and remotely sensed land surface data. Ecography 22:63–78.

GRAHAM, C. 2001. Habitat selection and activity budgets of Keel-billed Toucans at the landscape level. Condor 103:776–784.

GRIFFITH, J. T., AND J. C. GRIFFITH. 2000. Cowbird control and the endangered Least Bell's Vireo: a management success story, p. 342–357. *In* J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy [EDS.], Ecology and management of cowbirds and their hosts. University of Texas Press, Austin, TX.

HALL, L. S., AND S. I. ROTHSTEIN. 1999. Cowbird control: the efficacy of long-term control and proposed alternatives to standard control practices. Studies in Avian Biology 18:254–259.

JOHNSON, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

JONES, J. 2001. Habitat selection in avian ecology: a critical review. Auk 118:557–562.

KRABBE, N. 2004. Pale-headed Brush-Finch *Atlapetes pallidiceps* (Aves: Emberizidae): notes on population size, habitat, vocalizations, feeding, interference competition, and conservation. Bird Conservation International, in press.

MANLY, B. F. J. 1997a. Randomization, bootstrap and Monte Carlo methods in biology. Chapman & Hall, London.

MANLY, B. F. J. 1997b. RT: a program for randomization testing. Western EcoSystems Technology Inc, Cheyenne, WY.

OPPEL, S., H. M. SCHAEFER, V. SCHMIDT, AND B. SCHRÖDER. 2004a. Habitat selection of the Pale-headed Brushfinch, *Atlapetes pallidiceps*, the role of interspecific competition, and implications for management. Biological Conservation, in press.

OPPEL, S., H. M. SCHAEFER, V. SCHMIDT, AND B. SCHRÖDER. 2004b. Cowbird parasitism of the Pale-headed Brush-Finch *Atlapetes pallidiceps*: implications for conservation and management. Bird Conservation International, in press.

OSBORNE, P. E., J. C. ALONSO, AND R. G. BRYANT. 2001. Modelling landscape-scale habitat use using GIS and remote sensing: a case study with Great Bustards. Journal of Applied Ecology 38:458–471.

PAYNTER, R. A. 1972. Biology and evolution of the *Atlapetes schistaceus* species-group. Bulletin of the Museum of Comparative Zoology 143:297–320.

PULLIAM, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652–661.

RATCLIFFE, C. S., AND T. M. CROWE. 2001. Habitat utilisation and home range size of Helmeted Guineafowl (*Numida meleagris*) in the midlands of KwaZulu-Natal province, South Africa. Biological Conservation 98:333–345.

RIDGELY, R. S., AND P. J. GREENFIELD. 2001. The birds of Ecuador—field guide. Cornell University Press, Ithaca, NY.

SANDKÜHLER, K., AND B. SCHRÖDER. 1999. GIS-unterstützte Habitatstrukturanalyse wiesenbrütender Kleinvögel im Drömling (O-Niedersachsen). NNA-Berichte 3/99:41–50.

VAN HORNE, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901.

WHITE, G. C., AND R. A. GARROTT. 1990. Analyses of wildlife tracking data. Academic Press, New York.

WHITFIELD, M. J., K. M. ENOS, AND S. P. ROWE. 1999. Is Brown-headed Cowbird trapping effective for managing populations of the endangered Southwestern Willow Flycatcher? Studies in Avian Biology 18:260–266.