PHILOPATRY, NEST-SITE FIDELITY, AND REPRODUCTIVE PERFORMANCE IN BUFFLEHEADS

GILLES GAUTHIER

Département de Biologie, Université Laval, Sainte-Foy, Province Québec G1K 7P4, Canada

ABSTRACT.—I examined the consequences of breeding-site fidelity and natal philopatry on reproductive performance in Buffleheads (*Bucephala albeola*). Return rates of breeding females averaged 44% over 4 years. Females were twice as likely to return after their second breeding year than after their first. This difference was not associated with a poor reproductive performance in the previous year because birds that failed to return to the study area had a reproductive performance similar to those that returned, irrespective of breeding experience. Probability of return for successful breeders (45%) did not differ significantly ($P > 0.1$) from failed nesters (29%). However, nest-site fidelity was high (68%) and was associated with nesting success because successful breeders (83%) were much more likely to reuse the same nest site than were failed breeders (29%). Nest-site fidelity provided some benefits to females. Birds who used the same site laid earlier and laid more eggs.

The return rate of females banded as ducklings was 13% in the first two years after banding. Natal philopatry was strongly female-biased and no male ducklings were known to have returned to the study area. The average distance of natal dispersal for returning females was 0.99 km. My results supported Rohwer and Anderson's (1988) prediction that female ducks should gain in terms of reproductive success by returning to a familiar area. *Received 9 November 1988, accepted 16 August 1989.*

COSTS and benefits associated with natal philopatry and breeding-site fidelity have been analyzed extensively (e.g. Greenwood 1980, 1987; Greenwood and Harvey 1982; Shields 1982, 1983). Benefits of site fidelity have commonly been measured in terms of breeding performance. In several avian taxa, successful birds tended to return at a higher rate, while birds that returned to the same nest site or territory had generally a higher breeding success (Harvey et al. 1979, Newton and Marquiss 1982, Gratto et al. 1985, Drilling and Thompson 1988, Gavin and Bollinger 1988).

Dispersal patterns are unusual in waterfowl (Anatidae) because females show a higher degree of philopatry than males (Cooke et al. 1975, Dow and Fredga 1983, Lessells 1985, McKinney 1986). In a recent review of waterfowl mating system, Rohwer and Anderson (1988) suggested that site fidelity benefits females more than males because females are largely responsible for parental care in ducks. Winter pairing, another unusual feature of waterfowl mating system, also forces males to follow their mates to the breeding ground. Rohwer and Anderson (1988) further predicted that homing by females should increase their reproductive success. To date, few waterfowl studies have documented benefits to site fidelity in terms of reproductive success (but see Dow and Fredga 1983).

I studied both natal and breeding philopatry, and their consequences for reproductive performance, in the migratory Bufflehead (*Bucephala albeola*). Buffleheads nest in tree cavities, which makes nest-site fidelity easy to quantify. Site fidelity of adult and young female Buffleheads has been reported by Erskine (1961) but not in association with reproductive performance. My objectives were to examine site fidelity of adult female Buffleheads and of young of both sexes, to test if return rate is dependent on past reproductive performance, and to evaluate the consequence of site fidelity on reproductive success.

METHODS

This study was conducted from 1982 to 1986 in the Cariboo Parkland of British Columbia, Canada, 15 km north of 100 Mile House (51°46'N, 121°24'W). The study area included 26 permanent wetlands ranging from 0.5 to 61 ha (although 80% of these were <8 ha in area). Gauthier (1989) gives details of the study area.

In all years, females were trapped on the nest and marked individually with color-coded nasal saddles (Doty and Greenwood 1974) and a USFWS metal band. A few females (<10%) were also marked when they were caught with their brood in the drive trap (see below).

I found nests by searching intensively for natural cavities around ponds. Nest boxes were installed in

1982 and 1983, and many of them were used by Buffleheads in subsequent years (Gauthier 1988a). Of nests initiated on the study area, 45–62% were found each year (Gauthier and Smith 1987). Nests were checked every 2–5 days during egg laying and every 7–10 days during incubation. For nests found during incubation, the date of nest initiation was estimated by backdating from hatching (assuming a mean incubation length of 30 days and a mean egg-laying rate of 1 egg per 1.5 days [Erskine 1972]). I defined *nesting success* as the percentage of nests where at least one duckling left the nest (usually 24 h after hatching). *Hatching success* was the percentage of eggs that hatched in each nest.

From 1982 to 1984, I web-tagged young (Haramis and Nice 1980) before they left the nest. Young were recaptured between 18 and 40 days of age in a drive trap (modified from Cowan and Hatter 1952). Ducklings were sexed (see Gauthier 1987a) and banded permanently with a metal band and up to 3 plastic color bands. Nasal saddles were not used on ducklings because of their small bill size. More than 75% of ducklings that fledged on the study area were banded during the 3 yr that brood drives were conducted. Brood survival and the number of young fledged were calculated from weekly censuses conducted in June and July (Gauthier 1989). The mean number of young fledged was calculated using all nesting attempts, including total nest or brood loss.

I defined *breeding-site fidelity* as the return rate to the study area of females banded as breeding adults in a previous year. Females were classified as returning if their nest was found or if they were seen for at least two consecutive censuses and were accompanied by a male (lone marked females were never seen during the nesting period). From 1983 to 1985, weekly censuses were conducted on all ponds in the study area, and intensive behavioral observations were made on many ponds. Because adult females were marked with conspicuous nasal saddles, used open water, and were easy to observe, I am confident that I saw all marked females returning to the study area from 1983 to 1985 and determined their breeding status, even though I found only ca. 50% of the nests. In 1986, minimum return rates were estimated from females found on the nest and from casual observations of females on ponds.

I defined *nest-site fidelity* as use of the same nest site in two consecutive years. Nest-site fidelity was known accurately for all years of the study because all cavities and nest boxes were checked every year.

Natal philopatry was calculated from the return of birds banded as ducklings. The colored leg-bands were much less conspicuous than nasal saddles of adult females, and they were much more difficult to read from a distance. Thus, despite intensive censuses, an unknown number of color-banded birds may have gone undetected. Therefore, the return rates of ducklings in this study are minimum estimates of natal philopatry. The *distance that females dispersed* from their natal area was defined as the distance between the brood territory (Gauthier 1987a) where they were banded as ducklings and the site where they were sighted or where they nested for the first time.

TABLE 1. Return rates of female Buffleheads banded as breeding adults (the sample sizes are in parentheses).

Year banded	Returning *i*th year after banding			
	Year 1	Year 2	Year 3	Year 4
1982 (10)	5	3	0	1
1983 (24)	12	6	1	—
1984 (20)	7	5	—	—
1985 (10)	4	—	—	—
Total (64)	28	14	1	1
% returning	44	26	3	10
			6[a]	

[a] Average % returning for years 3 and 4.

Some measures of reproductive performance differed among years (date of nest initiation, clutch size) and between natural and box nests (date of nest initiation and number of young fledged) (Gauthier 1989). These variables were standardized by expressing them as deviations from annual means, or as deviations from the mean for each type of nest site. For several analyses, I classified females according to their breeding experience as follows: *first-time breeders* are birds breeding for the first time (all assumed to be 2 yr of age, Gauthier 1989), whereas *second-* and *third-time breeders* are birds which are known to have bred for *at least* 2 or 3 yr, respectively.

Statistical tests on nesting variables were performed using Student's *t*-test, and return data were analyzed with contingency tables. All tests were made using individual birds as the sampling unit. The angular transformation was applied to hatching success data (Sokal and Rohlf 1969). Tests were two-tailed, unless they dealt with a priori predictions.

RESULTS

BREEDING PHILOPATRY

Return rates of breeding females.—Of 64 female Buffleheads banded as breeding adults, 28 (44%) returned for at least 1 (and up to 4) breeding season. Annual return rates varied from 35 to 50% (Table 1). Return rates of females in the second year (26%) were higher than expected from their return rate in the first year ($[44\%]^2$ = 19%).

Return rates of female Buffleheads do not truly reflect their survival rates because some females may miss a breeding season. One female

TABLE 2. Return rates of female Buffleheads according to their previous breeding experience.[a]

Breeding year	Returned to breed	Did not return to breed	Probability of returning
1st	10	26	0.28
2nd	13	10	0.57
3rd	1	7	0.13

[a] $G_{adj} = 7.01$, $P = 0.03$, df = 2.

TABLE 4. Effect of previous nesting success on nest-site use by female Buffleheads in subsequent years (Fisher exact test, $P = 0.022$).

	Nesting success	
	Successful[a]	Failed
Use same nest site	24	2
Change nest site	7	5
Probability of using same nest site	0.77	0.29

[a] Successful nests are those where at least one duckling left the nest.

was banded in 1982, bred in 1983 and 1984, failed to return in 1985, but returned in 1986 (Table 1) to the same nest site she had used previously. This absence was not caused by the unavailability of her nest site because the cavity remained unoccupied in 1985.

Return rates and breeding experience.—Breeding experience influenced return rates of females. Females were twice as likely to return after their second breeding year than after their first breeding year (Table 2), but they were less likely to return after their third breeding year, although sample sizes were small. For this analysis, I included the data from 13 individuals recorded in two different years.

I tested the association between the higher return rate of birds after their second breeding year with differences in reproductive performance. In first-time breeders, the reproductive performance of birds that returned did not differ from those that did not return ($P > 0.1$), although returning birds tended to have a higher nesting success and a smaller clutch size (Table 3). I found no difference in reproductive performance between female second-year breeders that returned and those that did not return (Table 3). This result was unchanged when all experienced (second- and third-year) breeders were pooled together (for all tests, $P \geq 0.28$). Overall, return rate of successful females was 45% ($n = 40$) compared with 29% ($n = 17$) for failed nesters ($G_{adj} = 1.03$, $P > 0.1$). Thus, birds that failed to return to the study area had a reproductive performance in the previous year similar to birds that did return, whether they were first-time or experienced breeders.

Nest-site fidelity.—Of returning females, 68% used the same nest site ($n = 38$). Reuse of a nest site was affected by the nesting success of the female on that site. Only 2 of 7 (29%) females with nesting failures used the same nest site in the following year compared with 24 of 31 (77%) successful females ($P < 0.05$, Table 4). Of the 7 females that changed nest sites after a successful nesting attempt, 2 were forced to move because

TABLE 3. Comparison of nesting variables between female Buffleheads (experienced and inexperienced) that returned to breed in the following year and females that did not return to breed. For date of nest initiation, clutch size, and number of young fledged, data ($\bar{x} \pm$ SE) are standardized according to the type of nest site and the year (see Methods). Sample sizes are in parentheses.

Nesting variables	Returned to breed	P[a]	Did not return to breed
First time breeders			
Date of nest initiation	2.08 ± 2.49 (10)	0.83	1.42 ± 1.67 (25)
Clutch size	−0.85 ± 0.35 (10)	0.13	0.12 ± 0.38 (23)
Nesting success (%)	80.0 (10)	0.24	60.0 (25)
Hatching success (%)	92.0 ± 2.8 (8)	0.78	93.5 ± 3.2 (14)
Number of young fledged	−0.69 ± 0.74 (10)	0.84	−0.51 ± 0.44 (25)
Second time breeders			
Date of nest initiation	−4.13 ± 1.97 (13)	0.17	0.37 ± 2.48 (9)
Clutch size	0.32 ± 0.57 (13)	0.82	0.54 ± 0.70 (9)
Nesting success (%)	76.9 (13)	0.68	77.8 (9)
Hatching success (%)	94.8 ± 2.2 (10)	—	100 ± 0.0 (7)
Number of young fledged	0.53 ± 0.98 (13)	0.34	1.99 ± 1.03 (8)

[a] t-test except for nesting success, Fisher exact test.

TABLE 5. Comparison of nesting variables between female Buffleheads returning to the same nest sites as the year before and those moving nest sites between years. For date of nest initiation, clutch size, and number of young fledged, data ($\bar{x} \pm$ SE) are standardized according to the type of nest site and the year (see Methods). Sample sizes are in parentheses.

Nesting parameters	Returning to same nest site	P[a]	Moving to new nest site
Date of nest initiation	−5.78 ± 1.41 (24)	0.06	−0.84 ± 2.01 (11)
Clutch size	0.90 ± 0.37 (23)	0.02	−0.59 ± 0.42 (11)
Nesting success (%)	89.0 (26)	0.12	66.7 (12)
Hatching success (%)	93.0 ± 3.3 (22)	0.73	95.1 ± 2.5 (8)
Number of young fledged	0.72 ± 0.80 (18)	0.66	1.29 ± 0.96 (10)

[a] *t*-test except for nesting success, Fisher exact test.

their cavity tree fell during winter. If we exclude these 2 females, the probability of reusing a nest site after a successful nesting attempt was 83%. Data from 12 individuals were included twice in Table 4. Six of these females retained the same nest site over three consecutive years, whereas six changed site in at least one year.

Although females changed nest sites more often after a nesting failure, they did not move farther than females that changed nest sites after a successful nesting attempt (distance [$\bar{x} \pm$ SE] between nest sites: 348 ± 184 m [$n = 5$] vs. 432 ± 166 m [$n = 5$]; $t = 0.34$, $P = 0.74$). Females that changed nest sites either moved to a site elsewhere on the same pond or on the nearest neighboring pond.

I examined the reproductive consequences of changing nest site. Females that returned to the same nest site laid, on average, 5 days earlier and 1.5 more eggs than females that changed nests (Table 5). Other measures of reproductive success did not differ ($P > 0.1$), although nesting success of females that returned to the same nest site tended to be higher than those changing nest site (Table 5).

NATAL PHILOPATRY

Overall, 27 Buffleheads banded as ducklings returned to the study area for at least 1 yr. Of these, 19 were females, 0 were males, and 8 were of "unknown" sex (Table 6). Those labeled "unknown" sex were birds whose band combination was read incompletely but fully enough to establish the banding year. At least 13% of females returned to their natal site, but no males were ever known to return. If we assume that those of unknown sex were also females, female natal philopatry could be as high as 19%. Among the 27 returning birds, 14 were first seen at 1 yr of age, and 13 at 2 yr.

Natal dispersal ranged from 0 to 4.5 km with a mean of 0.99 ± 0.23 km (Fig. 1). The distribution of dispersal distances for females that were found nesting did not differ from that for females that were sighted only (Kolmogorov-Smirnov test, $D = 0.23$, $P = 0.13$; Fig. 1).

DISCUSSION

Breeding philopatry.—The return rate for adult female Buffleheads (44%) was slightly lower than the rate (50%) reported by Erskine (1972: 177). These return rates were lower than those reported for female goldeneyes (*Bucephala clangula* and *B. islandica*) in the same area (70%; J. P. Savard and J. Eadie pers. comm.). Bufflehead female return rates are similar or slightly higher than those reported in several species of dabbling ducks (range: 15–45%; McKinney 1986).

Return rate of birds is the product of site fidelity and survival rate. Based on 10 yr of banding data in British Columbia, Erskine (1972) estimated survival rate of adult females at 43%. This value may be too low because it implies 100% site fidelity (Table 1). In Mallards (*Anas platyrhynchos*) and American Black Ducks (*A.*

TABLE 6. Return rates of Buffleheads banded as ducklings.

Year banded	Banded (n)		Returning (n)		
	♂	♀	♂	♀	U[a]
1982	42	33	0	3	3
1983	44	59	0	10	3
1984	40	51	0	6	2
Total	126	143	0	19	8
Percent return (by sex)			0	13	—
Percent return (total)				10	

[a] U = Unknown.

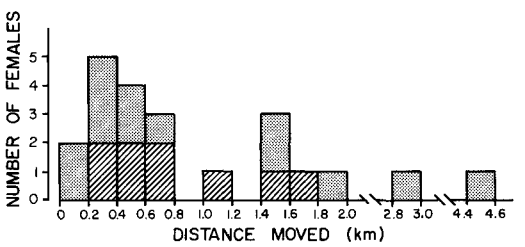

Fig. 1. Distribution of dispersal distances of female Buffleheads from their natal area for birds that returned to breed (hatched area) and those that were only sighted on the study area (stippled) in subsequent years.

rubripes), survival rates of adult females range from 48 to 58% (Krementz et al. 1987, Nichols and Hines 1987, Nichols et al. 1987). Assuming a similar survival rate for female Buffleheads, this would require site fidelity of 85% to account for the return rates I report (Table 1).

It is unclear why females in their second breeding year had a higher return rate than first-time breeders (Table 2). Although first-time breeders usually have lower reproductive success (Gauthier 1989), I found no differences between the reproductive performance of females that returned and those that did not, either as first-time or as second-time breeders (Table 3; but see below).

Return rate, nest-site fidelity, and breeding success.—Contrary to many studies (e.g. Newton and Marquiss 1976, Oring et al. 1983, Gratto et al. 1985, Gavin and Bollinger 1988, Reynolds and Cooke 1988), Bufflehead breeding success did not affect return rate of females in the following year. Admittedly, the power of the statistical test to detect a significant difference was low because sample sizes were small (Table 3). Therefore, I cannot rule out the possibility that small differences in reproductive success existed between females that returned and those that did not. Drilling and Thompson (1988), however, also reported a lack of association between reproductive success and the probability of returning in House Wrens (*Troglodytes aedon*). It is possible that, under some circumstances, the advantages of site fidelity outweigh the cost of dispersing a long distance even after a nesting failure.

Nesting failures were generally sufficient to deter females from reusing the same nest site in the following year (Table 4), although the distance moved between nest sites was generally small (<1 km). This implies that philopatry and nest-site fidelity are distinct decisions made by female Buffleheads. There was probably a balance between the advantage of moving to a better nest site after a nesting failure and the cost of dispersing to a new, unfamiliar area.

Movements of females after a nesting failure are common in birds (e.g. Harvey et al. 1979, Newton and Marquiss 1982, Dow and Fredga 1983, Drilling and Thompson 1988). It is probably advantageous for females to move nest sites after an unsuccessful nesting attempt because some nest sites may be more prone to predation (Dow and Fredga 1985, Sonerud 1985), disturbance by other birds, or nest parasitism (Eadie and Gauthier 1985).

Female Buffleheads that returned to the same nest site laid earlier and laid more eggs (Table 5). Although they did not fledge more young, early nest initiation increased the probability that offspring would return to breed (Gauthier 1989). Reusing the same nest site frees females from the need to prospect for nest sites in late summer or early spring (Eadie and Gauthier 1985). These advantages may explain the high degree of nest-site fidelity (83%) exhibited by successful females. Dow and Fredga (1983) reported the same breeding advantages for female goldeneyes that reused their nest sites, although nest-site fidelity of female goldeneyes following a successful nesting attempt was lower (45%).

Natal philopatry.—In addition to strong breeding-site fidelity, female Buffleheads also showed natal philopatry. Return rates of females were as high in their first year as in their second year, although they breed first at 2 yr of age (Erskine 1972, Gauthier 1989). Females presumably return in their first year to prospect for nest sites (Eadie and Gauthier 1985). Finding a good nest site is important for an obligate cavity nester (Dow and Fredga 1985, Eadie and Gauthier 1985), and it is advantageous for young females to prospect in a familiar area. This may explain why >90% of returning females were resighted or found nesting within 2 km of their brood territory. Erskine (1961) also found several females nesting on the pond where they were banded as ducklings. The average dispersal distance of returning females in this study (0.99 km; Fig. 1) is almost identical to the dispersal distance reported by Dow and Fredga (1983) for female goldeneyes returning to their natal area (1.05 km).

Dispersal in the genus Bucephala.—My results (Gauthier 1987b, this study) and those of others (Limpert 1980, Eadie and Gauthier 1985, Savard 1985) shed new light on the overall dispersal pattern in the genus *Bucephala*. In their first year, females return to their natal area to prospect for nest sites (Eadie and Gauthier 1985). During that period, females also develop a site-attachment to a wintering area (Limpert 1980). Second-year females return to the area where they prospected for their first nesting attempt and then return to the same area regardless of breeding performance the previous year. Familiarity with an area during the processes of finding a good nest site and a brood territory (Gauthier 1987a) probably favors female philopatry.

The low return of males suggests that they disperse in their first year. Males pair for the first time in their second winter (Erskine 1972). After deserting the female during incubation, males return to the same wintering area to repair with their former mate (Savard 1985, Gauthier 1987b). Thus, male site-attachment to their wintering grounds (Limpert 1980) probably develops after the first pairing. Males which failed to re-pair are known to return to their previous breeding area (Savard 1985, Gauthier 1987b). However, males re-paired with a new mate were never observed returning to their former breeding area. This is consistent with the idea that males follow their mate to her breeding area.

Even if males of the genus *Bucephala* are strongly territorial during the breeding season (Savard 1984, Gauthier 1987c), they do not depart from the pattern of female-biased philopatry observed in ducks (Rohwer and Anderson 1988). This is probably because territoriality is associated with protection of the female rather than with defense of a resource per se (Gauthier 1987c, Savard 1988), as in most other ducks (McKinney 1986, Gauthier 1988b). *Bucephala* species conform to the pattern of an association between female-biased philopatry and male defense of the female reported by Greenwood (1980). Rohwer and Anderson (1988) recently suggested that female-biased philopatry and winter pairing in migratory ducks were a consequence of the requirement for nutrient storage by breeding females and of their exclusive participation in parental care. Rohwer and Anderson predicted that females should gain in reproductive success by returning to a familiar area. My study supports Rohwer and Anderson's prediction because female Buffleheads faithful to their nest site improved their breeding performance.

ACKNOWLEDGMENTS

This study was funded by the Canadian National Sportsmen's Fund, the Natural Sciences and Engineering Research Council of Canada, and the Canadian Wildlife Service. I thank Rory Brown and Ron Boychuck of Ducks Unlimited (Canada) for providing nest boxes. Danielle Gauthier, Barbara Peterson, Natalie Hamel, Linnie Nyland, Simon Richards, André Breault, and Dominique Chagnon helped in the field. Jean-Pierre Savard and James N. M. Smith provided invaluable assistance throughout this study, and W. Monical kindly allowed me to work on his property. I thank Luc Bélanger, John Eadie, and James N. M. Smith for their comments on earlier drafts of this manuscript.

LITERATURE CITED

COOKE, F., C. D. MACINNES, & J. P. PREVETT. 1975. Gene flow between breeding populations of the Lesser Snow Goose. Auk 92: 493–510.

COWAN, I. MCT., & J. HATTER. 1952. A trap and technique for the capture of diving waterfowl. J. Wildl. Manage. 16: 438–441.

DOTY, H. A., & R. J. GREENWOOD. 1974. Improved nasal saddle marker for Mallards. J. Wildl. Manage. 38: 938–939.

DOW, H., & S. FREDGA. 1983. Breeding and natal dispersal of the goldeneye, *Bucephala clangula*. J. Anim. Ecol. 52: 681–695.

———, & ———. 1985. Selection of nest sites by a hole-nesting duck, the goldeneye *Bucephala clangula*. Ibis 127: 16–30.

DRILLING, N. E., & C. F. THOMPSON. 1988. Natal and breeding dispersal in House Wrens (*Troglodytes aedon*). Auk 105: 480–491.

EADIE, J. M., & G. GAUTHIER. 1985. Prospecting for nest sites in cavity-nesting ducks of the genus *Bucephala*. Condor 87: 528–534.

ERSKINE, A. J. 1961. Nest-site tenacity and homing in the Bufflehead. Auk 78: 389–396.

———. 1972. Buffleheads. Can. Wildl. Serv. Monogr. Ser. 4.

GAUTHIER, G. 1987a. Brood territories in Buffleheads: determinants and correlates of territory size. Can. J. Zool. 65: 1402–1410.

———. 1987b. Further evidence of long-term pair bonds in ducks of the genus *Bucephala*. Auk 104: 521–522.

———. 1987c. The adaptive significance of territorial behavior in breeding Buffleheads: a test of three hypotheses. Anim. Behav. 35: 348–360.

———. 1988a. Factors affecting nest box use by Buffleheads and other cavity-nesting birds. Wildl. Soc. Bull. 16: 132–141.

———. 1988b. Territorial behaviour, forced copulations and mixed reproductive strategy in ducks. Wildfowl 39: 102–114.

———. 1989. The effect of experience and timing on reproductive performance in Buffleheads. Auk 106: 568–576.

———, & J. N. M. SMITH. 1987. Territorial behaviour, nest-site availability and breeding density in Buffleheads. J. Anim. Ecol. 56: 171–184.

GAVIN, T. A., & E. K. BOLLINGER. 1988. Reproductive correlates of breeding-site fidelity in Bobolinks (*Dolichonyx oryzivorus*). Ecology 69: 96–103.

GRATTO, C. L., R. I. G. MORRISON, & F. COOKE. 1985. Philopatry, site tenacity, and mate fidelity in the Semipalmated Sandpiper. Auk 102: 16–24.

GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Anim. Behav. 28: 1140–1162.

———. 1987. Inbreeding, philopatry and optimal outbreeding in birds. Pp. 207–222 *in* Avian genetics (F. Cooke and P. A. Buckley, Eds.). London, Academic Press.

———, & P. H. HARVEY. 1982. The natal and breeding dispersal of birds. Annu. Rev. Ecol. Syst. 13: 1–21.

HARAMIS, G. M., & A. D. NICE. 1980. An improved web-tagging technique for waterfowl. J. Wildl. Manage. 44: 898–899.

HARVEY, P. H., P. J. GREENWOOD, & C. M. PERRINS. 1979. Breeding area fidelity of Great Tits (*Parus major*). J. Anim. Ecol. 48: 305–313.

KREMENTZ, D. G., M. J. CONROY, J. E. HINES & H. F. PERCIVAL. 1987. Sources of variation in survival and recovery rates of American Black Ducks. J. Wildl. Manage. 51: 689–700.

LESSELLS, C. M. 1985. Natal and breeding dispersal of Canada Geese *Branta canadensis*. Ibis 127: 31–41.

LIMPERT, R. J. 1980. Homing success of adult Buffleheads to a Maryland wintering site. J. Wildl. Manage. 44: 905–908.

MCKINNEY, F. 1986. Ecological factors influencing the social systems of migratory dabbling ducks. Pp. 73–82 *in* Ecological aspects of social evolution (D. I. Rubenstein and R. W. Wrangham, Eds.). Princeton, New Jersey, Princeton Univ. Press.

NEWTON, I., & M. MARQUISS. 1976. Occupancy and success of nesting territories in the European Sparrowhawks. Raptor Research 10: 65–71.

——— & ———. 1982. Fidelity to breeding area and mate in sparrowhawks *Accipiter nisus*. J. Anim. Ecol. 51: 327–341.

NICHOLS, J. D., & J. E. HINES. 1987. Population ecology of the Mallard: VIII. Winter distribution patterns and survival rates of winter-banded Mallards. U.S. Fish and Wildl. Serv. Resour. Publ. 162.

———, H. H. OBRECHT III, & J. E. HINES. 1987. Survival and band recovery rates of sympatric American Black Ducks and Mallards. J. Wildl. Manage. 51: 700–710.

ORING, L. W., D. B. LANK, & S. J. MAXSON. 1983. Population studies of the polyandrous Spotted Sandpiper. Auk 100: 272–285.

REYNOLDS, J. D., & F. COOKE. 1988. The influence of mating systems on philopatry: a test with polyandrous Red-necked Phalaropes. Anim. Behav. 36: 1788–1795.

ROHWER, F. C., & M. G. ANDERSON. 1988. Female-biased philopatry, monogamy, and the timing of pair formation in migratory waterfowl. Pp. 187–201 *in* Current ornithology, vol. 5 (R. F. Johnston, Ed.). New York, Plenum Publ.

SAVARD, J.-P. 1984. Territorial behaviour of Common Goldeneye, Barrow's Goldeneye and Bufflehead in areas of sympatry. Ornis Scandinavica 15: 211–216.

———. 1985. Evidence of long-term pair bonds in Barrow's Goldeneye (*Bucephala islandica*). Auk 102: 389–391.

———. 1988. Winter, spring and summer territoriality in Barrow's Goldeneye: characteristics and benefits. Ornis Scandinavica 19: 119–128.

SHIELDS, W. M. 1982. Philopatry, inbreeding, and the evolution of sex. Albany, State Univ. New York Press.

———. 1983. Optimal inbreeding and the evolution of philopatry. Pp. 132–159 *in* The ecology of animal movement (I. R. Swingland and P. J. Greenwood, Eds.). Oxford, Oxford Univ. Press.

SOKAL, R. R., & J. R. ROHLF. 1969. Biometry. San Francisco, W. H. Freeman.

SONERUD, G. A. 1985. Nest hole shift in Tengmalm's Owl *Aegolius funereus* as a defence against nest predation involving long-term memory in the predator. J. Anim. Ecol. 54: 179–192.