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POLYGYNY IN BARROW'S GOLDENEYE[1]

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INTRODUCTION

A male is considered polygynous whenever he forms a prolonged pair bond with two or more females whose nesting cycles overlap in time (Wittenberger 1981). Polygyny is rare in waterfowl (Wittenberger and Tilson 1980, Ford 1983) but commonly occurs in two species, the Magpie Goose *Anseranas semipalmata* and the Comb Duck *Sarkidiornis melanotos* (Frith and Davies 1961, Siegfried 1979). Studies of captive birds have indicated that some southern hemisphere dabbling ducks are occasionally polygynous (McKinney and Stolen 1982, Stolen and McKinney 1983, McKinney and Bruggers 1983, McKinney 1985). Similar studies of North American dabbling ducks have not documented polygyny (Stolen and McKinney 1983; McKinney 1985). Among North American diving ducks, polygyny has been reported only in the Canvasback *Aythya valisineria* (M. Anderson in Ford 1983). Males of Common Goldeneye (*Bucephala clangula*) and Barrow's Goldeneye (*B. islandica*) have been observed defending two females, suggesting that polygyny may occur in these species (M. Erickson, pers. comm.; Savard 1985a). In this note, I describe four cases of polygyny observed in 1984 among 229 pairs of Barrow's Goldeneye during a study of territorial behavior in the interior of British Columbia, Canada (Savard 1982).

Paired Barrow's Goldeneye drakes defend territories on their breeding ponds until mid-incubation. They exclude all conspecifics except their mate from the territory (Savard 1982). Territorial boundaries are relatively stable during the breeding season as indicated by observation of marked individuals. Unpaired birds are restricted to the center of the ponds by the aggressiveness of territorial males. Such a system facilitates population estimates and also the detection of polygyny. The presence of two females within a male's territory would indicate polygyny. Normally strange females are chased off the territory (Savard 1982). Detection of polygyny was further enhanced by the presence of 98 individually marked individuals (13 males, 85 females) in the population. Four counts conducted in early May 1984 yielded an average of 222 ± 3 (SE) pairs for the study area.

Case 1. Pair A (female marked with nasal disks) arrived on its breeding pond (Lake 13) on 13 April when 90% of the lake was still covered with ice. By 15 April, two other pairs had joined them. Female B (marked) was first seen on 17 April on the pond and did not seem paired. This was unusual, as unpaired adult females are rarely seen on the breeding areas. On 18 April, Male A was defending a territory from which he excluded all goldeneyes but Females A and B. Three monogamous males also defended territories on the lake, and there were several unpaired males on neighboring ponds. No aggression was observed between Females A and B. Female A started laying on 20 April and Female B on 29 April; each laid eight eggs in the same nest boxes they had used the previous year. Female A started incubation on 3 May and Female B on 17 May. The nest of Female A was destroyed by a black bear (*Ursus americanus*) on 4 May, whereas that of Female B was deserted on 27 May because of egg predation by American red squirrel (*Tamiasciurus hudsonicus*). Both females remained with Male A in the territory until his departure on 5 June (Male A had been captured and marked on 13 May). The two females then spent most of their time on Lake 13 associating temporarily with other females but rarely together. They were last seen on 5 July.

Both females had been marked in earlier years so that their breeding history was partially known. Female A nested in 1982 and 1983 in the same nest box she had used in 1984 and raised a brood on Lake 13 each year. In 1983 her breeding territory was on Lake 13 and her mate was monogamous. Female B nested in 1983 in the same box she had used in 1984 and also raised a brood on Lake 13. Because no polygynous males were seen in the area in 1983 it is assumed that she was paired with a monogamous male. It is also likely that her mate's territory was also on Lake 13.

Case 2. In this case, I witnessed the acquisition of the second female; Pair C (female marked) was first seen on a lake beside their breeding pond at 0500 on 4 April. At 1600, they landed on their breeding pond and challenged an established pair. After a violent fight in which both sexes participated, Pair C took over the territory. On 5, 6 and 7 April, the male was observed defending the territory. There were only two other pairs defending territories in this section of the pond and none adjacent to Pair C. However on 8 April, five pairs were defending small territories, one of which (Pair D) was adjacent to Pair C's territory. At 0645 Pair D copulated. At 0655, Male C attacked Male D (unmarked), and after a violent fight Male D left the pond, abandoning his mate. Male C did not show any aggression toward Female D, but Female C did (threat). At 0710, Male C approached Female D and both displayed to each other (rotary pumping; Palmer 1976). Female C was ignored in the following days as Male C spent more time with Female D. However Male C still defended his original territory and chased all goldeneyes that approached Female C. On 13 April, Female C returned from her nest and landed in her territory. She was greeted by Male C and both did the rotary pumping display. Then Female C twice attacked Female D, who swam away. Female C again threatened Female D, but this time Male C left her and swam to Female D and both did the rotary pumping display and swam away from Female C. I did not witness any further aggression between the females and both remained with Male C. I witnessed two copulations: on 1 May at 0725, Male C copulated with Female C, and Female D swam toward them assuming a prone posture but Male C did not respond; on 6 May at 0901, Male C copulated with Female D. Female C initiated her clutch on 5 May and hatched 14 young. It is not known if Female D nested, but her occasional absence from the territory indicates that she may have attempted to nest.

Case 3. A male (G) with two females was observed on 30 April, defending a territory on a small pond that also

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TABLE 1. Comparison of the number of aggressive interactions observed between polygynous males and monogamous neighboring males.

Pair	Number of observation days	Total length of observation (hr)	Aggressor	
			Polygynous male	Monogamous male
C	5	8	12	17
G	8	13	42	18
H	3	6	16	18

supported another territorial pair. During 13 hours of observations between 30 April and 25 May, I did not observe any obvious aggression between the two females that occasionally rested on the same rock. However, they were usually spaced apart and engaged in different activities. On 1 May, I captured and marked the polygynous male. He was more aggressive than his monogamous neighbor, initiating twice as many aggressive interactions (Table 1). He did not behave aggressively toward his two mates, but he attacked and drove other female goldeneyes off the pond (four cases observed). The temporary absence of one of the females from the territory on 1 and 15 May indicates that she may have been laying. On 25 and 26 May, only one female was with the male. On 27 May, the male had left the pond.

Case 4. On 2 May, a male with two females, one of which was marked (H), defended a territory on a pond where three other pairs had also established territories. On 6 May, the trio was observed during two hours; no aggression was observed between the females, which stayed away from each other but remained within the territory. Female H had bred on that pond in 1982 and 1983. On 11 May we captured and marked the other female (I). Female H laid 12 eggs in the same box she had used in 1982 and 1983 and she started incubation by 12 May. Her box was destroyed by a black bear. On 10 and 12 May, the male was with Female I in the territory. We don't know if Female I bred, but she was seen flying from a treed island, which indicates that she may have attempted to breed.

I compared the aggressiveness of the polygynous males with that of neighboring pairs to see if polygynous males tended to be more aggressive than monogamous males (Table 1). All comparisons between monogamous and polygynous pairs on a lake were done simultaneously and were spread over a few days. The results are inconclusive. In only one case (Pair G) was the polygynous male more aggressive.

DISCUSSION

Polygynous Barrow's Goldeneye drakes formed simultaneous pair bonds with two females. Polygyny in Barrow's Goldeneye could be promoted by the following factors: (1) breeding ponds are very productive (Cannings and Scudder 1978), so the resources of the territory may not be significantly altered by the presence of a second female; (2) males do not provide parental assistance (Munro 1939); and (3) polygyny increases reproductive success of males (Wittenberger 1981). However, several factors also act to limit polygyny. They are (1) the existence of strong and stable pair bonds (Savard 1985b); (2) aggressiveness of both paired males and females toward strange females (Savard 1982); (3) pair formation that occurs on the wintering area and is not related to territory quality (Palmer 1976); (4) sex ratio biased toward males (Bellrose 1976); and (5) ability of females to find a new mate more readily than males.

The low degree of polygyny observed in the population studied (<2%, $n = 222$ pairs) suggests that polygyny in Barrow's Goldeneye is not a common breeding strategy, but is rather an unusual occurrence. Models based on habitat or male qualities to explain polygyny (Wittenberger 1981) do not apply here and have been questioned in other cases (Alatalo et al. 1981). I propose that strong philopatry and attachment to breeding territories and nest sites by females, loss of previous mate or his failure to establish or regain the female territory, and familiarity between birds involved lead in some cases to polygyny in Barrow's Goldeneye. These factors have not always been considered in previous studies of polygyny and may prove important in explaining the occasional occurrence of polygyny in other species.

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TRADITIONAL NEST-SITE USE BY WHITE-THROATED SWIFTS[1]

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Key words: Apodidae; site tenacity; site fidelity; swifts; Toiyabe Mountains; White-throated Swift; Aeronautes saxatalis.

Site tenacity, the tendency to return to an established breeding site (Austin 1949), has been recorded for a wide variety of avian species (Freer 1979, Greenwood 1980, Shields 1984). Prior reproductive success, sex and age of the nesting bird, and physical stability of the nest site are factors that are known to affect site tenacity (McNicholl 1975, Freer 1979). Site tenacity and site fidelity imply the repeated use of a nest or colony site by a given individual and thus constitute a behavioral property of the individual bird. However, specific nest sites may continue to be used through time by a succession of individual birds for a variety of reasons that are inherent properties of the site, leading to "recognition" of the site as a quality nest location. Such properties include physical stability, protection from predators, association with a rich food supply, and scarcity of suitable nest sites (e.g., Blancher and Robertson 1985). Clearly site tenacity will not develop in the absence of nest site qualities that lead to reproductive success. Moreover, site tenacity is neither necessary nor sufficient for the long-term use of a nest or colony site, although it seems likely that such use will often occur in species exhibiting site tenacity. In this report we document long-term use of a nest site, which we here designate as "traditional nest site use," by White-throated Swifts (*Aeronautes saxatalis*) using the same small rock outcrop in central Nevada's Toiyabe Mountains where Lindsdale (1938) reported this species nesting 54 years earlier.

Linsdale (1938) described and photographed a unique rock outcrop adjacent to the only meadow in the Toiyabe's Birch Canyon (elevation 2,120 m). On 21 June 1930, he noted White-throated Swifts entering a crevice approximately 6 m in length and approximately 23 m from the ground. Nest materials were recovered subsequently from within the crevice. On the following day, about 25 birds were seen flying around the cliff. On 25 June 1984, as part of an extensive survey of avian communities in riparian habitats of the Toiyabe Range (Dobkin and Wilcox, 1986), we visited Birch Creek Canyon and easily located this same rock outcrop. Four swifts were seen flying around the cliff and making repeated flights in which they called loudly as they approached a crevice in the rock face and then turned away at the last possible moment. Within a 3-min period, four birds entered the nearly horizontal crevice that was protected by an overhanging projection of rock. From Linsdale's description, it appeared to be the same crevice that swifts had used 54 years earlier.

Linsdale (1938) indicated the apparent importance of an accessible foraging area in the selection of nest sites by White-throated Swifts and noted that colonies in the Toiyabe were nearly always located near a meadow. In addition to its physical stability, the site in Birch Creek Canyon is located adjacent to a highly favorable feeding area, a moist meadow. This is the only meadow in the entire canyon, and this locale is the only place in Birch Creek Canyon that we found nesting swifts.

Traditional use of sites for breeding or roosting (often the same site is used for both functions) may be common among species of swifts (Apodidae), which tend to use physically stable sites that are largely inaccessible to terrestrial predators (reviewed by Lack 1956). Black Swifts (*Cypseloides niger*) were found nesting in a canyon in the province of Alberta, Canada (their only recorded nesting location in the province), 46 years after having first been reported breeding there, and they continued to breed there in each of the subsequent seven years that the site was checked (Kondla 1973). Chestnut-collared Swifts (*Cypseloides rutilus*) in Trinidad have nested and roosted in the same Guacharo Gorge site over a 46-year period (Belcher and Smooker 1936; Snow 1962; Collins 1968, 1974). Collins (1973) reported roost-site tenacity in banded White-throated Swifts that used a narrow crevice in a rock overhang for three consecutive years. Traditional use of structures constructed by humans has been documented for Short-tailed Swifts (*Chaetura brachyura*) that used vertical concrete cylinders of an abandoned underground drainage system in Trinidad (Snow 1962, Collins 1968), and for Chimney Swifts (*Chaetura pelagica*) that used the same nest site over a 30-year period in Ohio (Dexter 1978).

Swifts in general appear to be relatively long-lived and exhibit low rates of adult mortality (Collins 1973, 1974). Such demographic characteristics in combination with a propensity to use physically stable nesting and roosting sites enhances the likelihood of site tenacity being widespread among these species.

Despite their widespread occurrence throughout the mountainous regions of the western United States, little is known of the breeding biology and general ecology of White-throated Swifts. The propensity of this species to nest deep within cracks and crevices of vertical cliffs and to breed in small colonies (Dawson 1923, Bent 1940) may account in large part for the paucity of data. Given the factors found to affect site tenacity in other species (physical stability of the nest site, prior breeding success at the site, and age of the individual bird) it seems likely that site tenacity may be typical of White-throated Swifts.

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