SHORT COMMUNICATIONS

Female-female aggression in polygynously nesting Yellow Warblers.—Ford (1983) described the Yellow Warbler (*Dendroica petechia*) as primarily monogamous but facultatively polygynous. This classification has been supported recently by reports of polygyny in two populations (DellaSala 1986, Reid and Sealy 1986). Since male Yellow Warblers provide substantial parental care when mated monogamously (Biermann and Sealy 1982, Sutherland 1987), polygyny may threaten a female's reproductive success and promote female-female aggression (see Yasukawa and Searcy 1982). Both Reid and Sealy (1986) and DellaSala (1986) described the behavior of polygynous male Yellow Warblers but the behavior of females in this mating relationship has not been reported. Here we document another case of polygyny in this species and describe associated female-female interactions.

Study area and methods. – During 1986 and 1987, observations were made of Yellow Warblers nesting in a stand of sandbar willow (Salix interior) on the forested dune ridge, Delta Marsh, Manitoba (see Goossen and Sealy 1982, MacKenzie 1982). Four pairs nested on the 25×100 -m site in 1986, and one of two males that settled on the site in 1987 was polygynous. The polygynous male (M1), banded as an adult in 1986, was at least two years old. The primary female's (F1) age was not known; the secondary female (F2) was at least three years old, i.e., banded as an adult in 1985. F2 nested on the site in 1986 and, together with a 2-year-old male, fledged 5 young.

Observations were made for 1-2 h per observation day between 0630 h and 1030 h CDT. We observed individuals at 10-25 m, either from the ground or from a 2-m stepladder. The stage of the nesting cycle for each pair was determined by checking the contents of each nest daily. The males' territories were mapped based on the positions where they sang and where border disputes occurred. Areas of territories were later calculated by superimposing territory maps on a vegetation survey grid and counting squares. Nestlings were weighed daily to the nearest 0.1 g until 6 days old using a digital scale.

Nesting chronologies. -F1 began nestbuilding on 18 May, laid her first egg on 23 May, but after her third egg was laid on 25 May the nest and eggs were preyed upon. F1 started another nest by 27 May and the clutch of 4 eggs was initiated on 30 May. All 4 young hatched and fledged by 22 June. F2 settled on the site on 26 May just after F1's first nest was destroyed. Two successful copulations with M1 were observed on 29 May when nestbuilding began 7.5 m from F1's renest. F2 initiated a 4-egg clutch on 1 June but only 2 young hatched. They fledged by 24 June. The 2 unhatched eggs we removed on 18 June were infertile.

Parental feedings and nestling growth. — After mating with F2, M1 appeared to direct his efforts to F1's second breeding attempt. From 3–11 June, M1 fed F1 during incubation at a rate of 3.4 ± 2.6 [SE] trips/h (N = 5 h), within the range of values reported by Sutherland (1987) for older males in this population. However, M1 did not feed F2 while she incubated (N = 10 h). M1 averaged 2.3 ± 0.7 trips/nestling/h (N = 8 h) when feeding F1's nestlings. He first fed F2's nestlings 4 days after they hatched and averaged 0.8 ± 0.5 trips/nestling/h (N = 10 h) until they fledged. M1's feeding rates were within and below the range observed for older males in the population for the nestlings of F1 and F2, respectively (Biermann and Sealy 1982, Sutherland 1987). M1 continued to feed fledglings at least until 5 July but we could not identify them to nest.

Although we did not quantify such departures, during incubation F2 appeared to leave her nest to forage more frequently than F1. F2 also fed nestlings more frequently (4.5 ± 1.0 trips/nestling/h, N = 8 h) than did F1 (0.4 ± 0.3 trips/nestling/h, N = 10 h; t = 3.93, df = 8, P < 0.01), and this rate was considerably higher than the population average for older females (Sutherland 1987). No difference was found in the growth rates of nestlings in the primary and secondary nests (mean mass at 6 days of nestlings in F1's brood was 8.4 ± 1.3 g, N = 4; F2's brood, 9.2 ± 0.2 g, N = 2).

Female-female interactions. – During 16 h of observation from 27 May to 10 June, we recorded 29 aggressive interactions between F1 and F2. Only 13 interactions were observed between neighboring females of the 5 monogamously paired Yellow Warblers that nested on this site in both years of the study (N = 127 h of observation). No aggressive interactions between F1 and F2 were observed after 10 June when F1's brood hatched. Most interactions were initiated by F1 (N = 20; $\chi^2 = 9.0$, df = 1, P < 0.005) and, of these, 17 were displacements and 3 were contacts. F2 initiated 5 displacements and in 4 interactions the initiator was not identified. Although F1 initiated most interactions during incubation breaks, twice she left her nest while incubating to attack F2. Within M1's 474-m² territory, 2 female territories were apparent. These were exclusively used areas that were defended aggressively (see Searcy 1986). F1's territory was approximately twice the size of F2's but their commonly defended boundary was about half-way between their nests.

Discussion.—Females are expected to mate polygynously when the benefits of male or territory quality exceed the costs of reduced male parental care (Searcy 1982). Age and nestling feeding are two measures of male quality. Sutherland (1987) found that older (>1 yr) males more successfully raised young that returned to the study site than did yearling males. F2 may have chosen M1 because he was older (but see Reid and Sealy 1986) although M1 did not provide more parental care in the form of higher nestling feeding rates than other males in the population. M1's territory was located on the south side of the forested dune ridge, an area usually settled first by arriving Yellow Warbler males (Sutherland 1987). However, M1's territory was close to the average size for the site ($\bar{x} = 429 \text{ m}^2$, N = 6) and the vegetation density and composition was similar to territories held by monogamous males (Hobson 1988).

DellaSala (1986) suggested that polygyny in Yellow Warblers may be promoted by persistent disturbances by the brood-parasitic Brown-headed Cowbird (*Molothrus ater*) at the nest site causing a female to desert a male's territory in order to take a chance with an already-mated male. On our study site the incidence of cowbird parasitism is typically about 21% and may have been a proximate factor causing polygyny in this case. As well, the failure of F1's first nest may have contributed to the polygynous behavior of M1. Hence, M1 may have paired with F2 as "insurance" after F1's nest failed. When F1 renested, M1 appeared to resume interest in F1 and largely abandoned F2. Although male Yellow Warblers may benefit from polygynous matings, instead of being a male or female strategy *per se*, polygyny in this species may often be the result of chance nest failure (see DellaSala 1986).

Within territorial passerines, mated females may respond aggressively toward intruding conspecific females in order to defend territorial resources (Morton et al. 1978, Power and Doner 1980, Gowaty 1981) or the parental investment of their mates (see Yasukawa and Searcy 1982). In our population of Yellow Warblers, both males and females foraged primarily on their territories (Hobson 1988). This may have promoted female territoriality in the polygynous trio. Smith et al. (1982) found little evidence for female territoriality within polygynously nesting Song Sparrows (*Melospiza melodia*), but there females foraged away from their territories. While M1 fed primarily F1's young (see also Smith et al. 1982, Petit et al. 1988), the care he directed to this female was threatened by F2's presence. That most aggressive interactions were initiated by F1 toward F2 supports the hypothesis that primary females attempt to prevent polygyny in order to ensure their mates' parental care. This aggression may fail to exclude secondary females due to differential female quality or time constraints on females, such as egg laying and incubation (Wittenberger 1979, Yasukawa and Searcy 1982).

Acknowledgments.—This work was funded by a Natural Sciences and Engineering Research Council of Canada grant (A9556) to SGS and post-graduate scholarships from NSERC and the University of Manitoba to KAH. The officers of the Portage Country Club permitted us to conduct this work on their property. N. Ford and W. Searcy made useful comments on an earlier draft of this manuscript. This publication is contribution number 163 of the University of Manitoba Field Station (Delta Marsh).

LITERATURE CITED

- BIERMANN, G. C. AND S. G. SEALY. 1982. Parental feeding of nestling Yellow Warblers in relation to brood size and prey availability. Auk 99:332–341.
- DELLASALA, D. A. 1986. Polygyny in the Yellow Warbler. Wilson Bull. 98:152-154.
- FORD, N. L. 1983. Variation in mate fidelity in monogamous birds. Pp. 329–356 in Current ornithology. Vol. 1 (R. F. Johnston, ed.). Plenum Press, New York, New York.
- GOOSSEN, J. P. AND S. G. SEALY. 1982. Production of young in a dense nesting population of Yellow Warblers, *Dendroica petechia*, in Manitoba. Can. Field-Nat. 96:189–199.
- GOWATY, P. A. 1981. Aggression of breeding Eastern Bluebirds (*Sialia sialis*) toward their mates and models of intra- and interspecific intruders. Anim. Behav. 29:1013–1027.
- HOBSON, K. A. 1988. Protection of genetic parentage in the Yellow Warbler (Dendroica petechia). M.S. thesis, Univ. Manitoba, Winnipeg, Canada.
- MACKENZIE, D. I. 1982. The dune-ridge forest, Delta Marsh, Manitoba: overstory vegetation and soil patterns. Can. Field-Nat. 96:61–68.
- MORTON, E. S., M. S. GEITGY, AND S. MCGRATH. 1978. On bluebird "responses to apparent female adultery." Am. Nat. 112:968–971.
- PETIT, K. E., DIXON, M. D., AND R. T. HOLMES. 1988. A case of polygyny in the Blackthroated Blue Warbler. Wilson Bull. 100:132–134.
- POWER, H. W. AND C. G. P. DONER. 1980. Experiments on cuckoldry in the Mountain Bluebird. Am. Nat. 116:689-704.
- REID, M. L. AND S. G. SEALY. 1986. Behavior of a polygynous yearling Yellow Warbler. Wilson Bull. 98:315–317.
- SEARCY, W. A. 1982. The evolutionary effects of mate selection. Ann. Rev. Ecol. Syst. 13: 57-85.

_____. 1986. Are female Red-winged Blackbirds territorial? Anim. Behav. 34:1381–1391.

- SMITH, J. N. M., Y. YOM-TOV, AND R. MOSES. 1982. Polygyny, male parental care, and sex ratio in Song Sparrows: an experimental study. Auk 99:555-564.
- SUTHERLAND, D. L. 1987. Age-related reproductive success in the Yellow Warbler (Dendroica petechia). M.S. thesis, Univ. Manitoba, Winnipeg.
- WITTENBERGER, J. F. 1979. The evolution of mating systems in birds and mammals. Pp. 271-349 in Handbook of behavioral neurobiology. Vol. 3 (P. Marler and J. Vandenbergh, eds.). Plenum Press, New York.
- YASUKAWA, K. AND W. A. SEARCY. 1982. Aggression in female Red-Winged Blackbirds: a strategy to ensure male parental investment. Behav. Ecol. Sociobiol. 11:13–17.

KEITH A. HOBSON AND SPENCER G. SEALY, Dept. Zoology, Univ. Manitoba, Winnipeg, Manitoba R3T 2N2. (Present address KAH: Dept. Biology, Univ. Saskatchewan, Saskatoon, Saskatchewan S7N 0W0.) Received 29 March 1988, accepted 16 June 1988.