THE EFFECT OF EXPERIENCE AND TIMING ON REPRODUCTIVE PERFORMANCE IN BUFFLEHEADS

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ABSTRACT.—I investigated the relationship among breeding experience, timing of reproduction, and reproductive performance in female Buffleheads (*Bucephala albeola*) over a 5-yr period. There were significant yearly fluctuations in date of nest initiation and in clutch size. On average, first-time breeders began nesting later, had a lower nesting success, fledged less young, and tended to have smaller clutches (although not significantly so) than experienced breeders. Birds that used nest boxes also began to lay later, had lower nesting success, and fledged fewer young than those that used natural cavities. This could not be explained solely by the higher use of nest boxes by first-time breeders. Repeatability was moderate for date of nest initiation and clutch size, but low for the number of young fledged. There was a seasonal decline in clutch size for both first-time and experienced breeders, although the relationship was much stronger for the latter group. Nesting success also decreased throughout the season, but the number of young fledged did not decrease. More early-hatched than late-hatched females were recruited into the breeding population. Early nesting was advantageous for experienced breeders. *Received 9 November 1988, accepted 18 April 1989.*

REPRODUCTIVE success increases with age and experience in many species of birds. First-time breeders often nest later, lay smaller clutches, have lower nesting success and a lower fledging success than experienced breeders (Pugesek and Diem 1983, Rockwell et al. 1983, Afton 1984, Dow and Fredga 1984, Coulson and Thomas 1985, Perrins and McCleery 1985, Nol and Smith 1987, but see Hannon and Smith 1984, Bédard and LaPointe 1985). Delayed reproductive maturity is also common in long-lived species (e.g. Rockwell et al. 1983). Higher reproductive success in experienced breeders may result from several factors. These include greater overall experience of older parents (Newton et al. 1981, Raveling 1981), increased reproductive effort with age (Pugesek 1981, 1983; Curio 1983), differences in "quality" among individuals (Raveling 1981, Coulson and Thomas 1985), and selection against poor performers in their first breeding year (Curio 1983, Nol and Smith 1987).

The timing of reproduction affects reproductive success. Young that hatch earlier in the season often survive better and recruit at a higher rate to the breeding population (Cooke et al. 1984, Dow and Fredga 1984, Arcese and Smith 1985). This may result from the accumulated experience of early-hatched young which enables them to achieve a higher dominance status (Arcese and Smith 1985).

I investigated breeding experience, timing of reproduction, and reproductive performance over 5 yr in Buffleheads (*Bucephala albeola*), a small cavity-nesting duck. Buffleheads are relatively long-lived and breed for the first time when only 2 yr old (Erskine 1972). My study was restricted to females, because males desert their mates during incubation, provide no parental care, and are difficult to trap and mark. I attempted to determine the combined effect of breeding experience and timing of reproduction on clutch size, nesting success, fledging success, and recruitment rate of young to the breeding population.

METHODS

My study was conducted from 1982 to 1986 in the Cariboo Parkland of British Columbia, 15 km north of 100 Mile House (51°46′N, 121°24′W). The study area covered 23 km^2 and included 26 ponds and lakes. All wetlands are permanent and range in size from 0.5 to 61 ha, although 80% are <8 ha in area. The landscape in this area is a mosaic of rangeland, groves of aspen (*Populus tremuloides*), and forests of Douglas fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*).

Females were trapped on the nest and marked individually with color-coded nasal saddles (Doty and Greenwood 1974) and a USFWS metal band. Because females were trapped after mid-incubation to minimize desertion, the identity of females was unknown for nests deserted during egg laying or early incubation (19%). These nests were therefore excluded from most of the analyses. A few females were also caught and marked with their brood in a drive trap (see below).

I found nests by searching intensively for natural cavities around ponds. Most nests (>90%) were found during the laying stage. A few were found by following females to their nests during incubation. I added more than 200 nest boxes to the study area. Between 1984 and 1986, 25–50% of the population nested in these boxes (Gauthier 1988). Overall, I estimated that 45–62% of the nests initiated on the study area were found each year from 1983 to 1986 (Gauthier and Smith 1987).

During egg laying, nests were checked every 2–5 days. All eggs were counted and measured. For nests found during incubation, I estimated the date of initiation by backdating from hatching. I assumed a mean incubation length of 30 days and a mean egg-laying rate of 1 egg per 1.5 days (Erskine 1972). Nests were checked every 7–10 days during incubation. A *nest* was defined as a site where at least one egg was laid. I defined *nesting success* as the percentage of nests where at least one duckling left the nest (usually 24 h after hatching), and *hatching success* as the percentage of eggs that hatched in each nest.

From 1982 to 1984, I checked nests on the day of hatching (estimated by candling; Hanson 1954) and web-tagged the young (Haramis and Nice 1980) before they left the nest. Ducklings were caught again on the water in a drive trap (modified from Cowan and Hatter 1952) between 18 and 40 days of age. They were sexed and banded permanently with a USFWS metal band and a unique set of colored leg bands. More than 75% of all ducklings that fledged on the study area were banded during 1982–1984.

Brood survival and the number of young fledged were calculated from weekly censuses and intensive behavioral observations conducted in June and July from 1982 to 1985 (see Gauthier 1987a for methods). Although Buffleheads can fly at 50 days, I defined the number of young fledged as the total number of young that reached 28 days of age (class IIa of Bellrose 1976) because females started to desert their brood at that age and mortality of older ducklings was negligible (Gauthier 1987a). The number of young fledged was calculated for all marked females that attempted nesting, including those that deserted their nest or lost their brood entirely. The number of young fledged was not available for 1986 because no censuses were conducted in June or July of that year.

Statistical tests were performed using ANOVA, Least square difference (LSD) and Student's t-test, except for nesting success which was analyzed with contingency tables. The angular transformation was applied to data on hatching success (Sokal and Rohlf 1969).

RESULTS

I found 157 Bufflehead nests in the study area during 5 yr. Overall nesting success was 64%.

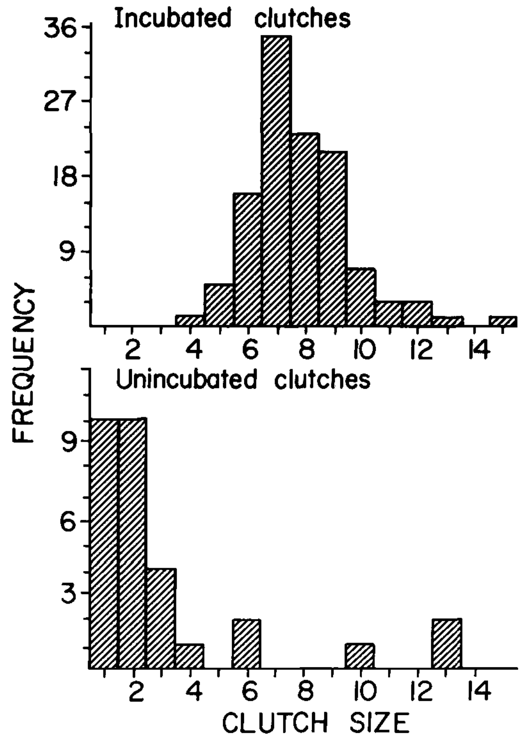

Fig. 1. Frequency distribution of clutch sizes of incubated and unincubated Bufflehead nests.

Desertion was the main cause of nest failure as nest predation was low (below 10% in most years; Gauthier and Smith 1987, Gauthier 1988). Thirty nests (19%) were deserted during the egg-laying process. Most of these had ≤3 eggs, well below the modal clutch size of incubated clutches (Fig. 1). A few large clutches were unincubated. Two of the three largest clutches were cases of nest parasitism (Gauthier 1987c). Date of nest initiation for nests deserted during laying did not differ from all other nests ($t = 0.27$, $P = 0.78$). The unincubated clutches were deleted from most of the remaining analyses because identity of females was unknown in most cases.

Year and type of nest site.—Nest initiation date and clutch size varied significantly among years whereas date of nest initiation and the number of young fledged varied significantly among nest type (Tables 1 and 2). Mean date of nest initiation was later in 1982 and 1985 than in other years, and was later in nest boxes compared with natural cavities (Table 1). Mean clutch size was larger in 1986 and smaller in 1985 than in other years. Finally, mean number

TABLE 1. Nesting variables for female Buffleheads according to year and type of nest site in the Cariboo Parkland, British Columbia ($\bar{x} \pm$ SE). Sample sizes are in parentheses.

	Date of nest initiation	Clutch size	Hatching success	Number of young fledged	% nesting success[a]
Year					
1982	137.2 ± 2.7[b] (11)	7.27 ± 0.51 (11)	97.7 ± 1.5 (9)	2.88 ± 1.03 (8)	81.8 (11)
1983	124.3 ± 1.6 (31)	8.04 ± 0.33 (26)	91.8 ± 2.3 (23)	2.26 ± 0.61 (23)	69.7 (33)
1984	126.6 ± 1.3 (44)	7.79 ± 0.30 (33)	93.3 ± 3.3 (22)	1.78 ± 0.51 (33)	55.8 (43)
1985	131.8 ± 1.8 (25)	7.20 ± 0.34 (25)	94.2 ± 2.7 (20)	2.57 ± 0.55 (28)	65.7 (35)
1986	126.0 ± 1.9 (21)	8.76 ± 0.37 (21)	92.6 ± 2.4 (20)	—	64.5 (31)
Nest type					
Cavity	126.4 ± 1.0 (72)	8.04 ± 0.21 (66)	93.1 ± 1.7 (58)	2.88 ± 0.44 (49)	80.5 (77)
Nest box	129.5 ± 1.1 (60)	7.58 ± 0.24 (50)	93.8 ± 1.8 (36)	1.49 ± 0.44 (43)	48.0 (75)
Overall	127.8 ± 0.8 (132)	7.84 ± 0.16 (116)	93.4 ± 1.2 (94)	2.23 ± 0.30 (92)	64.7 (153)

[a] This variable includes nests deserted during egg laying.
[b] Julian calendar (1 January = day 1).

of young fledged was lower in nest boxes than in natural cavities (in all cases, $P < 0.05$, LSD test). Nesting success was similar among years (Table 1; $\chi^2 = 3.28$, df = 4, $P = 0.51$) but was significantly higher in natural cavities (81%) than in nest boxes (48%) ($\chi^2 = 16.2$, df = 1, $P < 0.001$).

All nesting variables that differed significantly among years or types of nest sites were standardized for further analysis. Continuous variables were expressed as deviations from the mean by subtracting the mean from individual values in each year, or for each type of nest site. I analyzed nesting-success data separately for natural cavities and nest boxes. Untransformed data were used for the remaining variables.

Breeding experience of nesting females.—Only 10 females were of known age (i.e. banded as ducklings and recruited in the breeding population of the study area). All females of known age bred for the first time at 2 years of age, as found previously (Erskine 1972). For the remaining females, my only information was whether I found them nesting for the first, second, or third time. Females that nested for the second or third time were obviously experienced breeders. Those found breeding for the first time could be either first-time breeders or experienced breeders that nested elsewhere before. By the third year of the study (1984), >50% of the nesting females were banded. Because females show year-to-year fidelity to their nest site (Erskine 1961, Gauthier 1990), I assumed that unbanded females found nesting in known sites (i.e. cavities or nest boxes inspected the previous year) after 1983 were first-time breeders. This assumption is reasonable because breeding performance of these females was similar to that of known first-time breeders (i.e. those banded as ducklings) (Table 3). These two samples were combined and are thereafter referred to as first-time breeders.

Date of nest initiation was affected significantly by breeding experience (Table 4). Females in their second and third breeding year laid on average 4 and 9 days earlier than first-time breeders. Clutch size tended to increase for females in their second breeding year, but the difference was not significant (Table 4). Females in their second breeding year fledged more young than first-time breeders but not more than females breeding for their third year (Table 4). Sample size was small for the latter group. Overall, the mean number of young fledged by experienced females (second and third breeding year) was higher by 1.4 young

TABLE 2. Two-way analysis of variance of nesting variables for female Buffleheads according to breeding year (1982–1986) and type of nest site (natural cavity vs. nest box). Levels of significance: * = $P < 0.05$, ** = $P < 0.01$; all others, $P > 0.1$.

		Mean squares			
Source	df	Date of nest initiation	Clutch size	Hatching success	Number of young fledged
Year	4	543**	8.61*	0.071	3.49
Nest type	1	577**	7.85	0.023	40.70*
Year × nest type	3	101	1.29	0.041	0.89
Error	1	77	2.90	0.100	8.44

TABLE 3. Comparison of nesting variables between known and presumed first-time breeders. For date of nest initiation, clutch size, and number of young fledged, data were standardized according to the type of nest site and the year ($\bar{x} \pm$ SD). Sample sizes are in parentheses.

Nesting variables	Known first-time breeders	P[a]	Presumed first-time breeders
Date of nest initiation	4.05 ± 2.62 (9)	0.37	1.50 ± 1.04 (47)
Clutch size	−0.52 ± 0.54 (9)	0.54	−0.14 ± 0.29 (37)
Hatching success	86.7 ± 6.6 (6)	0.24	94.0 ± 2.0 (28)
Number of young fledged	−0.69 ± 0.88 (8)	0.86	−0.52 ± 0.42 (27)
Nesting success	60.0% (10)	0.68	61.5% (52)

[a] t-test except for nesting success (Fisher's exact test).

than first-time breeders (t = 2.09, P = 0.04). Finally, breeding experience did not affect hatching success.

Nesting success improved with each breeding year (Table 4). There was an interaction between breeding experience and the type of nest site used. Nesting success apparently increased with experience only for females in nest boxes (Table 5). Nesting success of first-time breeders using natural cavities was twice as high as the success of those using nest boxes, (P < 0.001, Table 5). Nesting success of experienced breeders was also higher for those using natural cavities but the difference was not significant.

Individual variation in reproductive performance.—Some of the variation in reproductive success may stem from differences among individual females. To test for this, I calculated repeatability of nesting variables (Lessells and Boag 1987). Repeatability of date of nest initiation and clutch size was moderate (r = 0.565, F = 4.08, P < 0.001, df = 23 and r = 0.550, F = 3.94, P < 0.001, df = 23, respectively). However, repeatability of hatching success and number of young fledged was low (r = 0.026, F = 1.06, P = 0.43, df = 18, and r = 0.145, F = 1.76, P < 0.10, df = 18, respectively).

Timing of reproduction.—In the previous analysis, date of nest initiation was the variable most strongly affected by breeding experience. Perhaps some benefits accrued to laying early. I looked for relationships between date of nest initiation and other measures of reproductive success. I found a significant inverse relationship between clutch size and date of nest initiation for both first-time and experienced breeders (Fig. 2). The slope was much steeper in experienced than in first-time breeders (b = −0.154 ± 0.034 vs. −0.047 ± 0.020, respectively; P = 0.01), but did not differ among experienced breeders (P > 0.1). There was also a seasonal decline in nesting success because early nesters were significantly more successful than late nesters (Fig. 3). When females were separated into first-time and experienced breeders, or into cavity and nest-box users, the trends were similar but no longer significant, possibly because of smaller sample size (Fig. 3).

Although clutch size and nesting success both decreased seasonally, the number of young fledged was not affected by date of nest initiation in either experienced breeders (b = −0.058, P > 0.1, n = 26) or in first-time breeders (b = −0.031, P > 0.1, n = 34) (Fig. 4). A better estimate of reproductive success is the number of young recruited in the breeding population

TABLE 4. Effect of breeding experience on nesting variables for female Buffleheads. For date of nest initiation, clutch size, and number of young fledged, data were standardized according to the type of nest site and the year. Means followed by the same letter did not differ significantly at the 0.05 level (LSD test).

			Breeding year[a]		
Nesting variables	Test	P	1st	2nd	3rd
Nest initiation date	F = 8.20	<0.001	1.91 ± 1.00A (56)	−2.36 ± 1.47B (26)	−7.31 ± 2.26C (11)
Clutch size	F = 1.26	0.29	−0.27 ± 0.26A (46)	0.34 ± 0.40A (24)	0.36 ± 0.50A (12)
Hatching success	F = 0.93	0.40	92.7 ± 2.2A (34)	96.7 ± 2.9A (19)	89.3 ± 3.6A (12)
Number of young fledged	F = 2.53	0.08	−0.56 ± 0.46A (35)	1.10 ± 0.57B (22)	0.15 ± 1.12AB (8)
Nesting success	χ^2 = 5.77	0.06	61% (62)	74% (27)	93% (14)

[a] $\bar{x}$ ± SE (n).

TABLE 5. Effect of breeding experience (first-time vs. experienced breeders) and type of nest site (natural cavity vs. nest box) on nesting success of female Buffleheads. Sample sizes are in parentheses.

Type of nest site	First-time breeders	P[a]	Experienced breeders[b]
Natural cavity	91% (23)	0.54	88% (25)
P[a]	<0.001		0.13
Nest box	44% (39)	0.08	69% (16)

[a] Fisher's exact test.
[b] Females in the 2nd and 3rd breeding year were combined because of small sample sizes.

(Cooke et al. 1984). To test for this, I used the sample of 10 females that were banded as ducklings and recruited in the breeding population. I calculated the deviation in the hatching date of the natal nest of these females from the mean hatching date of the sample of brood caught in banding drives each year. I used hatching date because it is highly correlated with date of nest initiation ($r = 0.95$, $P < 0.001$, $n = 93$) which was unknown for several of these females.

The average standardized natal hatching date of females that were recruited into the breeding population was -2.81 ± 2.75 (95% CI), which is significantly earlier than the standardized hatching date ($\bar{x} = 0$) of all banded ducklings. When I increased the sample size by adding females that were seen prospecting for nest sites in the study area at 1 year of age (Eadie and Gauthier 1985, Gauthier 1990), the trend was similar (mean standardized hatching date of all returning females: -2.75 ± 2.86, $n = 19$). Although early-laying females had larger clutches, this does not bias the result because early-laying females did not fledge more young than late-nesting birds. Early-hatched young had a higher return rate in their first year and appeared more frequently in the breeding population.

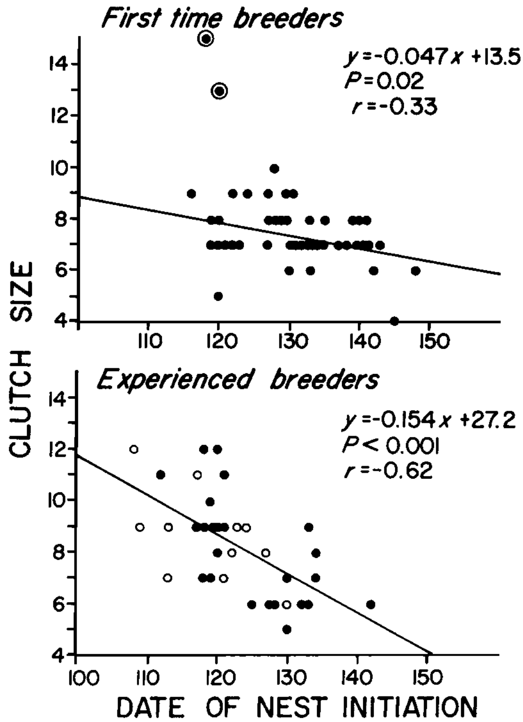

Fig. 2. Relationship of clutch size to date of nest initiation of first-time and experienced breeding female Buffleheads in their second (●) and third (○) breeding year. For first-time breeders, 2 parasitized clutches (◉) were excluded from the regression. When included, the regression equation is $y = -0.93x + 19.8$, $P < 0.001$, $r = -0.43$.

DISCUSSION

The exclusion from the analyses of females that deserted their nests during egg laying could bias my results (Fig. 1). Desertion was probably not induced by the observer because many nests were already abandoned when they were found, or the female was never disturbed on her nest (Savard 1986, Gauthier 1988). Desertion, however, was the major source of nesting failure (Gauthier and Smith 1987, Gauthier 1988) and, in most cases, its cause was unknown. Intraspecific competition for nest sites and nest parasitism are possible factors (Eadie and Gauthier 1985). Although this hypothesis explains the desertion of large, multiple clutches, it does not explain the desertion of many small clutches (≤3 eggs; Fig. 1).

An alternative explanation is that females who desert during egg laying are predominantly young and inexperienced birds which, for several reasons (physiological state, body condition, competition for territories, etc.), are unable to complete the laying process. Indeed, first-time breeders have a lower nesting success (Table 4), mostly because of nest desertion during incubation. It is possible that some females that abandoned their nests during laying renested elsewhere. I had circumstantial evidence of renests before completion of a full clutch (Gauthier 1988, unpubl. data), as did Erskine (1972), but this was uncommon. In 5 years, I never observed renesting by a female after completion of a full clutch.

Another confusing factor is that females re-

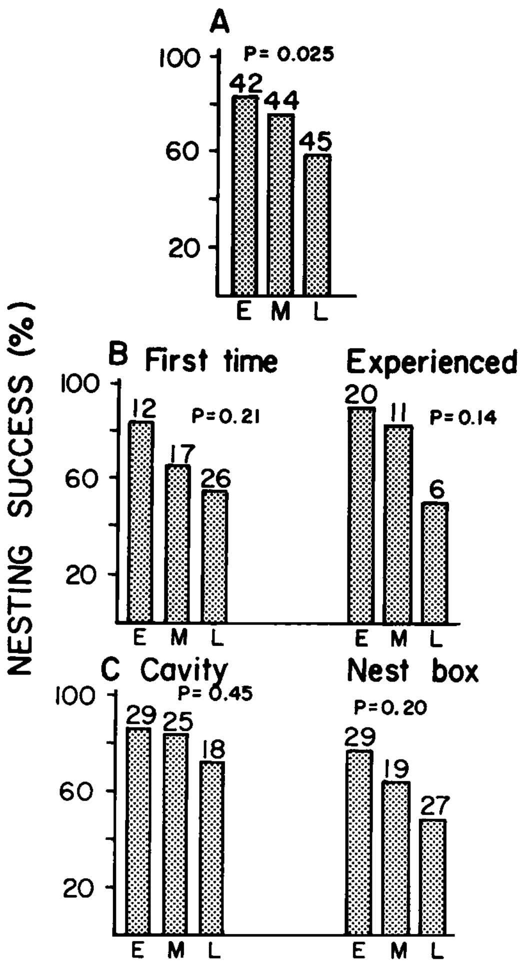

Fig. 3. Comparison of nesting success of early (E), middle (M), and late (L) nesters for all female Buffleheads (A), first-time and experienced breeders (B), and cavity and nest-box users (C). Sample sizes are above each bar. χ^2 test (except for experienced females: Fisher exact test combining middle and late nesters because of small sample size).

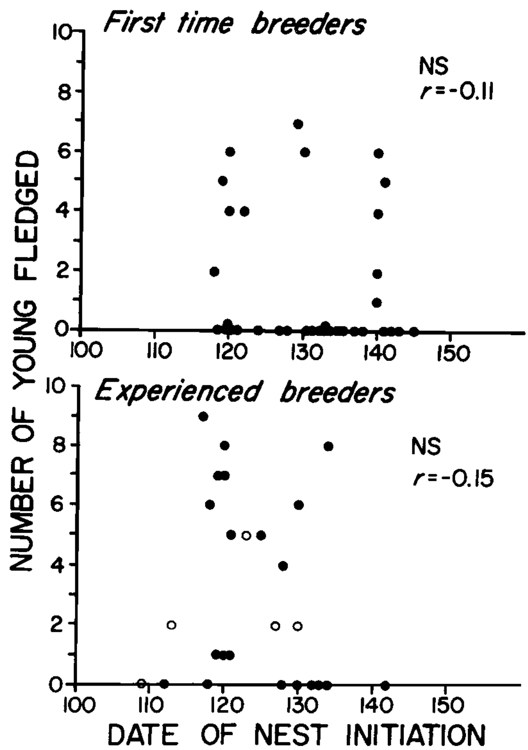

Fig. 4. Relationship of the number of young fledged to date of nest initiation of first-time and experienced breeding female (second [●] and third [O] breeding year) Buffleheads. None of the regressions were significant ($P > 0.1$).

corded breeding in their second and third year are a subsample of females recorded breeding in their first year. This would bias the analysis if the nesting performances of females that subsequently returned to breed differed from those that did not return to breed. However, this was not the case. I found that nesting performances of females that returned to breed were similar to those that did not (Gauthier 1990). Furthermore, repeatability of reproductive success (number of young fledged) was low.

Nest boxes vs. natural cavities.—The difference in reproductive performance between birds using natural cavities and those using nest boxes was unexpected (Table 2). Female Buffleheads began to nest later in boxes, had a lower nesting success, and fledged fewer young. The effect was especially marked in first-time breeders which had a much lower nesting success in nest boxes than in natural cavities (Table 5). One explanation is that nest boxes are closer to water and hence more conspicuous than natural cavities. This could have increased the probability of interference at the nest site. Increased competition with European Starlings (*Sturnus vulgaris*) in nest boxes could also be a factor (Peterson and Gauthier 1985, Gauthier 1988).

My results contrast with those of Nilsson (1984) who found that nesting success of Pied Flycatcher (*Ficedula hypoleuca*) was higher in nest boxes than natural cavities. These differences suggest prudence in interpreting nesting-success data obtained solely from birds using nest boxes. This is especially important when boxes are recently installed and are thus more likely to be used by inexperienced breeders, as I found (Table 5; see also Eriksson 1982).

Breeding experience and reproductive performance.—Breeding experience influenced most aspects of breeding performance in Buffleheads. Experienced breeders began to nest earlier, had a higher nesting success, and fledged more young. The effect was more pronounced for dates of nest initiation, which differed significantly among all three classes of breeding experience (Table 4). A progressively earlier date of nest initiation with increased breeding experience is usual in birds and has been reported many times in waterfowl (eg. Finney and Cooke 1978, Krapu and Doty 1979, Birkhead et al. 1983, Afton 1984, Dow and Fredga 1984).

Although experienced females tended to lay larger clutches than first-time breeders, it is difficult to determine if this was a direct effect of experience or an indirect consequence of an earlier date of nest initiation in experienced females. Based solely on the seasonal decline in clutch size (Fig. 2), we would expect that clutches of females in their second breeding year would increase by 0.66 egg because these females lay, on average, 4.3 days earlier than first-time breeders. This is very close to the observed difference of 0.61 egg between first-time and second-year breeders (Table 4). It is therefore not possible to conclude whether experienced females really increased their reproductive effort by laying more eggs (Pugesek 1981, 1983; Curio 1983) or whether their experience enabled them to initiate laying earlier and to benefit from better environmental conditions (Smith et al. 1980, Dijkstra et al. 1982, Ewald and Rohwer 1982). For instance, females begin to lay earlier on territories with higher food abundance (Gauthier 1987c). Experienced females that settle earlier could gain access to better territories, and lay earlier and have larger clutch sizes.

I found that experienced females fledged more young. Older, more experienced females fledged more young in many species including Canada Geese (*Branta canadensis;* Raveling 1981), Mute Swans (*Cygnus olor;* Birkhead et al. 1983), California Gulls (*Larus californicus;* Pugesek and Diem 1983), Great Tits (*Parus major;* Perrins and McCleery 1985), and Song Sparrows (*Melospiza melodia;* Nol and Smith 1987). There are, however, few reports of similar data in ducks because of the difficulty of following broods after they leave the nest. I found a considerable effect of female experience on the number of young fledged. Combining data from Tables 1 and 4, I found that experienced females fledged twice as many young as first-time breeders (3.07 vs. 1.67 young fledged; data standardized for type of nest site and yearly differences). A better measure of reproductive success is the number of young recruited into the breeding population (Cooke et al. 1984). Unfortunately, as in most studies of breeding biology, little of this information was available, because the mothers of many banded ducklings were unmarked, and their breeding history was unknown.

Timing of reproduction.—The advantage accrued to experienced females that laid early in terms of larger clutch size had disappeared by fledging time as early nesters did not fledge more young than late nesters. Experienced breeders reproduced more successfully because there was a trend for early-hatched young to be recruited at a higher rate into the breeding population. This further emphasizes the point that fledging success is an incomplete measure of fitness. Higher recruitment of early-hatched young has also been reported in Lesser Snow Geese (*Chen caerulescens caerulescens;* Cooke et al. 1984), Common Goldeneyes (*Bucephala clangula;* Dow and Fredga 1984), and Song Sparrows (Arcese and Smith 1985). Several mechanisms could account for this relationship. Early-hatched young may have access to better feeding territories and reach greater mass and better general condition at fledging (Dow and Fredga 1984, Gauthier 1987a). Alternatively, early-hatched young may achieve higher dominance status because of greater experience in agonistic encounters (Arcese and Smith 1985).

Variation among individuals.—Several authors have shown that much of the variance in reproductive success is due to variation among individuals (Raveling 1981, Woolfenden and Fitzpatrick 1984, Newton 1989). In Kittiwakes (*Rissa tridactyla*), quality of the individual is the most important factor to influence the breeding success of a pair, and successful breeders tend to be the same pairs from year to year (Coulson and Thomas 1985). In Buffleheads, repeatability was moderate for date of nest initiation and clutch size, which suggests that females were consistent in their reproductive effort. However, reproductive success of females was not consistent from year to year as indicated by the low repeatability of the number of young fledged.

I considered only experience of females. In species with male parental care, male age and breeding experience influences reproductive success (Raveling 1981, Birkhead et al. 1983, Perrins and McCleery 1985, Nol and Smith 1987). Because males generally desert their mates during incubation and provide no parental care, studies of reproductive success in waterfowl have traditionally neglected the effects of male experience. However, remating is common in several species of ducks including Buffleheads (Savard 1985, Gauthier 1987b). This suggests that male experience may contribute to the reproductive success of the pair.

Acknowledgments

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