SHORT COMMUNICATIONS

SURVIVAL AND BREEDING PHILOPATRY IN BARROW'S AND COMMON GOLDENEYES[1]

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Adults of many species of birds exhibit considerable fidelity to their previous breeding area (breeding philopatry) and may even use the same nest site in successive years. In many species of birds, breeding philopatry is male-biased (Greenwood 1980). Waterfowl differ from this pattern in that breeding philopatry is female-biased (Greenwood 1980, Lessells 1985), although it is not clear whether this pattern is ubiquitous among the Anatidae. Studies of breeding dispersal are necessary to understand the reproductive consequences of sex-biased philopatry, and also have implications for studies of gene flow and population dynamics (Geramita and Cooke 1982). If breeding philopatry is female-biased, information on return rates of females with known reproductive histories can provide insight into the costs of reproduction (e.g., Dow and Fredga 1984, Lessells 1986). To date, there have been few attempts to compare patterns of philopatry between areas, and few long-term studies of individually marked birds, although such studies are necessary to test current theories of breeding dispersal (e.g., Greenwood 1980). It has therefore been difficult to separate the influence of life history variation from the effects of environmental variability (Harvey et al. 1984). Finally, there has been no test of the reliability of the methods used to detect dispersal. For example, most estimates of philopatry in waterfowl are based on recaptures of females on their nests, usually late into incubation (e.g., Nilsson 1971, Dow and Fredga 1983, Hepp et al. 1987). Such methods would underestimate survival and philopatry because females that returned to their breeding area, but did not nest successfully, would be missed. The sample of philopatric females would be biased in favor of successful birds.

Our objectives in the present study are: (1) to provide comparative data on return rates of two species of hole-nesting ducks in two locations 100 km apart; (2) to assess the effects of previous breeding effort on return rates; (3) to compare two different methods to estimate return rates (i.e., nest recaptures and resightings of individually marked birds); and (4) to report preliminary findings on natal philopatry.

METHODS

Our study was conducted between 1982 and 1987 near Riske Creek and near 100 Mile House, British Columbia, Canada. Barrow's Goldeneyes (Bucephala islandica) and Common Goldeneyes (B. clangula) were studied on the 100 Mile House site, whereas only Barrow's Goldeneyes occurred on the Riske Creek study area. All birds nested in nest boxes (Savard 1988a). Nest boxes were checked at least twice each year near the end of incubation to identify nesting females. Adult females were caught in nest traps while laying, incubating, or prospecting for nest sites (see Eadie and Gauthier 1985). Adult males were caught in mirror traps (Savard 1985a). All captured birds were marked with individually color-coded nasal discs (Lokemoen and Sharp 1979) or nasal saddles (Doty and Greenwood 1974). Each year a minimum of three (usually five or six) surveys of ponds in both study areas were conducted in early spring to locate returning birds. Comparisons of return rates between categories (species, location, etc.) were conducted using contingency tests (x^2 with Yates correction for continuity). All tests are two-tailed.

RESULTS AND DISCUSSION

Return rate statistics are functions of three probabilities: (1) the probability that an individual survives from one year to the next (survival); (2) the probability that the individual returns to an area, given that it survives (philopatry); and (3) the probability that the individual is observed, given that it returns (sightability). The product of these three probabilities gives the proba-

TABLE 1. Return rates of Barrow's and Common goldeneye females to breeding areas in central British Columbia. Return rates based on resightings and nest recaptures.

Year x	Total no. of marked females seen in year x − 1	Return rate (%)			
		Resightings in year x	Nest recaptures in year x	No. of nest checks	Differences between methods
		Barrow's Goldeneye			
		Riske Creek			
1983	36	89	61	4–6	28
1984	82	71	52	4–6	19
1985	105	66	39	3–4	27
1986	119	66	24	1–2	42
1987	78	68	—[a]	—	—
		100 Mile House			
1985	32	53	38	4–27	15
1986	32	56	41	4–20	15
1987	49	65	41	2–11	24
		Common Goldeneye			
		100 Mile House			
1985	31	61	45	4–27	16
1986	30	53	40	4–20	13
1987	34	50	29	2–11	18
$\bar{x} \pm SE$		62.5 ± 3.6	41.0 ± 3.3		21.5 ± 2.4

[a] Nests not checked.

bility that an individual will be found in the same area the following year.

RETURN RATES OF ADULT FEMALES

We followed the return rates (% of marked birds that returned in a subsequent year) of 258 Barrow's Goldeneye females and 60 Common Goldeneye females (Table 1). Approximately 50 to 90% of all females returned to their previous breeding site, with an overall average of 63 ± 4% SE (Table 1). The proportion of birds returning did not differ significantly between years for either species at 100 Mile House (both $P > 0.10$, χ^2 tests). There was a difference for Barrow's Goldeneyes at the Riske Creek study site ($\chi^2 = 11.28$, df = 4, $P < 0.05$). However, the higher proportion returning in 1983 (Table 1) may be an effect of female age. The birds captured in 1983 were the first to breed in the nest boxes and may represent a biased sample of younger females. Consistent with this notion, Savard (1988a) found that clutch sizes were significantly smaller in 1983 than in 1984 or 1985 (see Heusman 1975, Baillie and Milne 1982, and Dow and Fredga 1983 for similar results). When 1983 data were excluded from the analysis, there was no significant difference between return rates in subsequent years ($\chi^2 = 3.24$, df = 3, $P > 0.10$). There were no significant differences in proportions of females returning between Barrow's Goldeneyes and Common Goldeneyes at 100 Mile House ($P > 0.10$ for each year analyzed separately and combined). Similarly, there were no significant differences in proportions returning for Barrow's Goldeneyes between the two study areas (all $P > 0.10$ for 1985, and 1986 and 1987, analyses conducted separately and combined).

Hepp et al. (1987) used capture-recapture data on female Wood Ducks (*Aix sponsa*) to estimate return rates, and band recovery data to independently estimate survival. By assuming that all returned birds were observed, they were able to estimate female philopatry. We did not have sufficient band recovery data to estimate philopatry. However, we believe that the return rates we observed closely approximate survival rates for the following reasons. First, we are confident that we saw all returning birds. Most ponds on our study areas lacked emergent vegetation and were easily accessible. This, coupled with the territorial behavior of goldeneye (Savard 1988b), their conspicuousness, and their habit of escaping to open water when disturbed, facilitated the localization of marked birds. Second, breeding dispersal appears to be very limited for female goldeneyes. None of our marked birds were sighted more than 3 km from their capture site and over 70% of the females used the same nest site and same pond each year. Unsuccessful birds usually changed nest sites but always remained within 0.5 km of their previous site.

During 6 study years, only four females and three males were missed in one year, but seen the following year. All cases but one occurred in 1986. The other, a male, was not seen in 1985 but was subsequently seen in 1986 and 1987. We assume that these birds were overlooked for the following reasons. First, four of these birds occupied large lakes where observation was difficult. Second, survey efforts were lower in 1985 and 1986 than in 1983 and 1984, which increased the chances of missing a bird. Third, no birds skipped breeding in 1983 or 1984, when surveys were intensive. Return rates of females are therefore considered here as estimates of annual survival rates and all surviving females are assumed to return to their previous breeding area.

TABLE 2.   Yearly return rates for cohorts of Barrow's and Common goldeneye females in central British Columbia.

Year marked	No. females marked	Number (%) of females returning in year				
		1983	1984	1985	1986	1987
		Barrow's Goldeneye				
		Riske Creek				
1982	36	32 (89)	22 (61)	15 (42)	8 (22)	7 (19)
1983	50		36 (72)	25 (50)	17 (34)	13 (26)
1984	47			29 (62)	17 (36)	14 (30)
1985	50				31 (62)	19 (38)
		100 Mile House				
1984	32			17 (53)	9 (28)	6 (19)
1985	15				9 (60)	5 (33)
1986	28					21 (75)
		Common Goldeneye				
		100 Mile House				
1984	31			19 (61)	11 (36)	5 (16)
1985	11				5 (46)	2 (18)
1986	18					10 (56)

Table 2 gives the yearly return rate for each cohort of marked females in the two study areas. These data indicate an annual mortality rate of 10–40%. For example, of the 36 Barrow's Goldeneyes marked at Riske Creek in 1982, 89% were still alive in 1983, 61% in 1984, 42% in 1985, 25% in 1986, and 19% in 1987. Average annual survival was 73% ($n = 5$) for this cohort. Annual survival rates of adult Common Goldeneyes averaged 74% in Sweden (Dow and Fredga 1984), 63% in Minnesota (Moyle et al. 1964), and 58% in Saskatchewan (Du Wors et al. 1984). We found no differences between the return rate of Barrow's Goldeneyes and Common Goldeneyes on our 100 Mile House study area, and our values are within the range reported for Common Goldeneyes elsewhere. Du Wors et al. (1984) noted that adult survival rates for species with delayed maturity, such as goldeneyes, tend to be higher than those for species that mature at an earlier age. Our data are consistent with that observation.

RETURN RATES OF ADULT MALES

Fewer data were available for males than for females. Return rates of adult males to their previous breeding areas averaged $67 \pm 11\%$ (range = 31–100%; Table 3). The overall return rate of males (60%; $n = 63$) did not differ significantly from that of females (69%, $n = 420$) ($\chi^2 = 1.88$, df = 1, $P = 0.17$). A similar result is obtained if birds returning for more than 1 year are excluded from the sample, thus assuring independence of the data (males: 63%, $n = 30$; females 71%, $n = 183$; $\chi^2 = 0.69$, df = 1, $P = 0.41$). The high return rate for males was surprising, as few previous studies have documented high levels of male breeding philopatry in anatids (see Bengtson 1972, Blohm 1978). The greater range observed in annual return rates of males than females could be due to the small sample size for males, but is expected as males that lose their mates occasionally remate with females from another locality.

Why is breeding philopatry so high in male goldeneyes? In Barrow's Goldeneye, the sex ratio is biased in favor of males by a factor of 1.5 (Savard, unpubl. data), which suggests intense competition for females among males. Barrow's Goldeneyes are also highly territorial and can maintain long-term pair bonds (Savard 1985b, 1988b). If a male that loses his mate fails to re-pair on the wintering area, there might be advantages in returning to his previous breeding area (e.g., familiarity with resources, potential mates, etc.). Return of unpaired males to their previous breeding areas could be a common feature in waterfowl (Bengtson 1972, Poston 1974, Alison 1975, Donaghey 1975, Blohm 1978).

TABLE 3.   Return rates of adult Barrow's Goldeneye males for the Riske Creek study sites.

Year marked x	No. of adult males marked	No. (%) of males returning in year					No. of marked males seen in year x	No. (%) returning in year x + 1
		1983	1984	1985	1986	1987		
1982	7	5 (71)	3 (43)	3 (43)	2 (29)	2 (29)	7	5 (71)
1983	8		6 (75)	3 (38)	0 (0)	0 (0)	13	9 (69)
1984	13			8 (62)	3 (23)	3 (23)	22	14 (64)
1985	2				0 (0)	0 (0)	16	5 (31)
1986	0						5	5 (100)

TABLE 4. The effect of previous breeding success on the return rates of Barrow's and Common goldeneye females.

Breeding attempt in previous year	Fate in following year		% return
	Returned next year	Did not return next year	
Barrow's Goldeneye			
Riske Creek			
Succeeded	151	64	70.2%
Failed or did not breed	54	21	72%
100 Mile House			
Succeeded	44	25	63.8%
Failed or did not breed	23	19	54.8%
Common Goldeneye			
100 Mile House			
Succeeded	26	21	55.3%
Failed or did not breed	26	21	55.3%

EFFECTS OF PREVIOUS BREEDING EXPERIENCE ON SURVIVAL

A major tenet of life history theory is that there is a cost to reproduction; viz., current fecundity can be increased only at the cost of future fecundity or survival (Williams 1966, Charnov and Krebs 1974). Tests of this hypothesis with wild birds have been equivocal (Askenmo 1979; de Steven 1980; Smith 1981; Nur 1984; Dow and Fredga 1984, 1985; Lessells 1986). We tested for an effect of current reproductive effort on survival of female goldeneyes by comparing the return rates of hens that bred successfully with those of females that did not nest or that failed to hatch a brood. We reasoned that females that hatched a brood and cared for offspring would have invested more in the current reproductive effort and therefore might be expected to exhibit reduced survival (after Lessells 1986). Contrary to this prediction, there was no trend for successful females to return less often (Table 4). We also did not find differences in survival between non-breeding females that were caught prospecting for nest sites (19 of 38 survived) and breeding females (31 of 52 survived; $\chi^2 = 0.479$, $P > 0.10$). These results suggest that trade-offs between current reproduction and future survival are weak or absent for goldeneyes.

Our findings contrast with Dow and Fredga's (1984) observation that survival of Common Goldeneye females was reduced if hens produced a large clutch early in their first year of breeding. However, both our study and Dow and Fredga's (1984) study were based on observational data and therefore may have confounded variation in reproductive efforts with effects of individual variation in parental abilities (e.g., Hogstedt 1981, Lessells 1986). For example, individuals that failed to breed could have had enhanced survival (because they did not invest as much in current reproduction), or reduced survival (if these individuals were simply poorer quality individuals). If both conditions apply, we might not see any trade-off between survival and reproductive effort even if such a trade-off existed. Alternatively, if survival rates and return rates are not equivalent as we have assumed, there is the possibility

that successful females suffer higher mortality but exhibit a higher degree of philopatry than unsuccessful females, which may counteract any negative effect of reproductive effort. Experimental brood manipulations are required to control for these effects (see Lessells 1986).

COMPARISON OF ESTIMATES OF SURVIVAL BASED ON NEST RECAPTURES AND ON SIGHTINGS

Estimates of return rates on resightings of marked birds were significantly higher than estimates based on nest recaptures (Wilcoxon's paired sample test $t = 0$, $n = 10$, $P < 0.01$ for both species combined; $t = 0$, $n = 8$, $P < 0.01$ for only Barrow's Goldeneyes; Table 1). In fact, return rates based only on nest recaptures were underestimated by as much as 42%, with an average of $21.5 \pm 2.4\%$ SE. The level of underestimation varied greatly between years and was influenced by the number of nest visits. Studies relying solely on nest recaptures are therefore likely to underestimate survival and breeding philopatry.

NATAL PHILOPATRY

We marked over 1,000 goldeneye ducklings at hatching on our study area from 1984–1987. To date, 17 females and no males have been resighted on their natal lake. Six of these females nested at 2 years of age, and one at 3 years of age. Five females nested on their natal lake (three within 100 m of their natal nest), and the other two females on an adjacent pond. Dow and Fredga (1983) reported that, of 17 Common Goldeneye females that returned to their natal area to breed, 94% nested within the immediate vicinity of their natal nest site. Current data, although limited, suggest that natal philopatry is biased in favor of females and that dispersal of males occurs prior to the first breeding season.

In summary, our study demonstrates that: (1) return rates are high for both female and male Barrow's Goldeneye; (2) return rates are comparable for the closely-related Common Goldeneye; (3) levels of return rates do not differ significantly among locations; and (4) natal philopatry is female-biased. Lessells (1985)

argued that female-biased philopatry has evolved in anatids because, in most species, females provide most or all of the parental care of ducklings. Females may therefore gain a greater advantage in exploiting information on brood-rearing areas. In cavity-nesting birds, females might further benefit through previous experience with the availability of nest sites. Both species of goldeneye exhibit delayed maturity, and Eadie and Gauthier (1985) have shown that nonbreeding females prospect for future nest sites in their natal area.

Natal dispersal is better understood for females than males. Resightings of marked birds on the wintering areas indicate that philopatry to wintering sites by males and females may be as high as to nesting sites (Savard 1985b, 1986, 1988b), and that birds from the same breeding area do not winter together (Savard 1987). This suggests that the young likely disperse prior to or during fall migration, ending up in different wintering areas. Subsequently, females returned as yearlings to their natal area, whereas it is still unknown whether, or what proportion of males do. In their second winter, females pair and return to nest on their natal area, whereas males follow their mates to their natal area and subsequently become philopatric to that area until they remate.

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SEX AND EGG SIZE IN GREAT-TAILED GRACKLES[1]

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Key words: Great-tailed Grackles; Quiscalus mexicanus; egg size; facultative manipulation; sexual dimorphism; sex control.

Trivers and Willard (1973) suggested that when the variance in reproductive success of one sex is greater than that of the other, females in good condition should produce more offspring of the sex that exhibits the higher variance. This assumes that the condition of the female is reflected in the condition of the offspring and that the survival and breeding success of an individual is at least partially dependent on the condition of the individual at the end of parental care. Although Trivers and Willard's model predicts different strategies for different females, it is clear that nestling quality within individual broods may vary greatly and that females may potentially influence this variability in an adaptive way. For example, sequence-related hatching trends found in Lesser Snow Geese (*Chen caerulescens,* Ankney 1982) and Bald Eagles (*Haliaeetus leucocephalus,* Bortolotti 1984) may function to provide a competitive advantage for the larger sex in both species.

Mead et al. (1987) recently found that eggs from which male White-crowned Sparrows (*Zonotrichia leucophrys*) hatched were larger than those from which females were hatched. Since the variance in reproductive success of males in this species is probably greater than that of females and since egg size has been shown in many studies to be correlated with nestling growth and survival, they interpreted these results as being an adaptive response in accordance with the predictions generated by the Trivers and Willard model. Because their study is one of few among altricial birds that provides evidence that parents might adaptively apportion their investment into sons and daughters, I decided to examine similar data for a species in which much greater difference in variance in breeding success for males and female would lead to the prediction of even greater size differences between eggs from which sons and daughters hatch.

Great-tailed Grackles (*Quiscalus mexicanus*) exhibit extreme sexual size dimorphism which becomes apparent shortly after hatching (Teather and Weather-
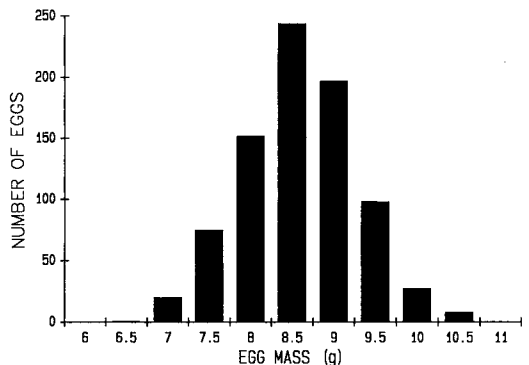

FIGURE 1. Distribution in the sizes of eggs laid by Great-tailed Grackles.