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Copulatory Behavior of American Avocets and Black-necked Stilts

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ABSTRACT.—I recorded details of 231 copulations of American Avocets (*Recurvirostra americana*) and 39 copulations of Black-necked Stilts (*Himantopus mexicanus*) in northern Utah. Those data are presented as quantitative descriptions of the copulatory behavior of each species, complementing and clarifying qualitative descriptions in the literature. I observed no qualitative differences between copulatory behavior of avocets and stilts. Small quantitative differences may be related to differences in morphology and habitat preference. Across the family Recurvirostridae, the distinctive copulatory displays of avocets (*Recurvirostra* spp.) and stilts (*Himantopus* spp.) seem relatively uniform, but the behavior of the monotypic Banded Stilt (*Cladorhynchus leucocephalus*) of Australia appears to differ somewhat from typical recurvirostrid copulatory behavior. Attempted copulation

with inanimate objects has been reported for at least 6 of the 10 recurvirostrid species.

Avocets and stilts (Charadriiformes: Recurvirostridae) exhibit eye-catching ritualized mating behaviors that have been described qualitatively for a majority of the world's species (Cramp and Simmons 1983, Marchant and Higgins 1993, Robinson et al. 1997, 1999). Their copulatory behavior includes a sequence of stereotypic elements arranged in pre- and postcopulatory displays. Copulatory behavior in recurvirostrids is relatively easy to observe because it typically occurs in shallow water with little vegetation to obscure the view. Pairs of some species have been estimated to copulate about seven times per day (Gibson 1978, Marchant and Higgins 1993). Nevertheless, there have been no quantitative studies of that behavior.

Gibson (1971) and Hamilton (1975) described copulatory behavior of the American Avocet (*Recurvirostra americana*). Hamilton (1975) noted that the oth-

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er North American member of the family, the Black-necked Stilt (*Himantopus mexicanus*), has similar copulatory behavior, although he personally observed only one stilt copulation. Additional observations reported by Robinson et al. (1999) support the similarity of behavior in the two species, as does existence of a hybrid American Avocet \times Black-necked Stilt in captivity (Principe 1977). In this paper, I present a quantitative description of copulatory behavior of American Avocets and Black-necked Stilts that shows some of the variation of the behavior, compare copulation in the two species, and survey copulatory behavior in the Recurvirostridae.

Study Area and Methods.—I recorded copulations of American Avocets and Black-necked Stilts opportunistically during field studies in northern Utah in 1977 and 1978. My study sites were the Barrens Company Hunting Club (41°52'N, 111°55'W) in Cache County and the Bear River National Wildlife Refuge (approximately 41°26'N, 112°10'W) in Box Elder County (sites are described in Sordahl 1982).

Field observations were made with 7 \times 35 binoculars and a 20 \times spotting scope, often from an automobile or dugout blinds scattered about the hunting club property. I used a stopwatch to time behaviors. In the field, I determined the sex of avocets by bill curvature and of stilts by color of the dorsal plumage (Hamilton 1975). An unknown number of pairs is included in the data (some pairs probably were recorded more than once). I considered copulations to be successful or complete when mounting occurred and was followed by normal postcopulatory behavior. In this paper, terminology for displays follows Hamilton (1975) and species-level taxonomy follows Sibley and Monroe (1990).

Results.—I recorded all or part of 231 copulation sequences (147 successful, 44 unsuccessful, and 40 uncertain) for avocets and 39 (31 successful and 8 unsuccessful) for stilts. Copulations were observed at the Barrens from 24 March to 23 June for avocets and from 11 April to 6 June for stilts (Sordahl 1981). There was a three to four week peak of copulatory activity for the populations each year (Fig. 1). Those peaks corresponded to the periods when most nests were initiated (see Sordahl 1996: figs. 1 and 2). Habitat in which copulations occurred was open shallow water (62 of 62 observations for avocets and 9 of 11 for stilts); one stilt copulation was observed in grass and one was observed on mud at the edge of open water.

Precopulatory sequences usually were initiated by the female (avocet, 25/28; stilt, 12/12) by sexual preening or the Neck Extended posture, or occasionally by mutual preening (avocet, 3/28). Females held the stylized Neck Extended posture (Fig. 2A), with head extended out just above the water and body tilted upward posteriorly, through the precopulatory and copulation stages. Males approached females from behind (avocet, 18/19; stilt, 3/3). Usually the male stepped up along the female's right side (avo-

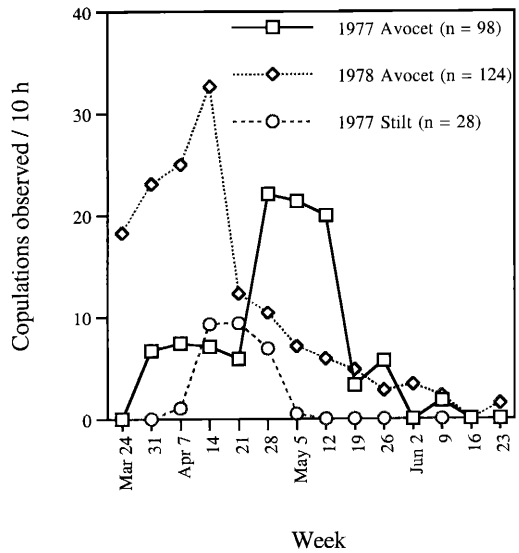


FIG. 1. Weekly copulatory activity of American Avocets and Black-necked Stilts at the Barrens, Cache County, Utah, during 1977 and 1978. The 1978 data for stilts are omitted due to small sample size.

cet, 30/39; stilt, 5/6) and then performed Upright Breast Preening and Bill Dipping displays while approximately parallel to her at her shoulder. The male usually circled behind the female several times (avocet, $\bar{x} \pm SD = 5.8 \pm 3.4$ times, $n = 38$, range = 2–16; stilt, 4.6 ± 1.9 times, $n = 9$, range = 2–8; $t = 0.916$, $df = 45$, two-tailed test, $P > 0.20$), pausing to continue sexual preening displays at her side each time. Intensity of sexual preening and water splashing during Bill Dipping increased during the precopulatory stage until mounting occurred.

Mounting occurred from the female's right side 56 of 89 times in avocets and 8 of 10 times in stilts. Males held their wings above their back (Fig. 2B), balancing on the female as they flexed their legs and the members of the pair brought their cloacas into apposition. Females slowly moved their heads from side to side during copulation (avocet, 35/36; stilt, 3/3). Mount time lasted a few seconds (avocet, 4.90 ± 1.75 s, $n = 75$, range = 2.8–13.6; stilt, 5.54 ± 1.5 s, $n = 16$, range = 2.8–7.6; $t = 1.168$, $df = 89$, two-tailed test, $P > 0.20$). Morphological sex determination always corresponded to a male-on-top position during mounting. I observed no reversal of position in either species.

Postcopulatory behavior began with dismounting. Males dismounted to the side determined by the direction of tail twisting during copulation—that is, toward the right if the right side of the male's tail twisted downward (avocet, 46/81 right side; stilt, 6/8 right side). A male usually extended his inside wing over the female's back as he dismounted (avocet, 53/55; stilt, 4/4). With their bills crossed, the pair then

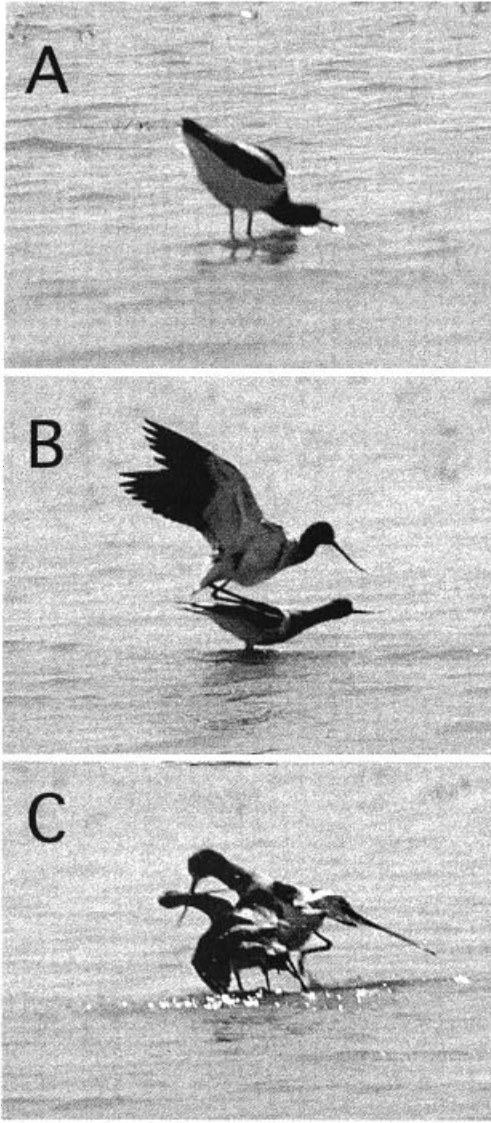


FIG. 2. Copulatory behavior of American Avocets: (A) a female in the Neck Extended posture, initiating a copulatory sequence; (B) a copulating pair (note the female's more strongly recurved bill); (C) a pair performing the Bills-crossed Run postcopulatory display (note the male's wing extended over the female).

ran forward a few steps (avocet, 6.76 ± 2.11 steps, $n = 54$, range = 3.5–12; stilt, 4.27 ± 1.56 steps, $n = 13$, range = 1.5–8; $t = 3.458$, $df = 65$, two-tailed test, $P < 0.001$) in the Bills-crossed Run before separating. The path of the Bills-crossed Run usually curved (avocet, 29/31; stilt, 2/3), toward the female's side (see Fig. 2C).

Total duration of a copulatory sequence from first sexual preening to separation of the pair in the Bills-crossed Run was at most a few minutes (avocet, 103.3 ± 37.7 s, $n = 17$, range = 46–179; stilt, 51 s, $n = 1$) (note: those total-duration data were incorrectly reported as duration of precopulatory display only in Robinson et al. 1997). Members of a pair usually engaged in the same activity after copulation (avocet, 68/73; stilt, 15/16), and usually that activity was feeding (avocet, 137/146; stilt, 27/32). Other activities observed after copulation were maintenance behaviors (avocet $n = 4$; stilt $n = 3$), intraspecific interactions (avocet $n = 4$; stilt $n = 2$), and interspecific interactions (avocet $n = 1$).

Unsuccessful or incomplete copulation attempts failed for a variety of reasons. Sometimes the female walked away while the male engaged in sexual preening (avocet $n = 5$; stilt $n = 1$). Sometimes the male did not respond to solicitation behavior of the female, continuing to bathe, preen, or feed instead (avocet $n = 15$; stilt $n = 3$). Other copulations were disrupted by conspecifics (avocet $n = 11$), heterospecific birds (avocet $n = 2$; stilt $n = 2$), or humans (avocet $n = 8$). And some copulation attempts failed for unknown reasons (avocet $n = 3$; stilt $n = 2$).

I observed copulation with inanimate objects twice. On one occasion, a male avocet mounted a clump of vegetation, and on another a male avocet mounted a long-necked bottle. That represents 0.86% of avocet and 0.74% of recurvirostrid copulations that I recorded.

Discussion.—I observed no qualitative differences between copulatory behavior of avocets and stilts, as noted also by Hamilton (1975). Cramp and Simmons (1983) made a similar generalization for the copulatory behavior of the Pied Avocet (*Recurvirostra avocetta*) and the Black-winged Stilt (*Himantopus himantopus*).

I did, however, find small quantitative differences in some components of copulatory behavior of American Avocets and Black-necked Stilts. Those may be related to morphological differences between the two species and preference of stilts for habitats with more vegetation (Hamilton 1975, Sordahl 1996). First, although all avocet copulations occurred in open water areas, two stilt copulations were observed elsewhere, in grass and at the edge of the water. Second, although the difference was statistically nonsignificant, stilt males circled behind the female fewer times than did avocet males during precopulatory behavior. Third, also not statistically significant, stilts had slightly longer mount times than avocets, a likely consequence of their longer legs, which appear awkward during mounting. Fourth, avocets took significantly more steps in the postcopulatory Bills-crossed Run display. And fifth, avocet copulation sequences may be longer than those of stilts.

The sparse quantitative information available in the literature for recurvirostrid copulatory displays agrees well with mine. For example, the ranges of

mount times I found for American Avocets and Black-necked Stilts of 2.8–13.6 s and 2.8–7.6 s, respectively, are similar to the 5–10 s reported by Gibson (1971) for the American Avocet and by Marchant and Higgins (1993) for the White-headed Stilt (*Himantopus leucocephalus*). The monotypic Banded Stilt (*Cladorhynchus leucocephalus*) of Australia seems atypical, however, with a reported mount time of about 30 s (Marchant and Higgins 1993).

Major elements of copulatory behavior in American Avocets and Black-necked Stilts are found in their relatives around the world. The family Recurvirostridae contains three genera: *Himantopus* (five species), *Cladorhynchus* (one species), and *Recurvirostra* (four species). Descriptions in the literature indicate that typical recurvirostrid copulatory behavior includes the following selected elements: (1) precopulatory—sexual preening, Neck Extended posture by the female, Bill Dipping and circling by the male; (2) copulatory—female swings head from side to side; (3) postcopulatory—Bills-crossed Run, male wing extended over the female. Those elements usually are present in the American *H. mexicanus* and *R. americana* (Hamilton 1975, T. A. Sordahl pers. obs.), and in the Eurasian *H. himantopus* and *R. avocetta* (Cramp and Simmons 1983). They also are present in the Australasian *H. leucocephalus*, except that males were not reported to extend a wing over females in postcopulatory display, and in New Zealand's *H. novaehollandiae* (Black Stilt), except that precopulatory sexual preening was not reported (Marchant and Higgins 1993). It is important to note that the North American and Eurasian species have been studied in more detail than other recurvirostrids, and that lack of mention of a behavior in any species does not necessarily mean it does not occur. For example, even in the relatively well-studied American Avocet, for which my data indicate that males usually extend a wing over the female's back during postcopulatory display (53 of 55 observations), Hamilton (1975) said that occurs "sometimes" and Robinson et al. (1997) did not mention the behavior. However, J. A. Robinson (pers. comm.) agreed that is the more usual behavior and that figure 4 in Robinson et al. (1997) would have better depicted typical American Avocet postcopulatory display if it had shown the male's wing over the female's back.

Breeding biology of the South American taxa, *H. melanurus* (White-backed Stilt) and *R. andina* (Andean Avocet), and the Australian *R. novaehollandiae* (Red-necked Avocet), has been little studied, but I suspect copulatory behavior of those species is similar to that of other typical recurvirostrids, as is that of the distinctive Hawaiian subspecies *H. mexicanus knudseni* (Robinson et al. 1999). The Banded Stilt, however, is an aberrant member of the family in its breeding biology. Available descriptions of its rarely observed copulatory behavior are reminiscent of avocet and stilt displays (Marchant and Higgins 1993,

Pierce 1996), but appear to differ in some details. For example, there is no mention of bills of the pair crossing (although their necks apparently do, as sometimes occurs in other recurvirostrids), or of the male extending a wing over the female's back (which sometimes does not occur in other recurvirostrids), during postcopulatory display, and there is a final stage in the postcopulatory run that does not seem to correspond to anything observed in other recurvirostrids. Overall, however, the distinctive copulatory behavior of avocets and stilts seems relatively uniform across the family.

Copulation with inanimate objects has been reported for at least 6 of the 10 species in the Recurvirostridae: Black-necked Stilt (Hamilton 1975), Black Stilt (Marchant and Higgins 1993), Banded Stilt (Minton and Collins 1998), American Avocet (Hamilton 1975, this study), Pied Avocet (Makkink 1936), and Red-necked Avocet (Marchant and Higgins 1993). The proximate mechanisms causing that behavior are poorly understood. However, Hamilton (1975) observed that those attempted copulations occurred early in the season and that the inanimate objects approximated the size of females, which suggests that male copulatory behavior may be redirected toward substitutes when females are not sexually responsive (Ficken and Dilger 1960).

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Fitness-related Consequences of Relaying in an Arctic Seabird: Survival of Offspring to Recruitment Age

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ABSTRACT.—Seasonal declines in rates of renesting following clutch loss are common features of avian breeding, and are generally thought to reflect underlying seasonal declines in food availability that lower survival prospects for late-season offspring. However, in Thick-billed Murres (*Uria lomvia*), long-lived Arctic seabirds that lays a single-egg clutch, previous research has shown that early laying females will continue to relay until late in the laying period. Moreover, hatching success is similar between first and replacement attempts, as are nestling growth and survival, when parental quality is controlled. I compared survival between departure from the breeding site and recruitment age (4–5 years) for Thick-billed Murres that hatched from first and replacement eggs, but that were raised by parents that laid their first eggs early in the season. Replacement-egg offspring hatched and departed the colony about

three weeks later than did first-egg offspring, but despite that, they were no less likely to survive to recruitment age. That result indicates that the potential fitness payoff from a replacement egg is similar to that from a first egg for the more capable members of the population. I suggest that an adequate and predictable late-season food supply ultimately underlies the considerable relaying capacity exhibited by Thick-billed Murres.

Replacement clutches can make important contributions to an individual's lifetime reproductive success, especially in avian species or populations prone to clutch loss (Martin et al. 1989, Keegan and Crawford 1993). However, offspring from replacement clutches tend to experience low rates of survival to recruitment (Martin and Hannon 1987, Verboven and Visser 1998), often because late-fledged young are socially subordinate and fare poorly in competition with those that fledge early (Nilsson and Smith 1988, Spear and Nur 1994). From an evolutionary standpoint, uncertain prospects for late-season offspring, combined with adverse effects of late breed-

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