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Intraspecific brood parasitism in three species of prairie-breeding shorebirds.—Intraspecific brood parasitism has been reported in fewer than 100 avian species (Yom-Tov 1980). For precocial birds it is common among ratites, phasianids, and, particularly, anatids (Andersson 1984). Shorebirds are characterized by small, fixed clutch sizes, and abnormally large clutches are uncommon (Cramp and Simmons 1983). Intra- and interspecific egg-dumping account for many of these large clutches. Other instances result when more than one female contributes to the laying and care of combined clutches (Walters and Walters 1980). Here I document three shorebird nests that each contained eggs from more than one female of the same species.

The three nests included those of a Western Willet (*Catoptrophorus semipalmatus*), a Marbled Godwit (*Limosa fedoa*), and a Wilson's Phalarope (*Phalaropus tricolor*) at Last Mountain Lake Wildlife Management Unit in southcentral Saskatchewan. From 1982 to 1985, when I studied shorebirds in the area, water conditions changed dramatically. All observed cases of brood parasitism occurred in 1984, a year of severe drought in which 75% of local wetlands were dry. The severity of the drought reduced available breeding sites for

TABLE 1

DENSITY OF PAIRS OF SHOREBIRDS AT TWO SITES IN SOUTHCENTRAL SASKATCHEWAN FROM 1982 TO 1985

Species	Ephemeral wetland				Permanent wetland[b]	
	1982	1983[a]	1984[a]	1985	1984	1985
Killdeer	10	7	1	12	10	5
American Avocet	8	0	0	25	8	1
Western Willet	3	2	0	5	5	3
Spotted Sandpiper	0	0	0	0	3	2
Upland Sandpiper	2	1	1	2	4	3
Marbled Godwit	5	1	1	5	7	4
Common Snipe	0	0	0	0	3	2
Wilson's Phalarope[c]	45	20	0	30	55	80

[a] Wetland was dry during most (1983) or all (1984) of the breeding season.
[b] Incompletely censused in 1982 and 1983.
[c] Densities are of nesting males, as this species is occasionally polyandrous (Colwell, in press).

several species of shorebirds, and the few remaining wetlands supported high densities of breeding pairs (Table 1).

Each year, I monitored nesting pairs of all shorebird species to obtain accurate egg-laying chronologies. During the four years, I found 336 nests of nine species (109 nests in 1984), including nests of 3 Piping Plovers (*Charadrius melodus*), 38 Killdeers (*C. vociferus*), 35 American Avocets (*Recurvirostra americana*), 8 Western Willets, a Spotted Sandpiper (*Actitis macularia*), 2 Upland Sandpipers (*Bartramia longicauda*), 14 Marbled Godwits, 3 Common Snipes (*Gallinago gallinago*), and 232 Wilson's Phalaropes. The following observations describe the three instances of brood parasitism I observed.

Observations.—On 7 May 1984 I found an unlined scrape of a Western Willet that contained one egg. A 4-egg clutch was completed late on 12 May or early on 13 May. When I next visited the nest on 22 May, it held a fifth, distinctly differently colored egg. No additional eggs were laid. Both adults were color banded. The pair hatched two chicks from the initial four eggs on 7 June and lost the remaining three eggs to a predator on the same day. As the laying date for the fifth egg was unknown, I cannot be certain that it was laid by a second female. However, the egg's unique color suggests that it was.

Between 5 and 10 May, a color-banded pair of Marbled Godwits performed courtship scraping on their territory. One of their scrapes contained three eggs on 14 May. The 4-egg clutch was completed on 15 May. During the morning of 22 May the nest held a fifth egg. Two more eggs were laid on 23 and 24 May. Shortly thereafter the 7-egg clutch was destroyed by an unknown predator. Another, unbanded godwit pair initiated a clutch less than 300 m away on 18 May. The first egg in this nest was taken by a predator, suggesting that the three eggs deposited in the parasitized nest could have belonged to this female.

During the afternoon of 26 June, I flushed an unbanded male Wilson's Phalarope from a nest that contained three eggs. On the morning of 27 June the nest held four eggs, and that afternoon it contained five eggs. The morning of 28 June a sixth egg was laid. Sometime between 13:00 and 14:15, on the same day, a seventh egg was laid in the nest. No additional eggs were laid and the male deserted the clutch at that time. The laying of five eggs in less than 76 hours indicates that at least two females laid the eggs. The male's breeding rela-

tionship to the females was unknown. It may have been that two pairs were using the same nest as has been recorded for other shorebirds (Cramp and Simmons 1983).

Discussion.—Andersson (1984) discussed two evolutionary routes that favor brood parasitism among precocial birds. The limited breeding-site hypothesis suggests that brood parasitism occurs when a shortage of breeding opportunities forces two females to lay in the same nest. Selection would favor this behavior if one female subsequently obtained another breeding site that allowed her to produce additional offspring. The predation hypothesis states that nest failure prior to clutch completion leads females to parasitize nests because they possess fertilized eggs that need to be laid. The common occurrence of nest parasitism among ground nesters that suffer high levels of predation supports this hypothesis (Andersson 1984).

For prairie-breeding shorebirds, ecological conditions promoting nest parasitism may occur during drought years when breeding sites are limited, predation is high, and brood parasites can readily locate nests in habitats with high nest densities. For all shorebirds, nest loss to predators was highest during the dry years of 1983 and 1984 ($G = 39.4$, df = 3, $P < 0.001$).

Perhaps the most important biological features restricting nest parasitism among shorebirds are small clutch size and daily laying interval (Andersson 1984). Together, they impose strict limits of synchrony between the parasite's and host's reproductive cycles. Failure to lay eggs during the host's laying period may result in eggs hatching asynchronously and therefore being deserted. Other precocial birds that commonly parasitize nests are characterized by large clutch sizes allowing for a greater window of vulnerability to parasitism (Andersson 1984).

Although brood parasitism may not be common in shorebirds, I suggest that its occurrence may be linked to ecological conditions that restrict breeding opportunities and, at the same time, increase levels of predation.

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