

- the White-throated Sparrow, *Zonotrichia albicollis* (Gmelin). *Evolution* 29:611-621.
- THORPE, W. H. 1961. Bird song. Cambridge Univ. Press, London.
- WASSERMAN, F. E., C. DOWD, B. A. SCHLINGER, D. BYMAN, S. P. BATTISTA, AND T. H. KUNZ. 1984. The effects of microwave radiation on avian dominance behavior. *Bioelectromagnetics* 5:331-339.
- WINGFIELD, J. C. 1985. Short-term changes in plasma levels of hormones during establishment and defense of a breeding territory in male Song Sparrows, *Melospiza melodia*. *Horm. Behav.* 19:174-187.

The Condor 92:530-532
© The Cooper Ornithological Society 1990

SEXUAL DIFFERENCES IN ANTIPREDATOR BEHAVIOR OF BREEDING AMERICAN AVOCETS AND BLACK-NECKED STILTS¹

TEX A. SORDAHL

Department of Biology, Luther College, Decorah, IA 52101

Key words: *American Avocet; Recurvirostra americana; Black-necked Stilt; Himantopus mexicanus; Recurvirostridae; antipredator behavior; sexual dimorphism.*

One hypothesis for the evolution of biparental care in species with precocial young is that two adults are needed for predator defense (Pitelka et al. 1974, p. 194, Lenington 1980). However, even when both parents participate in predator defense, their contributions are unlikely to be equal because of differences in selective pressures on males and females (Trivers 1972, Montgomerie and Weatherhead 1988). In a review of sexual differences in nest protection behavior in shorebirds, Gochfeld (1984) listed 42 species for which differences have been reported and 40 species for which relatively equal participation by the sexes has been reported. Neither the American Avocet (*Recurvirostra americana*) nor the Black-necked Stilt (*Himantopus mexicanus*) appear on the lists but their Eurasian congeners, the Eurasian Avocet (*R. avocetta*) and the Black-winged Stilt (*H. himantopus*), are included as species in which the sexes have relatively equal antipredator roles.

American Avocets and Black-necked Stilts are relatively monomorphic, monogamous shorebirds that exhibit biparental care of eggs and young. They produce a wide variety of mobbing and diversionary displays, which are associated exclusively with breeding (Sordahl 1986). The displays, which are similar for these two members of the Recurvirostridae, have been well described (Gibson 1971a, Hamilton 1975, Sordahl 1986). They include aerial displays such as dive-bombing or circling a predator and ground displays such as crouch-running, false-incubation, and displays in which the wings are extended and moved erratically. No sex-specific displays or other sexual differences in antipredator behavior have been reported in avocets or stilts.

Gibson (1971a, 1978) found no difference between male and female American Avocets in the amount of time spent in diversionary behavior. However, during parts of five field seasons in which I observed many interactions between recurvirostrids and natural predators and staged hundreds more with models of eight predator species or myself as predator, males seemed more aggressive than females. In this paper I describe quantitatively this sexual difference in antipredator behavior.

METHODS

I spent about 1,000 hr studying American Avocets and Black-necked Stilts in northern Utah during the 1977 and 1978 breeding seasons. Additional observations were made in 1979, 1980, and 1987. My two study sites, the Barrens Company Hunting Club in Cache County and the Bear River National Wildlife Refuge in Box Elder County, are described in Sordahl (1982). About 85 avocet and 25 stilt pairs nested at the Barrens (Sordahl 1981a); breeding populations at the Bear River Refuge were much larger, probably numbering about 2,500 avocet and 1,000 stilt pairs (pers. comm. with refuge personnel). Potential predators of eggs or young were abundant and diverse at both sites, enabling me to record over 500 interactions between recurvirostrids and more than 20 predator species. Predators included at least three species in each of the following groups: ardeids, raptors, gulls, corvids, and mammals. For each observed instance of mobbing, I attempted to record the sex and number of mobbers. Although both avocets and stilts are relatively monomorphic, the sexes usually can be distinguished in the field (Hamilton 1975). However, the distances at which predator interactions were observed often precluded identification of a mobber's sex.

I further studied the antipredator behavior of avocets and stilts experimentally, using myself as a stimulus. Nineteen avocets (13 males, six females) and seven stilts (four males, three females) were nest-trapped (Sordahl 1980) and color-marked. I used a standardized procedure for testing marked adults, which con-

¹ Received 18 August 1989. Final acceptance 2 January 1990.

sisted of approaching the nest, stopping about 10 m from it, and recording displays and approach distances (measured with an optical tape measure) of the parents for a 10-min period on alternate days. My methods are described in more detail in Sordahl (1986).

RESULTS

Recurvirostrids typically perform distraction displays to a human near the nest at about 40 m distance. I have observed them at distances as close as 1 m and as far as 183 m from me. I recorded the nearest distance at which each member of a pair displayed to me during a test period. In this analysis, any effects of repeated testing are controlled by using the distances measured on the first day to represent pairs that were tested on more than one day. This sample includes pairs at different stages of incubation. However, comparing the members of a mated pair on the same day reveals sexual differences by controlling for the changes in approach distance that occur as incubation progresses (Sordahl 1986). American Avocet males displayed at a mean nearest distance of 27.5 m from me and females at a mean nearest distance of 42.1 m ($n = 11$ pairs). For Black-necked Stilt males the mean nearest distance was 30.0 m and for females it was 47.6 m ($n = 5$ pairs). Thus male avocets approached 14.6 m nearer than their mates on the average ($t = 4.00$, $df = 10$, $P < 0.01$, two-tailed paired t -test). In two of the 11 pairs the male and female distances were the same, but no female approached closer than her mate. Male stilts distracted 17.6 m closer than their mates on the average ($t = 4.80$, $df = 4$, $P < 0.01$), and none of the five females approached nearer than her mate. Repeated tests of some pairs through the incubation period, as well as numerous qualitative notes in my field journals that the males of other pairs came closer, are consistent with the conclusion that male avocets and stilts approach a human near the nest more closely than do their mates.

Aerially, females tended to circle predators at greater distances than males did, and males were more likely to swoop at predators (i.e., dive-bombing of Hamilton 1975; attack-mobbing of Sordahl 1981b). I was able to determine the sex of 124 avocets and 25 stilts observed mobbing nonhuman predators. Although some individuals might have been counted more than once, making statistical tests that require independent samples inappropriate, the large breeding populations and 5-year sampling period make it unlikely that there are many such replicates in these data. Eighty-six (69.4%) of the avocets and 19 (76.0%) of the stilts were males. Thus males were seen mobbing predators more often than were females. This sexual difference was more pronounced when a single bird mobbed the predator. Ninety-two of the 124 avocets observed mobbing were engaged in solo mobbing and 69 (75.0%) were males. Fourteen of the 25 stilts observed mobbing were engaged in solo mobbing and 13 (92.9%) were males.

DISCUSSION

In both American Avocets and Black-necked Stilts the sexes share all major types of parental investment (including nest building, incubation and brooding, agonistic and territorial behavior, and antipredator behavior) except egg laying. The results presented here indicate that male avocets and stilts approach a human

predator at the nest more closely than their mates do, and that males are more often seen mobbing nonhuman predators than are females. Thus, even though antipredator behavior is shared by the members of a pair, there is role specialization, with males being somewhat more aggressive and assuming a greater antipredator role. Also, males often continue their predator defense role longer than females; in my study, males attended 39 of 44 broods over 2 weeks old that had been deserted by one parent. Females may play a slightly lesser role in predator defense and be more likely to desert broods because of energetic considerations—following egg laying and in some cases re-nesting, the incubation and brood-rearing periods are overlapped by the prebasic molt and preparation for migration (Sordahl 1981a).

For avocets, Gibson (1978) found little difference between the sexes in seasonal time budgets, except that females spent 6.5% more time incubating. He also found that avocets spent little time engaged in diversionary behavior (due in part to rigorous predator control at his study site [Gibson 1971b, p. 452; Gibson 1978, p. 73]). However, for antipredator behavior the risk incurred may be a better measure of parental investment than is time or energy expenditure (Trivers 1972, p. 141). Risk is probably a significant cost of defense against predators (Montgomerie and Weatherhead 1988, Sordahl 1990).

That male avocets and stilts approach predators more closely and mob predators more often than females implies that they incur greater risks in antipredator behavior. Approaching a predator more closely probably increases both the likelihood of eliciting an attack from the predator and its chance of success in the attack. And a greater tendency to mob alone rather than with a group is probably more risky because a predator can retaliate more easily against a single attacker (see Brown and Hoogland 1986). I also found male avocets and stilts less wary and easier to nest-trap than females (Sordahl 1980), an attribute that could make them more susceptible to predation at a disturbed nest.

An interspecific analysis of mobbing in shorebirds shows that it occurs only in larger species, suggesting that size is an important factor in determining the effectiveness of shorebird mobbing (Sordahl 1981b). It is interesting to speculate whether subtle intraspecific differences, as between populations or the sexes, could also relate to size. The data presented here that male recurvirostrids approach humans more closely and mob predators more frequently than females do is consistent with Hamilton's (1975) data showing males to be slightly larger than females. Furthermore, the trends in my data suggest that behavioral dimorphism in antipredator behavior may be greater in stilts than in avocets, as is size dimorphism (Hamilton 1975).

I thank K. L. Dixon for helpful suggestions throughout the study. J. R. Walters, D. W. Mock, and K. Kraus provided valuable reviews of the manuscript, and J. W. Eckblad and W. Nitschke contributed advice about data presentation. I appreciate the cooperation of the members of the Barrens Company Hunting Club and the personnel of the Bear River National Wildlife Refuge. My work was supported by the Utah State University Biology Department, the Frank M. Chapman

Memorial Fund of the American Museum of Natural History, and by Sigma Xi, The Scientific Research Society.

LITERATURE CITED

- BROWN, C. R., AND J. L. HOOGLAND. 1986. Risk in mobbing for solitary and colonial swallows. *Anim. Behav.* 34:1319-1323.
- GIBSON, F. 1971a. Behavioral patterns and their temporal organization in breeding American Avocets. Ph.D. diss., Oregon State Univ., Corvallis.
- GIBSON, F. 1971b. The breeding biology of the American Avocet (*Recurvirostra americana*) in central Oregon. *Condor* 73:444-454.
- GIBSON, F. 1978. Ecological aspects of the time budget of the American Avocet. *Am. Midl. Nat.* 99: 65-82.
- GOCHFELD, M. 1984. Antipredator behavior: aggressive and distraction displays of shorebirds, p. 289-377. *In* J. Burger and B. L. Olla [eds.], *Behavior of marine animals*. Vol. 5. Shorebirds: breeding behavior and populations. Plenum Press, New York.
- HAMILTON, R. B. 1975. Comparative behavior of the American Avocet and the Black-necked Stilt (*Recurvirostridae*). *Ornithol. Monogr.* No. 17. American Ornithologists' Union, Washington, DC.
- LENINGTON, S. 1980. Bi-parental care in Killdeer: an adaptive hypothesis. *Wilson Bull.* 92:8-20.
- MONTGOMERIE, R. D., AND P. J. WEATHERHEAD. 1988. Risks and rewards of nest defence by parent birds. *Q. Rev. Biol.* 63:167-187.
- PITELKA, F. A., R. T. HOLMES, AND S. F. MACLEAN, JR. 1974. Ecology and evolution of social organization in arctic sandpipers. *Am. Zool.* 14:185-204.
- SORDAHL, T. A. 1980. A nest trap for recurvirostrids and other ground-nesting birds. *N. Am. Bird Bander* 5:1-3.
- SORDAHL, T. A. 1981a. Phenology and status of the shorebirds in northern Utah. *West. Birds* 12:173-180.
- SORDAHL, T. A. 1981b. Predator-mobbing behaviour in the shorebirds of North America. *Wader Study Group Bull.* 31:41-44.
- SORDAHL, T. A. 1982. Antipredator behavior of American Avocet and Black-necked Stilt chicks. *J. Field Ornithol.* 53:315-325.
- SORDAHL, T. A. 1986. Evolutionary aspects of avian distraction display: variation in American Avocet and Black-necked Stilt antipredator behavior, p. 87-112. *In* R. W. Mitchell and N. S. Thompson [eds.], *Deception: perspectives on human and nonhuman deceit*. State Univ. of New York Press, Albany.
- SORDAHL, T. A. 1990. The risks of avian mobbing and distraction behavior: an anecdotal review. *Wilson Bull.* 102:349-352.
- TRIVERS, R. L. 1972. Parental investment and sexual selection, p. 136-179. *In* B. Campbell [ed.], *Sexual selection and the descent of man, 1871-1971*. Aldine, Chicago, IL.

The Condor 92:532-534
© The Cooper Ornithological Society 1990

OBSERVATIONS OF AGGRESSIVE INTERACTIONS BY BALD EAGLES OF KNOWN AGE AND SEX¹

DAVID K. GARCELON

Institute for Wildlife Studies, P.O. Box 127, Arcata, CA 95521

Key words: Bald Eagle; *Haliaeetus leucocephalus*; interactions; supplanting; dominance.

Bald Eagles (*Haliaeetus leucocephalus*) are widely known to compete with conspecifics for food both by pirating small prey items and by supplanting other individuals at large prey items (McClelland 1973, Stalmaster 1976, Sherrod et al. 1977, Knight and Knight 1983). The effect of plumage (adult, subadult, immature) and relative size on the outcome of these interactions has been described by others (Griffin 1981, Stalmaster and Ges-

saman 1984, Hansen 1986, Knight and Skagen 1988), however, the actual sex of the eagles was unknown in these studies.

As part of a reintroduction attempt on Santa Catalina Island, California, Bald Eagles that were reared and released from artificial nest (hacking) platforms from 1980 through 1984 were observed to determine their time and activity budgets. Here I report on the outcome of supplanting attempts between 11 individuals of known age and sex.

METHODS

Eagles were sexed by morphometrics or karyotyping (Garcelon et al. 1985), or by observing a bird's behavior during nesting (e.g., egg laying). Weights were obtained on eight of the 11 eagles that we observed in

¹ Received 25 August 1989. Final acceptance 15 January 1990.