

# DUCKLING MORTALITY IN BARROW'S GOLDENEYE AND BUFFLEHEAD BROODS

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**ABSTRACT.**—We compared duckling mortality patterns in Barrow's Goldeneyes (*Bucephala islandica*) and Buffleheads (*B. albeola*) in the aspen parkland of central British Columbia, Canada. Hatching phenology of both species varied between years in relation to spring temperatures. Buffleheads hatched on average a few days later than Barrow's Goldeneyes each year. Mortality estimates for ducklings differed by as much as 55%, and depended on the technique used. Estimates of mortality rates per brood were higher and more variable than those calculated per duckling. The Mayfield estimate of mortality per duckling day, adjusted for duckling age, was the most accurate. Mortality rates of Barrow's Goldeneyes and Buffleheads varied similarly between years. Mortality patterns in relation to duckling age, however, varied between species and between years. The highest mortality usually occurred in the week after hatching. Hatching date influenced mortality rates in 3 of 5 yr, but there was no consistent pattern. Barrow's Goldeneye ducklings suffered higher mortality than Bufflehead ducklings in 4 of 5 yr. This pattern was reversed in 1984, when the largest number of Barrow's Goldeneye broods occurred. Duckling mortality was higher on ponds with several broods than on ponds with single broods, which implies density-dependent mortality. This may have been due to intra- and interspecific aggression. The high mortality of Barrow's Goldeneye ducklings in 1983 was followed by lowered female recruitment in 1985. Because aggressiveness by Barrow's Goldeneyes has more impact on conspecifics, Barrow's Goldeneyes and Buffleheads can coexist at low to moderate densities of goldeneyes. At high goldeneye densities, Buffleheads may be excluded from some ponds. Received 1 June 1990, accepted 23 December 1990.

COMPETITION occurs when two species exploit common resources in short supply or when they interfere with one another, even if resources are sufficient (Birch 1957). For two populations to coexist stably, each must inhibit its own growth more than that of the other species (Pianka 1978). In areas of sympatry, interference competition between Barrow's Goldeneye (*Bucephala islandica*) and the Bufflehead (*B. albeola*) is strong (Savard 1982, 1984), and Barrow's Goldeneyes dominate Buffleheads in aggressive interactions (Savard and Smith 1987).

In some regions of central British Columbia, densities of Barrow's Goldeneyes are almost twice as high as those of Buffleheads (Savard 1982), when the reverse pattern might be expected from relative body size and availability of nest sites (Gauthier 1985, Gauthier and Smith 1987). Female Barrow's Goldeneyes with young do not tolerate Buffleheads within their territory and are particularly aggressive toward Bufflehead broods (Savard 1982, 1988a; Gauthier 1985; Savard and Smith 1987). Bengtson (1972) found that Barrow's Goldeneye ducklings suf-

fered greater mortality at higher densities and that high densities of goldeneyes were also correlated with increased mortality of ducklings in other sympatric waterfowl species. Bengtson (1972) and Einarsson (1985) quantified mortality in broods of Icelandic Barrow's Goldeneye, and Erskine (1972) and Gauthier (1987) did so for Buffleheads in British Columbia. However, mortality of Barrow's Goldeneye and Bufflehead ducklings has not been compared directly in areas of sympatry.

Our aim was to compare hatching chronology and duckling mortality of the two species. We also compare the effectiveness of six methods to estimate mortality.

## METHODS

Barrow's Goldeneye and Bufflehead broods stay in open water and rarely seek cover. This, and the lack of emergent vegetation on most of our study ponds, greatly facilitated brood checks. In 1980 and 1981, we counted broods on 100 ponds at intervals of 14 days. In 1982, 1983, and 1984, we counted every 3 days. During each visit, we recorded the location of the

brood, the age of the young and the number of young in each brood. Most broods were identified from census to census by a combination of the mother's nasal disk, age, number of young, and location of the brood. We determined ages of ducklings by the criteria of Gollop and Marshall (1954) and Taber (1971). We used age classes for Lesser Scaup (*Aythya affinis*) as an approximation of Bufflehead age classes (Taber 1971). Bufflehead and Lesser Scaup have similar growth patterns (Erskine 1972). As data on plumage growth and age are not available for Barrow's Goldeneye, we assumed their growth to be similar to that of Common Goldeneye (Gibbs 1961).

Many Barrow's Goldeneye females were marked with nasal disks (26% in 1982, 47% in 1983, 56% in 1984) (Lokemoen and Sharp 1979, Savard and Eadie 1989). Females were captured in mirror traps (Savard 1985) and on the nest during the last week of incubation. We assumed that reduction in brood size between consecutive censuses indicated duckling mortality. On some ponds, broods amalgamated (Savard 1987). In most cases, we could identify such occurrences from duckling age and numbers. We assigned the young to their respective broods. Broods that could not be followed individually were excluded from some analyses.

Major nest predators were the black bear (*Ursus americanus*), Douglas squirrel (*Tamiasciurus douglasii*), and marten (*Martes americana*). Potential duckling predators were Raven (*Corvus corax*), Great Horned Owl (*Bubo virginianus*), Northern Harrier (*Circus cyaneus*), coyote (*Canis latrans*), and red fox (*Vulpes vulpes*).

Each year, we divided broods into three equal-sized groups (early, middle, late) based on their hatching date. We estimated mortality in 6 ways: 2 direct estimates and 4 obtained from the Mayfield method. In Method 1 we recorded the number of young present when a brood was first sighted and used that value to calculate the number of young that hatched on the study area. We compared this value with the number of young present on the study area just before fledging. All first sightings were of broods <1 week old. The last count for each brood was done at least 4 weeks after the first sighting. This method allowed us to estimate minimum duckling mortality on lakes where broods could not be followed individually because of mixing.

The second direct estimate (Method 2) assumed an average initial brood size based on values reported in the literature. Over 4 yr, the average number of young that hatched from successful Barrow's Goldeneye nests in the study area was 10 (Savard 1988b). An average of 8 young hatched from successful Bufflehead nests (Erskine 1972). This allowed us to account for the mortality that occurred before the first sighting of a brood.

The Mayfield method (Mayfield 1961, 1975) accounts for bias related to the time when a nest or brood is first found by considering the period that

the nest or brood is under observation. Ringelman and Longcore (1982) and Gauthier (1987) have modified the method to estimate survival rates of ducklings. For each period, an exposure index is calculated. *Exposure* is defined as the number of ducklings multiplied by the length of period (i.e. 3 ducklings alive for 2 days represent 6 duckling-days). *Mortality* is expressed as losses per exposure, where losses are the number of ducklings that disappeared in each period. When the exact time of duckling loss was unknown, we assumed that the mortality rate was constant, and we estimated losses and exposure for each day of the period (Johnson 1979). We also assumed that losses were constant during the period, or that losses occurred mid-way through the period. Results were almost identical for all three assumptions because of our frequent surveys. Thus, we use only the assumption of constant mortality rate here.

We derived two estimates of daily mortality from the Mayfield method: a weighted estimate, where exposures and losses were summed for all broods and the daily mortality rate was calculated, and an unweighted estimate, where mortality rates were calculated for each brood individually and then averaged. When mortality varies with age, these two estimates can be further refined by the product-moment method (Klett and Johnson 1982). Survival rates are then calculated as the product of age-class survival rates. Thus four estimates (3-6) were obtained from the Mayfield method: (3) a weighted estimate, (4) the weighted estimate refined by the product-moment method, (5) an unweighted estimate, and (6) the unweighted estimate refined by the product-moment method. Depending on sample size and type of analyses, mortality is expressed as either daily mortality rate, mortality over a 4-week period, or mortality over a 6-week period.

We used the jackknife technique (Cochran 1977) to estimate the variability of the weighted daily mortality rates. To test for differences among several means, multiple comparison tests cannot be used here because the jackknife method was used to compute standard errors. To make such comparisons, we used paired *z*-tests and adjusted  $\alpha$  (probability level) to  $\alpha/c$ , where *c* is the number of comparisons made.

## RESULTS

*Hatching chronology.*—During the 5 yr of the study, mean hatching dates of Barrow's Goldeneye broods ranged from 14-24 June and those of Bufflehead broods from 16-25 June (Table 1). Mean hatching date varied significantly between years (two-way ANOVA  $P < 0.001$ ), and Buffleheads hatched slightly—but significantly ( $P < 0.001$ )—later than Barrow's Goldeneye. There were no interactions between year and species. For both species, 1983 was an early

TABLE 1. Mean hatching date ( $\pm$ SD) of Barrow's Goldeneyes and Buffleheads in relation to average temperatures ( $^{\circ}$ C) in April and May.

Year	Temperature		Barrow's Goldeneye		Bufflehead	
	April	May	<i>n</i> <sup>a</sup>	Hatching date	<i>n</i>	Hatching date
1980	9.4	14.3	84	19 June $\pm$ 7 A <sup>b</sup>	67	22 June $\pm$ 8 AC
1981	6.8	13.1	84	19 June $\pm$ 7 A	73	20 June $\pm$ 8 A
1982	5.3	11.5	85	24 June $\pm$ 7 C	78	25 June $\pm$ 7 C
1983	8.6	14.5	95	14 June $\pm$ 8 B	73	16 June $\pm$ 9 B
1984	7.5	10.1	108	19 June $\pm$ 10 A	78	20 June $\pm$ 9 A

<sup>a</sup> Number of broods.

<sup>b</sup> Student-Newman-Keuls test was used to test for differences in hatching dates within species between years. Dates followed by different letters differ significantly ( $P < 0.05$ ) between years.

hatching year and 1982 a late one. In all years, >70% of the broods hatched within 3 weeks. The earliest brood hatched in the first week of June in 1983, and the latest hatched in the second week of July in 1982.

*Estimation of duckling mortality.*—Mortality estimates varied with the techniques used to calculate them (Tables 2 and 3), and Method 1 yielded the lowest estimates. The six estimates ranged from 37% to 69% for Barrow's Goldeneye, and from 10% to 65% for Bufflehead. Adjustments for age differences influenced estimates based on broods more than those based on ducklings. The estimates were affected in some years but not in others. Differences were high between estimates with broods as units (2–37%) especially in 1983–1984, and relatively low for those with ducklings (2–8%). Estimates made by assuming an average initial brood size (Method 2) were usually higher than those based on the weighted Mayfield method adjusted for

age differences (Method 3). Although estimates were slightly different, both methods tracked yearly differences in mortality rates similarly.

Analyses of mortality on a brood basis permit the use of standard statistical techniques. A four-way analysis of variance of the effect of species, year, age, and hatching date on brood daily mortality rates indicated that daily mortality rates varied significantly with species and year, decreased with increasing duckling age ( $P < 0.001$ ), but did not vary with hatching date ( $P < 0.199$ ). Interaction terms indicated that age-specific mortality differed between years ( $P < 0.001$ ). The absence of significant interactions between species and year ( $P = 0.067$ ), and between species and hatching dates ( $P = 0.547$ ), indicates that goldeneyes and Buffleheads responded similarly to factors that influenced mortality between years and periods.

Weighted mortality estimates (on a duckling basis) were less variable and permitted a more

TABLE 2. Estimates of mortality of Barrow's Goldeneye ducklings ( $\pm$ SE). All estimates are for 43 days following hatching. Mortality is expressed in %.

Year	<i>n</i> <sup>a</sup>	Mayfield estimate						
		Direct estimate		Weighted estimate (on a duckling basis)		Unweighted estimate (on a brood basis)		
		% dead		Adjusted for age difference	Not adjusted for age difference	<i>n</i> <sup>d</sup>	Adjusted for age difference	Not adjusted for age difference
1980	84 (584)	35	55					
1981	84 (612)	21	43	31 $\pm$ 4 B	33 $\pm$ 1	54	49 $\pm$ 10	76 $\pm$ 16
1982	87 (621)	21	44	28 $\pm$ 3 B	29 $\pm$ 1	67	38 $\pm$ 8	58 $\pm$ 10
1983	95 (779)	46	56	62 $\pm$ 2 A	70 $\pm$ 1	69	79 $\pm$ 5	98 $\pm$ 2
1984	110 (922)	21	34	30 $\pm$ 3 B	32 $\pm$ 1	93	55 $\pm$ 9	90 $\pm$ 7

<sup>a</sup> Number of broods on the study area (maximum number of young seen).

<sup>b</sup> Estimate derived from the number of young seen.

<sup>c</sup> Estimate assuming an initial brood size of 10 young (Savard 1988b).

<sup>d</sup> Number of broods used for the Mayfield estimates.

<sup>e</sup> Similar letters indicate that the estimate did not differ significantly at the  $P = 0.05$  level.

TABLE 3. Estimates of mortality of Bufflehead ducklings ( $\pm$ SE). All estimates are for 43 days after hatching. Mortality is expressed in %.

Year	Mayfield estimate							
	Direct estimate			Weighted (on a duckling basis)		Unweighted (on a brood basis)		
	$n^a$	% dead A <sup>b</sup> B <sup>c</sup>		Adjusted for age difference	Not adjusted for age difference	$n^d$	Adjusted for age difference	Not adjusted for age difference
1980	68 (433)	32	46	38 $\pm$ 4 A <sup>e</sup>	44 $\pm$ 1	48	43 $\pm$ 8	48 $\pm$ 6
1981	75 (514)	12	25	17 $\pm$ 4 B	15 $\pm$ 1	36	21 $\pm$ 10	22 $\pm$ 5
1982	78 (541)	12	24	20 $\pm$ 4 BC	22 $\pm$ 1	49	24 $\pm$ 10	34 $\pm$ 11
1983	73 (475)	36	48	45 $\pm$ 4 A	50 $\pm$ 1	47	59 $\pm$ 9	77 $\pm$ 7
1984	74 (520)	26	35	32 $\pm$ 3 AC	37 $\pm$ 1	70	54 $\pm$ 13	91 $\pm$ 8

<sup>a</sup> Number of broods (maximum number of young seen).

<sup>b</sup> Estimate based on the maximum number of young seen.

<sup>c</sup> Estimate assuming an initial brood size of 8 young (Erskine 1972).

<sup>d</sup> Number of broods used for the Mayfield estimates.

<sup>e</sup> Similar letters indicate that the estimate did not differ significantly at the 0.05 level.

detailed analysis of the factors affecting mortality rates of both species. All subsequent analyses here are on a duckling basis unless otherwise specified.

*Effect of duckling age on mortality rates.*—Daily mortality rates of Barrow's Goldeneye and Bufflehead ducklings generally declined with duckling age (Figs. 1 and 2), but the pattern of variation differed between years. In 4 of 5 yr (1980 was the exception), daily mortality rates of Barrow's Goldeneye ducklings were highest in the first week after hatching, and declined subsequently. This decline was gradual in 1983, but in 1981, 1982, and 1984, mortality rates dropped sharply in the second week and remained similar thereafter. In 1980, fluctuations in daily mortality rates with duckling age were smaller than in other years, although the rates themselves were often higher. Patterns observed in 1980 and 1981 are less precise than in other years because surveys were less frequent.

As with Barrow's Goldeneye, daily mortality rates of Bufflehead ducklings were highest in the first week post-hatch and decreased subsequently. Again, fluctuations in mortality rates in 1980 were less dramatic than in other years, and there was an unusually high mortality in the fifth week of 1983. Variability between years in daily mortality rates for both species was highest for the first week post-hatch than for any other duckling age classes.

Because female Barrow's Goldeneyes were marked for only some of the broods we studied, we repeated the analysis for the sample of 120

marked females. We found no differences in the patterns of mortality between this subsample and the total sample. The sample of marked females, however, allowed us to estimate the loss of eggs before hatching. Egg losses were 6% ( $n = 234$  eggs) in 1982, 11% ( $n = 519$ ) in 1983, and 15% ( $n = 631$ ) in 1984.

We believe the most crucial time for duckling survival was the first week post-hatch. Even within the first week, we observed declines in mortality rates in each of the 3 yr (Fig. 3).

*Effect of hatching date on mortality rates.*—Mortality rates of Barrow's Goldeneye during the first 4 weeks of life varied significantly in some years in relation to hatching date (Fig. 4). The pattern of variation, however, differed between years. In 1980, mortality was significantly lower for broods that hatched in midseason, whereas in 1983 it was lower for early hatching broods. In 1982, late-hatching broods suffered higher mortality than midhatching broods ( $P = 0.004$ ); differences with early-hatching broods were not significant ( $P = 0.03$ ) at the adjusted Bonferroni significance level (0.02).

Mortality rates of Bufflehead ducklings did not vary significantly in relation to hatching date in any year (Fig. 5), and no clear patterns were apparent. Yearly effects tended to dominate seasonal effects on mortality rates for both species. In 1983, mortality of ducklings was higher for all hatching dates, but the pattern reversed in 1981.

*Mortality rates of Barrow's Goldeneye and Bufflehead ducklings.*—Seasonal mortality rates of

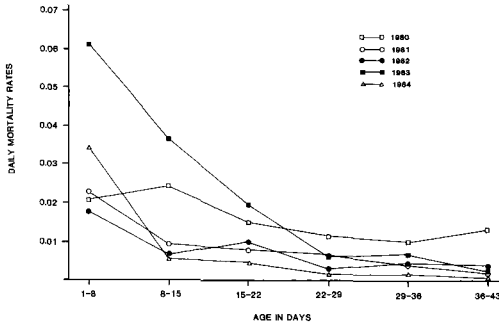


Fig. 1. Daily mortality rates of Barrow's Goldeneye ducklings in relation to duckling age.

Barrow's Goldeneye ducklings were higher than those of Bufflehead ducklings except in 1984 (Tables 2 and 3). Significant differences between species occurred in 1980 ( $P = 0.03$ ), 1981 ( $P = 0.01$ ), and 1983 ( $P < 0.01$ ).

We compared daily mortality rates of the two species for various duckling ages. There were no clear effects of duckling age on the relative mortality rates of Barrow's Goldeneye and the Bufflehead. In all five comparisons where mortality differed significantly, Barrow's Goldeneye had a higher mortality rate than Bufflehead.

Mortality rates of Barrow's Goldeneye and Bufflehead ducklings did not differ consistently in relation to hatching periods over 5 yr (Table 4). Differences in mortality rates between the species were slightly more common for early-hatching broods than for late ones.

*Mortality rates in relation to brood density.*—To assess if interactions between broods affected duckling mortality, we compared duckling mortality on lakes with single broods and on lakes with two or more broods. Because duckling mortality varied between years, we ana-

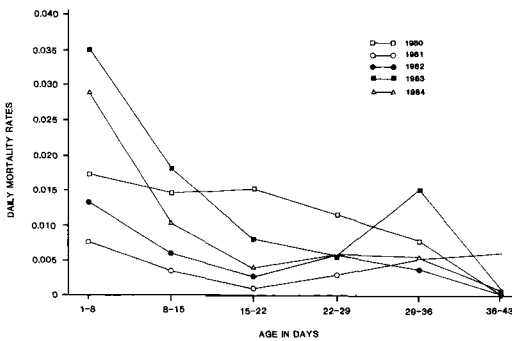


Fig. 2. Daily mortality rates of Bufflehead ducklings in relation to duckling age.

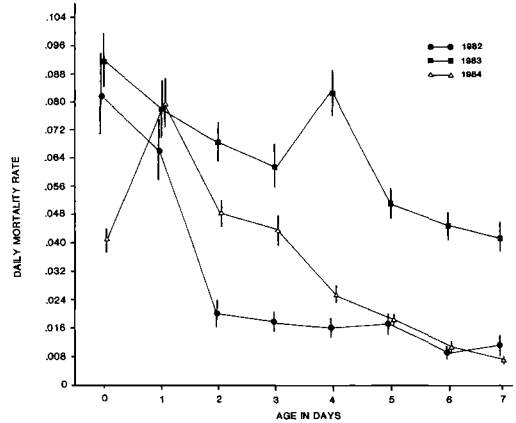


Fig. 3. Daily mortality rates of Barrow's Goldeneye ducklings during the first week post-hatch (calculated from broods of marked females only;  $\bar{x} \pm 2$  SE).

lyzed each year individually. This reduced sample sizes and thus our ability to detect differences. We compared daily mortality rates of ducklings for the first week post-hatch only, because most mortality occurred at that time, and ducklings of this age are most susceptible to intraspecific aggression. In 1984, mortality of Barrow's Goldeneye ducklings was significantly higher on lakes with several broods than on lakes with single broods (Table 5). Although no other comparison differed significantly, the mortality values found were all higher on lakes with several broods and higher for the second brood to hatch on a given lake than for the first

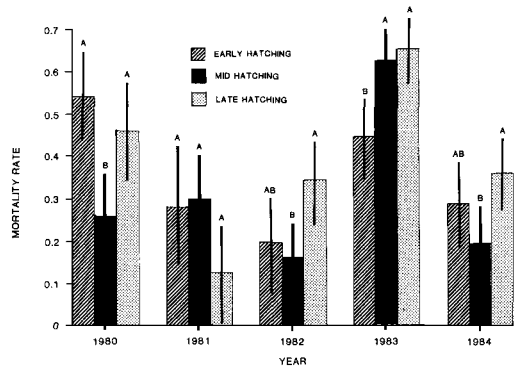


Fig. 4. Mortality estimates ( $\pm$ SE) of Barrow's Goldeneye ducklings in relation to hatching date for the first 4 weeks post-hatch. (Comparison within years only. Similar letters indicate no significant difference at  $P = 0.05$ .)

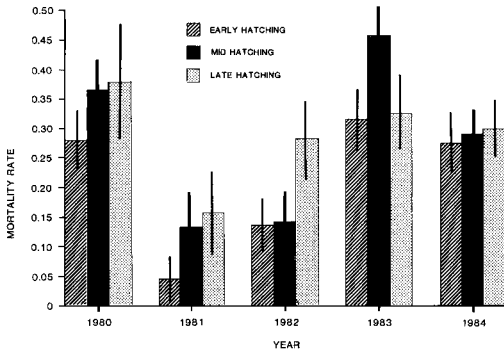


Fig. 5. Mortality estimates ( $\pm$ SE) of Bufflehead ducklings in relation to hatching date for the first 4 weeks post-hatch. (Comparison within years only. No significant difference at  $P = 0.05$  in any of the years.)

one. In 1984, there was also a tendency for higher daily mortality rates of ducklings for Bufflehead broods that shared a lake with goldeneyes ( $0.057 \pm 0.02$ ) compared with solitary broods ( $0.003 \pm 0.002$ ;  $P < 0.05$ ). Samples were too small for robust comparisons in other years.

*Effect of duckling mortality on recruitment.*—We looked at relationships between recruitment and mortality rates in Barrow’s Goldeneye. From the proportion of marked adult females returning (Savard and Eadie 1989), we estimated female mortality and calculated the expected number of unmarked females in the population (Table 6). We assumed that mortality rates were similar for marked and unmarked females. Then, the difference between the expected number of females in the population and the number actually present provides an estimate of the number of new females recruited into the population. In 1983, duckling mortality was nearly twice as high as in the three other years (Table 2), which corresponded with an unusually low recruitment in 1985 (Table 6).

DISCUSSION

*Hatching chronology.*—Hatching chronology varied among years due to the timing of spring thaw, which was related to April temperatures. In 1980, 1981, and 1982, some breeding ponds were still frozen in late April. In 1983 and 1984, all ponds were free of ice by the third week of April. More broods hatched late in 1984 than in 1983, perhaps because cold weather in early May 1984 delayed laying by some females (Ta-

TABLE 4. Differences in mortality rates<sup>a</sup> of Barrow’s Goldeneye and Bufflehead ducklings in relation to hatching period.

Year	Hatching group		
	Early	Mid	Late
1980	0.26*** <sup>b</sup>	-0.11	0.08
1981	0.25***	0.17*	-0.03
1982	0.06	0.02	0.06
1983	0.13*	0.17***	0.33***
1984	0.02	-0.09	0.06

<sup>a</sup> Mortality rates were calculated by the product method over 4 age classes (1-8, 8-15, 15-22, and 22-29 days old).

<sup>b</sup> Barrow’s Goldeneye mortality rate-Bufflehead mortality rate: \* =  $P < 0.10$ ; \*\* =  $P < 0.05$ ; \*\*\* =  $P < 0.017$ .

ble 1). Spring weather may determine the onset of laying in several species of prairie waterfowl (Hammond and Johnson 1984).

*Estimation of duckling mortality.*—Mortality estimates varied with the technique used to calculate them. Estimates expressed on a brood basis were higher and more variable than those expressed on a duckling basis as expected from statistical considerations. When the brood is the unit, a brood of 1 duckling has the same weight as a brood of 15 ducklings, whereas the brood of 15 has 15 times more weight when the duckling is taken as a unit. Thus, both estimates sometimes differed considerably. Biologically, both estimates are useful, but each has limitations. Mortality sometimes acts on whole broods (e.g. during overland movements or in territorial interactions among broods; Savard 1987), but more often mortality affects individual ducklings (e.g. bad weather, partial predation).

That the Method 1 based on duckling counts underestimates mortality is not surprising, because of the high mortality during the first few days of life. Peak mortality often occurs before the brood is sighted for the first time. However, when an average initial brood size is assumed, the direct method (2) provides estimates similar to those derived from the Mayfield method. Because broods of Barrow’s Goldeneyes and Buffleheads are easy to survey as they frequent open water, direct method (2) can be used. The method provides a good estimate of the total number of young produced in a given area. By estimating the initial number of broods in the area, one can then estimate duckling mortality for a given area. Because of significant differences in mortality rates of ducklings with age, we recommend the product-moment method for estimating mortality with the Mayfield method.

TABLE 5. Comparison of daily mortality rates ( $\pm$ SE) of Barrow's Goldeneye ducklings in the first week after hatching in relation to the presence of other Barrow's Goldeneye broods. Number of broods is in parentheses.

Year	Solitary brood	1st brood to hatch	2nd brood to hatch	$\geq 2$ Barrow's broods
1982	0.018 $\pm$ 0.010 (14)	0.000 (4)	0.036 $\pm$ 0.030 (4)	0.023 $\pm$ 0.015 (7)
1983	0.045 $\pm$ 0.015 (14) <sup>a</sup>	0.044 $\pm$ 0.021 (21)	0.066 $\pm$ 0.031 (14)	0.088 $\pm$ 0.022 (17) <sup>a</sup>
1984	0.01 $\pm$ 0.008 (12) <sup>b</sup>	0.024 $\pm$ 0.016 (14)	0.067 $\pm$ 0.028 (14)	0.057 $\pm$ 0.018 (17) <sup>b</sup>

<sup>a</sup> Difference between solitary and  $\geq 2$  broods are statistically significant only at  $P < 0.10$ .

<sup>b</sup> Differences between solitary and  $\geq 2$  broods are statistically significant at  $P < 0.05$ .

Unweighted estimates, which were particularly affected by age difference in mortality rates, provided overestimates of mortality.

Mortality of both species' ducklings was higher in 1983 than in the four other years. We suspect that the cold temperature coupled with constant rain during the peak hatching period in 1983 contributed. Bad weather can depress the survival rate of precocial birds markedly either directly (Hilden 1964, Mendenhall and Milne 1985) or through food reduction (Erikstad and Andersen 1983).

Mortality was highest in the first week post-hatch for both species as reported in other waterfowl (Patterson 1982, Hill and Ellis 1984, Mendenhall and Milne 1985). At hatching, ducklings are vulnerable to predators, bad weather, and intraspecific aggression (Makepeace and Patterson 1980). Bengtson (1972), Koskimies and Lahti (1964), and Hilden (1964), found that mortality of young ducklings increased in bad weather. Sjöberg and Danell (1982) found that aquatic insect availability was reduced in adverse weather, and Hill and Ellis (1984) showed that ducklings are inefficient divers at hatching and depend on small prey near the surface. Within the first week of life, we found especially high mortality in the first 2 days post-hatch. Travel from the nest site to the water (up to 2 km away) may contribute. Also, territorial behavior among females may cause duckling losses (Petrie 1984, Savard 1987). As ducklings get older, they are better equipped to escape attacks by territorial females. The high daily mortality rate (0.04–0.09) of ducklings in the first 2 days has important implications for studies of mortality.

We found no consistent pattern of an effect of hatching date on mortality rates among years. Bengtson (1972) found a decrease in survival for late-hatching Barrow's Goldeneye in Iceland. In some years, mortality rates were higher later in the season for both Barrow's Goldeneye and the Bufflehead, but this trend was not sta-

tistically significant. Other factors, unrelated to hatching date had greater effects on duckling mortality. Our definitions of early and late hatching (first third and last third of the season) may not have reflected ecological divisions. Data on the effects of intra- and interspecific aggression on mortality suggest an advantage of early hatching. This advantage, however, could be negated by other factors in some years. Some studies suggest that hatching date affects duckling survival (Grice and Rogers 1965, Ringelman and Longcore 1982), while other studies do not (e.g. Dzubin and Gollop 1972, McAuley 1986). Fluctuating directional selection based on hatching date has been demonstrated in the Great Tit (*Parus major*).

*Comparison of mortality rates of Barrow's Goldeneye and Bufflehead ducklings.*—Barrow's Goldeneye ducklings suffered higher mortality than Bufflehead ducklings in 4 of 5 yr. Both species frequent similar habitat and have similar breeding behavior and ecology (Savard 1982, 1984; Gauthier 1985). Several factors might contribute to the higher mortality of goldeneye ducklings:

1. Barrow's Goldeneyes often nest farther from brood-rearing ponds than Buffleheads do, because of lower nest-site availability (Erskine 1972, Peterson and Gauthier 1985, Gauthier and Smith 1987). The longer overland journey to water by Barrow's Goldeneyes may cause mortality directly or may weaken ducklings and increase their vulnerability once they reach the pond.
2. Goldeneye ducklings are twice the size of Bufflehead ducklings and thus have greater daily energy requirements (Kendeigh 1970, King 1973).
3. Aggressive neglect (Ripley 1961) could contribute to this higher mortality. Barrow's Goldeneye females spend on average 12% of their time in aggressive intra- and interspecific interactions, leaving their young unprotected during these events (Savard 1988a).

TABLE 6. Relationship between Barrow's Goldeneye duckling mortality (%) and recruitment into the breeding population.

Year $x$	% of marked birds returning <sup>a</sup>	No. of unmarked females in year $x - 1$	Expected no. of unmarked females in year $x$	No. of unmarked females in year $x$	New females in year $x$	Mortality in year $(x - 2)$ <sup>b</sup>
1983	89 (36)	165	147	233	86	31
1984	71 (82)	233	164	264	100	28
1985	66 (105)	264	172	184	12	62
1986	66 (119)	184	121	200	79	30

<sup>a</sup> Number of birds marked the previous year ( $x - 1$ ) is in parentheses (Savard and Eadie 1989).

<sup>b</sup> Weighted estimate adjusted for age differential in mortality (over a 6-week period). Mortality rate 2 yr before, as female goldeneye recruit into population when 2 yr old (Eadie and Gauthier 1985).

Comparatively, female Buffleheads spend on average only 5% of their time in aggressive interactions (Savard 1986).

4. Intraspecific aggression causes more duckling deaths in Barrow's Goldeneye than in the Bufflehead. Bufflehead ducklings are rarely killed by conspecifics (Erskine 1972; Donaghey 1975; Gauthier 1985, 1987), but such deaths are common in Barrow's Goldeneye (Bengtson 1972, Savard 1988a).

In 1984, levels of mortality were similar in ducklings of both species. We suggest that this was due to interspecific aggression by Barrow's Goldeneye, which were at their highest density (Savard 1988b). Survival of Bufflehead ducklings was significantly lower in 1984 on lakes with Barrow's Goldeneye broods. The interspecific aggressiveness of Barrow's Goldeneye is well known and often results in duckling death (Sugden 1960, Robertson and Stelfox 1969, Bengtson 1972, Einarsson 1985, Savard and Smith 1987, Savard 1988a). Inter- and intraspecific aggression within the genus *Bucephala* may be a response to limited food resources (Savard 1982, Savard and Smith 1987). Barrow's Goldeneye and Bufflehead ducklings overlap in size due to hatching asynchrony between broods; older Buffleheads are similar in size to younger goldeneyes, and potentially compete for the same food resources. Food limitation restricts reproductive success of some species of waterfowl (Hunter et al. 1984, Pehrsson 1973).

There was higher mortality of Barrow's Goldeneye ducklings on ponds with several broods than on those with single broods. Also, newly arrived broods on a lake tended to suffer higher mortality than previously established broods. Similar patterns have been observed in Shel-

ducks (Williams 1974, Makepeace and Patterson 1980, Pienkowski and Evans 1982), and elsewhere in Barrow's Goldeneyes (Einarson 1988) and in Buffleheads (Gauthier 1987). Established territorial females should have an advantage over arrivals with newly hatched broods (Savard 1987, Petrie 1984, Figler and Einhorn 1983), because they regained some of the weight lost during incubation. Newly arrived broods could also belong to less experienced first-time breeders, who tend to breed later (Afton 1984, Gauthier 1989) and may be less efficient in protecting their young. Goldeneye females are highly philopatric (Dow and Fredga 1983, Savard and Eadie 1989, Gauthier 1990), thus the population size of an area should be influenced by the number of young produced in that area. This low dispersal has important management applications.

The methodological difficulty of measuring productivity in waterfowl populations is apparent in our results. We believe that territorial aggression should be considered in the management of Barrow's Goldeneye and Bufflehead populations. Efforts to reduce nest predation and increase reproductive success could be negated in years when density-dependent mortality factors may operate. It appears that aggressiveness in Barrow's Goldeneye has a greater intraspecific than interspecific effect, which allows Buffleheads and Barrow's Goldeneye to coexist (Pianka 1978).

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