

SHORT COMMUNICATIONS

The Condor 99:798–803
© The Cooper Ornithological Society 1997

A TEST OF AN ENVIRONMENTAL ADVERTISEMENT HYPOTHESIS FOR THE FUNCTION OF DRUMMING IN YELLOW-BELLIED SAPSUCKERS¹

LURIE S. EBERHARDT²

Department of Zoology, 223 Bartram Hall, University of Florida, Gainesville, FL 32611

Abstract. The woodpecker drum is unusual among avian acoustic display because woodpeckers employ material outside their own bodies to produce sound. This allows an opportunity for acoustic analysis of instruments used for drumming that is not possible with other types of acoustic display. Examination of the drum sites of Yellow-bellied Sapsuckers (*Sphyrapicus varius*) revealed that sapsuckers do not use drumming to advertise the presence of nesting and feeding sites in their environment. Controlled hits on a variety of substrates in the sapsuckers' environment were used to compare acoustic properties of spots chosen for drumming to other non-drum spots. In general, sapsuckers drummed in locations that could produce louder and longer lasting sounds than surrounding non-drum substrate including nest trees, feeding trees, and other substrate near the site of drumming. My evidence suggests that sapsucker drumming is an acoustic signal designed for long distance transmission.

Key words: *acoustic display, communication, drumming, Sphyrapicus varius, woodpecker, Yellow-bellied Sapsucker.*

Drumming is a loud, rhythmic series of sounds produced when a woodpecker hammers its bill in split-second repetitions against a resonating object. Drumming is never produced when the substrate is being altered for feeding or nest building and is thus defined as a signal or display behavior (Lawrence 1967). Among acoustic displays, drumming is unusual because a separate instrument is required to produce the sound in addition to the bird's body parts (Skutch 1985). Like many acoustic displays, drumming is likely to have multiple functions depending upon context, season, and species (Short 1982). One intriguing function for drumming was proposed by Winkler and Short (1978): drumming could contain valuable information about habitat quality if sound quality varies with the substrate that is used for the display. I call this the environmental advertisement hypothesis (EAH). This hypothesis can be used to explain how potential mates

use information contained in the sound of the drum to assess environmental quality and make territory settlement choices. Thus, the EAH applies to the mate attraction aspect of communication systems.

Although the EAH was originally proposed to explain drumming in woodpeckers, it could apply to other acoustic displays that employ external substrate for sound production including Ruffed Grouse (*Bonasa umbellus*) (Palmer 1963, Schemnitz 1976), lycosid spiders (Harrison 1969, Rovner 1975, Stratton and Uetz 1981), and kangaroo rats (*Dipodomys* sp.) (Kenagy 1976, Randall and Stevens 1987, Randall 1989). In addition, the EAH has broader applications to the more typical acoustic displays that organisms make with their own bodies such as bird song, insect stridulation, or amphibian trills. All airborne sounds are altered by environmental factors such as vegetation, humidity, temperature, and wind (Aylor 1972, Linskens et al. 1976, Wiley and Richards 1978). By choosing specific sites for acoustic display, organisms may be able to advertise locations of high quality if the sounds that they produce are altered by the environment in particular ways. Although the EAH may have many broad applications, in this paper I will focus on the EAH as it may apply to woodpeckers, the taxon for which it was first proposed.

The EAH predicts that woodpeckers will choose to drum on substrates that advertise the quality of their location. A high-quality territory for a woodpecker includes wood that is valuable for constructing nest holes, roosting sites, or for feeding. Most species of woodpeckers use dead wood for feeding, nesting, and roosting. Several studies have shown the importance of keeping dead wood standing in a forest to maintain healthy woodpecker populations (Peterson and Grubb 1983, Swallow et al. 1986, Welch and Capen 1992). Dead wood, without the high water content of a living tree, probably would have a different sound than live wood. Thus, for the majority of woodpecker species, the EAH predicts that they will choose dead wood rather than live trees as a drum substrate.

A review of the drumming of woodpeckers of the world (Short 1982) shows that the majority of woodpeckers use dead wood for drumming, thus fitting the predictions of the EAH. A more in-depth study of Red-headed Woodpeckers (*Melanerpes erythrocephalus*) (Venables and Collopy 1989) showed that this species preferred to drum specifically on the dead wood of a

¹ Received 18 July 1996. Accepted 16 April 1997.

² Current address: Department of Biology, Valparaiso University, Valparaiso, IN 46383, e-mail: leberhardt@exodus.valpo.edu

nest tree and not on other dead wood available, providing even stronger evidence for a possible environmental advertisement function. In this study, I examined the EAH for Yellow-bellied Sapsuckers (*Sphyrapicus varius*). Yellow-bellied Sapsuckers do not use dead wood like other woodpeckers, making them an intriguing species for a test of this hypothesis.

Adult Yellow-bellied Sapsuckers feed on the phloem sap of live trees from shallow holes that they peck in the bark (Beal 1911, Kilham 1964, Tate 1973). Nestlings are fed a mixture of insects and sap. The insects are gleaned from the leaves and trunks of trees or caught in flight. Yellow-bellied Sapsuckers rarely obtain food from excavations in dead, rotting wood as do many other woodpeckers. In addition, Yellow-bellied Sapsuckers generally make nesting cavities in live aspen that have been infected with a heart-rot fungus (Kilham 1962, 1977, Lawrence 1967). Thus, dead wood generally is not used for nesting, roosting or feeding by Yellow-bellied Sapsuckers.

Given these peculiarities, the EAH predicts that Yellow-bellied Sapsuckers should drum upon substrates that could be used to indicate the presence of their living food and nest trees. Consequently, the preferred drum substrate for sapsuckers predicted by the EAH is living wood and more specifically, something that sounds like food or nest trees. In this study, I test these predictions that Yellow-bellied Sapsuckers advertise the presence of nest and food trees by their choice of drum substrate. In the process of this test I describe specific acoustic properties of the drum substrates used by the sapsuckers.

METHODS

STUDY SITE AND OBSERVATIONS

I observed Yellow-bellied Sapsuckers in 1991 and 1992 at the University of Michigan Biological Station in Cheboygan county, Michigan. The habitat in this area consists of an 80-year-old mixed hardwood forest which grew up after extensive clear cutting of the original pine forest in the early 1900s.

Data on types of substrate used for drumming were collected from the time the first adults arrived from migration in early April until just after young were fledged from the nest in early July. Two sampling methods were used. Ad libitum observations of all drumming birds encountered were made in April and May 1991. In 1992, five individual sapsuckers were followed for up to 4 hr at a time, and all drumming substrates of each focal individual were identified. Individual birds were marked with colored leg bands or identified by unique color patterns of red head and nape feathers. These focal-animal data were collected in April before the deciduous trees had developed new leaves which meant that long distance observations were possible through the branches in the forest canopy.

A drum site was defined as the specific location on a substrate where a bird made its drumming bouts. A drum roll was defined as a series of rapid taps followed by a pause that was longer than any of the intervals between individual taps. I defined a drumming bout as a series of drum rolls made continuously on the same

drum site. An individual bout of drumming ended when the bird moved away from the drum site.

MEASUREMENTS OF SOUND QUALITY

Four aspects of the sound-producing potential of nest, food, and drum substrate were measured. A comparison of the loudness of sounds that could be produced from different substrates was made with a knocking device. The knocking device consisted of a 5 cm diameter solid oak mallet mounted on a board with a screen-door spring which was attached at the end of the mallet's 24 cm handle. For each knock on a substrate, the mallet was pulled back to a designated mark on the board and released 22 cm in front of a substrate. In combination with the spring, this system allowed approximately equal knocks to be repeated on a variety of substrates. The amplitude of the resulting sounds of these controlled knocks was measured with a Realistic sound level meter also mounted on the apparatus at a fixed distance of 25 cm from the mallet's striking surface. The amplitudes of three knocks per test substrate were measured and averaged for later analysis. A second device was used to measure three additional aspects of sound quality involving frequency and loudness. This implement was made with a 15 cm plastic crochet hook mounted perpendicular to one end of a small board (2 × 4 × 36 cm) and also was used to make hits against the different substrates. Strikes with the crochet-hook device were recorded 30 cm away with an Audio-Technica AT815a directional microphone and a Sony Professional Walkman cassette tape recorder. One strike per substrate spot was used for analysis of the crochet hook strike sounds. Sound properties of these crochet hook strikes were measured using a UNISCAN II model 14600 sound analyzer (Multigon Industries, range = 5 Hz). These measurements included frequency (Hz) of the longest lasting frequency component in the recording, length (sec) of the longest lasting frequency component, and frequency (Hz) of the sound component with the greatest power (loudest). Neither of the knocking devices described above was designed to simulate woodpecker drumming. Rather, the sound properties of the knocks were used to compare the sound producing potential of different test substrates.

SUBSTRATES TESTED

To show whether the drum substrates had similar sound qualities to food or nest substrates as the EAH predicts, the sound-producing potential of nest and food substrates were compared with all accessible drum substrates located in 1991. Nest substrates were defined as sites on trees 5–10 cm above or below active nest-cavity entrances. A site on a tree that had 100 or more sap holes with some newly made wounds was defined as food substrate. Drum sites were assessed from knocks made directly on the spot where sapsuckers had produced drum sounds.

A second experiment was performed by making controlled knocks and strikes on substrates chosen for drumming and those not chosen. Specific drum sites were easy to locate because sapsuckers leave small indentations in the wood during drumming from the force of their blows. I identified 12 drum sites and for each one I located a close non-drum spot 20 cm below

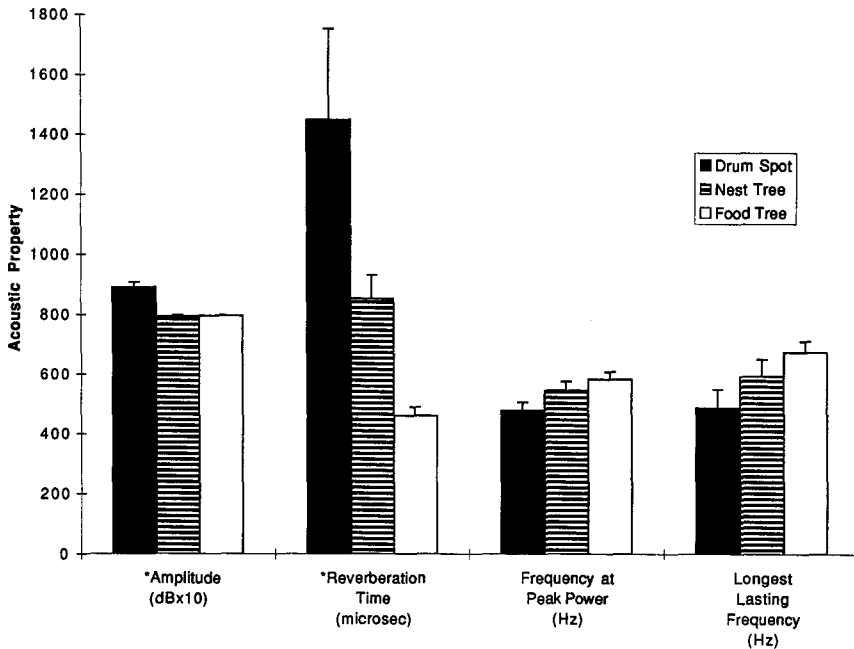


FIGURE 1. Comparisons of four acoustic properties between substrate used for drumming, nesting and feeding. Bars are means + SE. * denotes an acoustic property that is significantly different for drum substrate ($P < 0.01$).

the drum site if possible. If there was no testable substrate below the drum site, I located a non-drum spot 20 cm to the side or up from the drum site. Also for each drum site, I randomly chose one of the closest five neighbor trees that had not been used for drumming. I made the controlled knocks and strikes on neighboring trees at the same height and in the same orientation as the matched drum substrate. Thus, for this second experiment, I had samples of the acoustic properties of 12 drum sites, 12 non-drum close spots, and 12 non-drum neighbor trees all matched for location.

STATISTICAL ANALYSES

I used ANOVA to detect differences in the four sound quality measurements among drum, nest, and food substrates. Because multiple comparisons were made, Bonferroni's approximation was used to determine a suitable level of significance ($P = 0.012$) for each test (Fry 1993). A Friedman Rank Sum analysis (Hollander and Wolfe 1973) was used to compare acoustic properties of the paired drum sites, non-drum close spots and non-drum neighbor trees. Bonferroni's approximation of α -levels also was employed in this case.

RESULTS

SUBSTRATE USED FOR DRUMMING

Yellow-bellied Sapsuckers never drummed at feeding or nesting sites (0/142 drumming bouts). Non-living substrate was used in 100% of the drum bouts that I observed. The majority of individuals (32/40) that I watched nested in live trees, and all individuals that

were observed feeding ate sap extracted from living trees. Out of 142 bouts of drumming from 23 individuals, the preferred drum substrate was a dead aspen branch still attached to the living tree (81% of bouts observed). Also frequented were the old skeletons of huge pine stumps (8%) and the dead wood of other species of trees (7%). A few birds drummed on human-made substrate including telephone poles, chimneys of cabins and an upturned metal boat (4%).

SOUND QUALITY COMPARISONS

Drum spots had significantly louder sounds ($F_{2,40} = 28.95$, $P < 0.001$) and longer reverberation times ($F_{2,40} = 10.10$, $P < 0.001$) than nest and food trees. Post-hoc Fisher PLSD tests indicated that drum substrates significantly differed from nest and food substrates in both cases. With the Bonferroni adjustment in the significance level, I found no clear differences between drum, nest, and food trees in the frequency of peak power ($F_{2,40} = 4.1$, $P = 0.02$) or the longest lasting frequency ($F_{2,40} = 3.7$, $P = 0.03$) (Fig. 1). However, in both cases there was a trend for drum substrates to produce lower sounds than nest or food substrates. In summary, drum substrates had louder sounds that lasted longer than the sound produced on the nesting and feeding substrates.

I found significantly louder sounds produced on the drum substrate than on close non-drum substrate and non-drum neighbor trees (Friedman, $n = 13$, $\chi^2_2 = 14.2$, $P < 0.001$). A post hoc multiple comparison test (Hollander and Wolfe 1973) showed only a significant difference between drum spots and their neighbor trees

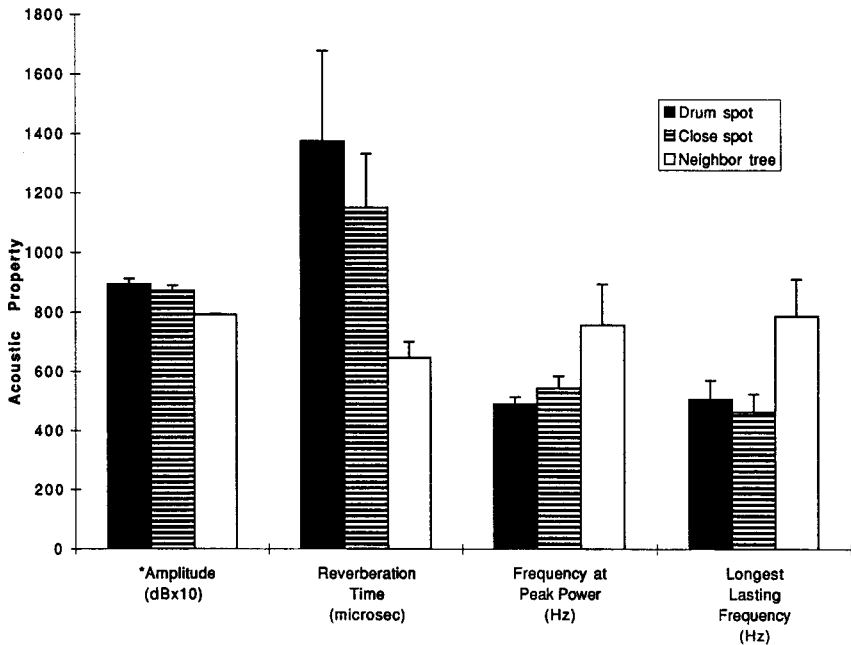


FIGURE 2. Comparisons of four acoustic properties between matched drum substrate and two non-drum substrates (close spots on the same drum material and neighbor trees). Bars are means + SE. * denotes an acoustic property that is significantly different for drum substrate ($P < 0.01$).

($P < 0.01$) but not between drum spots and their close non-drum substrate ($P > 0.05$). There were no differences between substrate in any of the other three acoustic measurements when Bonferroni approximations were used. In short, drum substrates had louder sounds than matched substrate on neighbor trees but did not differ from other spots on the same drum material (Fig. 2).

DISCUSSION

The EAH predicts that sapsuckers should drum on nesting or feeding sites or both. Because I never saw a Yellow-bellied Sapsucker drum on the trunk of a nesting or feeding tree, this first prediction was not supported. Furthermore, sapsuckers did not choose drum substrate that had sounds typical of food or nest substrate. Thus, I conclude that sapsuckers do not advertise the quality of particular nesting or feeding spots with their drumming.

Although I did not find evidence that sapsuckers advertise environmental quality with their drum display, it is clear that drum substrates had unusual sound properties. Drum substrates could be used to produce an acoustic signal with particularly loud sounds and possibly lower sounds than would come from the nest and food substrates. Sounds from drum substrate had long-lasting acoustic components. Studies of sound transmission in forested environments have shown that lower frequencies (below 3 kHz) travel farther through most habitats (Marten and Marler 1977). Louder sounds also would transmit greater distances. Thus, my data suggest that sapsucker drumming is designed for

long-distance transmission, much like the song of most passerine birds (Richards and Wiley 1980). As anecdotal corroboration of this, I and others (Rushmore 1973) have heard distant birds drumming apparently in response to a focal sapsucker's drumming or to artificial drums. Although outside the scope of this study, drumming offers a unique opportunity to further test a long-distance transmission hypothesis because various types of artificial drums could be broadcast easily in a forest habitat and their transmission properties tested.

Sapsuckers appeared to choose drum sites that could be used to produce louder sounds than neighboring trees within a specific area, thus strengthening the above conclusions that drumming is a signal designed for long-distance transmission. However, within specific dead branches or stumps, drum sites did not differ significantly from other non-drum spots in the acoustic properties that I measured. Perhaps other factors in addition to long-distance transmission of acoustic signals are considered by drumming birds. For example, sapsuckers are vulnerable to aerial attack by hawks and owls (pers. observ.). Within a snag suitable for drumming, sites chosen for drumming may have provided a better vantage point for predator detection rather than a better acoustic signal. Although I did not record information on specific orientation and vulnerability of drumming sapsuckers, most drumming sapsuckers were situated in a way that appeared to offer excellent positions for predator vigilance. Producing loud acoustic signals could easily make a drummer more vulnerable to predator detection and it would follow that a

drumming sapsucker must use positions that minimize predation risk.

As demonstrated by the results of controlled knocks on various substrates, woodpecker drumming offers an unusual opportunity to study acoustic display as an advertisement. Normally, when only an organism's own body is involved in sound production, it is impractical or impossible to define the range of sounds that the organism is capable of making. Such a question involves difficult long-term study, invasive manipulations, or studies of captive animals. In species that use substrates however, one can measure the sound-producing properties of the substrate used to make the display and a range of possible sounds can be identified. Knowing the sound-producing capabilities of an organism helps in understanding the function of advertisement because the sounds it chooses to make when performing a particular acoustic display can reveal how far and therefore to whom that display is directed. For example, in Yellow-bellied Sapsuckers I have shown that they make sounds on substrates that can be used to produce louder and longer lasting sounds than other trees in an area. This suggests that they are covering the greatest possible range with their type of acoustic display. In conclusion, drumming by sapsuckers does not appear to have the unusual function of advertising environmental quality as first hypothesized by Winkler and Short (1978) for woodpeckers. However, drumming is a unique signal among birds and my study has shown that use of controlled knocking devices allows an analysis of this acoustic signal's properties that is not easily possible for song.

H. J. Brockmann, A. E. Eberhardt, M. A. Eberhardt, and P. W. Martin offered invaluable help, support, and guidance throughout this study. Special thanks is extended to D. B. McDonald for his advice on statistical analysis, R. J. Vande Kopple for his technical advice in the field, and the maintenance staff at the University of Michigan Biological Station for their careful revisions of my device for measuring amplitude of controlled hits. F. J. Cuthbert provided excellent advice on the local site and color-marked sapsuckers. I am grateful to H. J. Brockmann, S. D. Duncan, D. B. McDonald, L. L. Short, and two anonymous reviewers for their comments on the manuscript. The Florida Museum of Natural History Bioacoustic Laboratory provided sound recording and analysis equipment. Funding for this study came from the University of Florida Zoology Department, the University of Michigan Biological Station, a Sigma Xi Grant-In-Aid of Research, and the Frank M. Chapman Memorial Fund.

LITERATURE CITED

- AYLOR, D. 1972. Sound transmission through vegetation in relation to leaf area density, leaf width, and breadth of canopy. *J. Acoust. Soc. Am.* 51: 411-414.
- BEAL, F. E. L. 1911. Food of the woodpeckers of the United States. U.S. Dept. Agric. Biol. Surv., Bull. 37.
- FRY, J. C. 1993. Biological data analysis: a practical approach. Oxford Univ. Press, Oxford.
- HARRISON, J. B. 1969. Acoustic behavior of a wolf spider, *Lycosa gulosa*. *Anim. Behav.* 17:14-16.
- HOLLANDER, M., AND D. A. WOLFE. 1973. Nonparametric statistical methods. John Wiley and Sons, New York.
- KENAGY, G. J. 1976. Field observations of male fighting, drumming, and copulation in the great basin kangaroo rat, *Dipodomys microps*. *J. Mammal.* 57:781-784.
- KILHAM, L. 1962. Breeding behavior of Yellow-bellied Sapsuckers. *Auk* 79:31-43.
- KILHAM, L. 1964. The relations of breeding Yellow-bellied Sapsuckers to wounded birches and other trees. *Auk* 81:520-527.
- KILHAM, L. 1977. Nesting behavior of Yellow-bellied Sapsuckers. *Wilson Bull.* 89:310-324.
- LAWRENCE, L. K. 1967. A comparative life history study of four species of woodpeckers. *Ornithol. Monogr.* 5.
- LINSKENS, H. R., M. J. M. MARTENS, H. F. G. M. HENDRIKSEN, A. M. ROESTENBERG-SINNIGE, W. A. F. M. BROUWERS, A. L. H. C. VAN DER STAACK, AND A. M. J. STRIK-JANSEN. 1976. The acoustic climate of plant communities. *Oecologia* 23:165-177.
- MARTEN, K., AND P. MARLER. 1977. Sound transmission and its significance for animal vocalization. *Behav. Ecol. Sociobiol.* 2:271-290.
- PALMER, W. L. 1963. Ruffed Grouse drumming sites in Northern Michigan. *J. Wildl. Manage.* 27:656-663.
- PETERSON, A. W., T. C. GRUBB, JR. 1983. Artificial trees as a cavity substrate for woodpeckers. *J. Wildl. Manage.* 47:790-798.
- RANDALL, J. A. 1989. Individual footdrumming signatures in banner-tailed kangaroo rats *Dipodomys spectabilis*. *Anim. Behav.* 38:620-630.
- RANDALL, J. A., AND C. M. STEVENS. 1987. Footdrumming and other anti-predator responses in the bannertail kangaroo rat (*Dipodomys spectabilis*). *Behav. Ecol. Sociobiol.* 20:187-194.
- RICHARDS, D. G., AND H. WILEY. 1980. Reverberations and amplitude fluctuations in the propagation of sound in a forest: implications for animal communication. *Am. Nat.* 115:381-399.
- ROVNER, J. S. 1975. Sound production by nearctic wolf spiders: a substratum-coupled stridulatory mechanism. *Science* 190:1309.
- RUSHMORE, F. M. 1973. Techniques for calling sapsuckers and finding their nesting territories. USDA For. Serv. Res. Paper, Northeastern Region, Publ. No. 281.
- SCHEMNITZ, S. D. 1976. Characteristics of Maine Ruffed Grouse drumming sites. *Res. Life Sci.* 11.
- SHORT, L. L. 1982. Woodpeckers of the World. Delaware Mus. Nat. Hist., Greenville, DE.
- SKUTCH, A. F. 1985. Life of the woodpecker. Ibis Publishing, Santa Monica, CA.
- STRATTON, G. E., AND G. W. UETZ. 1981. Acoustic communication and reproductive isolation in two species of wolf spiders. *Science* 214:575-577.
- SWALLOW, S. K., R. F. GUTIERREZ, AND R. A. HOWARD, JR. 1986. Primary cavity-site selection by birds. *J. Wildl. Manage.* 50:576-583.
- TATE, J., JR. 1973. Methods and annual sequence of foraging by the sapsucker. *Auk* 90:840-856.

- VENABLES, A., AND M. W. COLLOPY. 1989. Seasonal foraging and habitat requirements of Red-headed Woodpeckers in North-central Florida. Florida Game and Fresh Water Fish Commission Non-game Wildl. Prog. Final Rep., Gainesville, FL.
- WELCH, C. J. E., AND D. E. CAPEN. 1992. Availability of nesting sites as a limit to woodpecker populations. *Forest Ecol. Manage.* 48:31–41.
- WILEY, R. H., AND D. G. RICHARDS. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. *Behav. Ecol. Sociobiol.* 3:69–94.
- WINKLER, H., AND L. L. SHORT. 1978. A comparative analysis of acoustical signals in pied woodpeckers (Aves, *Picoides*). *Bull. Am. Mus. Nat. Hist.* 160:1–110.

The Condor 99:803–806
© The Cooper Ornithological Society 1997

MIXED SEXUAL DIMORPHISM IN SEMIPALMATED PLOVERS¹

KEVIN L. TEATHER AND ERICA NOL

*Department of Biology, Trent University, Peterborough, Ontario, Canada K9J 7B8,
e-mail: kteather@trentu.ca*

Abstract. Sexually dimorphic species generally are characterized by having one sex consistently larger, and often brighter, than the other. Semipalmated Plovers (*Charadrius semipalmatus*) exhibit a pattern of mixed dimorphism with females that are heavier and having longer wings than males, whereas males have longer toes and bills, and are more colorful than females. Although we found weak evidence that male and female plovers mate assortatively with respect to body size, this likely resulted from birds of certain phenotypes breeding at different times. The mixed pattern of dimorphism in Semipalmated Plovers has probably resulted from different selection pressures, ecological and sexual, operating on different characters.

Key words: *Semipalmated Plover*, *Charadrius semipalmatus*, *sexual dimorphism*, *assortative mating*.

Hypotheses concerning the evolution and maintenance of sexual size dimorphism in birds generally focus upon benefits to one sex in terms of mating advantages (Darwin 1871) or benefits to both sexes in terms of reduced competition (Selander 1972). Most dimorphic taxa contain species that exhibit either “normal” size dimorphism, in which males are larger than females (e.g., Icterinae), or “reversed” size dimorphism, in which females are larger than males (e.g., Falconiformes). The suborder Charadrii (order Charadriiformes) is of particular interest in studies of sexual dimorphism because its species range from those in which males are much larger than females (e.g., Ruffs *Philomachus pugnax*, Prater et al. 1977) to those in which females are significantly larger than males (e.g., Jacanas *Jacana spinosa*, Jenni and Collier 1972). In rare cases, there is evidence for both normal and reversed size

dimorphism (mixed dimorphism) for different morphological characters within a species (e.g., Common Ringed Plover *Charadrius hiaticula*, Dement'ev et al. 1956, in Jehl and Murray 1986). Here we report on mixed dimorphism in the closely related Semipalmated Plover *Charadrius semipalmatus*.

Selection pressures responsible for the evolution and maintenance of sexually dimorphic characters may be ecological, for example if males and females are adapted to different feeding regimes, or sexual, if the possession of certain traits results in increased mating success for individuals of one sex. Assortative mating, defined as nonrandom mating with respect to some phenotypic character (Findley et al. 1988), may be indicative of active mate choice; if so, the expression of sexual dimorphism in such traits is likely maintained by sexual selection. Our second objective, therefore, is to test whether males and females mate assortatively with respect to any characters that differ between the sexes.

METHODS

We studied Semipalmated Plovers in the 1992–1996 breeding seasons in and around Churchill, Manitoba (58°45'N, 95°04'W). Adults were captured during the last two weeks of the 24-day incubation period, using walk-in traps, and were weighed to the nearest 0.1 g using a Pesola spring balance. Sexes were easily distinguished on the basis of auricular plumage (Cramp and Simmons 1983); ear coverts of females are the same brown as on the back, whereas those of males are solid black, contrasting with the brown back. Lengths of tarsus, culmen, and middle toe were measured with vernier calipers to the nearest 0.01 mm, whereas wing length was measured to the nearest 1 mm with a ruler. To document potential color differences between the sexes in addition to those used for sexing birds, we counted the number of brown feathers in the breast band and quantified (by length) the

¹ Received 14 November 1996. Accepted 22 April 1997.