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A COMPARISON OF THE CHARACTERISTICS AND FATE OF BARROW'S GOLDENEYE AND BUFFLEHEAD NESTS IN NEST BOXES AND NATURAL CAVITIES

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birds in North America and Europe use boxes (Eadie et al. 1998).

Nest boxes are also valuable for conservation programs aimed at augmenting target species' abundance, having increased populations for 22 of 23 studied species (Eadie et al. 1998). Highly successful programs have included Eastern Bluebirds (*Sialia sialis*, Gowaty and Bridges 1991), Wood Ducks (*Aix sponsa*, Nichols and Johnson 1990), and American Kestrels (*Falco sparverius*; Hamerstrom et al. 1973).

Despite the utility of nest boxes for birds, researchers, and managers, the behavior and demographics of birds nesting in boxes are likely to differ from those of birds nesting in natural sites (Nilsson 1986). Nest box studies may be biased in two important ways: they often reduce nest predation levels to a fraction of their natural levels, and they reduce ectoparasite loads when researchers consistently remove old nests at the end of each breeding season (Møller 1989). In fact, it has long been believed that cavity nesters have higher nesting success rates than do ground-nesting birds (Lack 1954), a belief that has arisen primarily from the results of nest box studies. Some now argue that this belief may be inaccurate, as studies of populations using natural cavities have begun to show (Purcell et al. 1997). Nilsson (1984a) found nest predation to be 62% lower in nest boxes than cavities for five passerine species, and nesting success in natural holes was nearly identical to that of open-nesting species (Nilsson 1986). Other studies have reported that nest-box populations experience lower rates of predation, lay larger clutches (Robertson and Rendell 1990), and fledge more young (Nilsson 1986, Kuitunen and Aleknonis 1992) than populations in natural sites.

Nest boxes may alter other key ecological processes such as population dynamics and intraspecific social interactions like conspecific brood parasitism (Møller 1989, Eadie et al. 1998). The addition of artificial nesting structures may also produce artificially high densities of breeding birds, which may have negative influences on other species' breeding ecology, such as increasing competition for nest sites. In some species, these changes may even lead to precipitous declines in productivity and result in population instability and decline (Eadie et al. 1998). More information on birds nesting in cavities will allow further understanding of the factors that regulate populations of secondary cavity nesters and influence community structure (Purcell et al. 1997).

Barrow's Goldeneye (*Bucephala islandica*) and Bufflehead (*B. albeola*) are cavity-nesting waterfowl that have received considerable attention in studies using boxes (Gauthier 1985, Savard 1986, Eadie 1989, Thompson 1996). However, little is known about the nesting ecology of these birds in natural cavities. This is also true for Common Goldeneyes (*B. clangula*), which now nest predominately in nest boxes across their range in northwestern Europe (Eriksson 1982, Fredga and Dow 1984). The purpose of this study was to compare nest characteristics, fate, and sources of predation of Barrow's Goldeneyes and Bufflehead breeding in nest boxes and natural cavities.

METHODS

STUDY AREA

This study was conducted between April and September, 1997–1999, on approximately 200 km^2 in the Cariboo Parklands, 45 km west of Williams Lake, British Columbia (52°07′N, 122°27′W). The area is characterized by a rich mixture of naturally fragmented deciduous and

TABLE 1. Nest box dimensions and number of boxes made available each year to Barrow's Goldeneye and Bufflehead at Riske Creek, British Columbia, Canada, 1997–1999.

Species	Number of boxes available	Length × width × height (cm)	Volume (L)	Floor area (cm^2)	Entrance size (cm)
Barrow's Goldeneye					
	139	39 × 25 × 26	25.4	650	11 × 13
	71	50 × 25 × 28	35.0	700	11 × 10
	24	41 × 25 × 26	26.7	650	12 × 12
Bufflehead					
	43	28 × 15 × 15	6.3	225	7 × 7
	54	32 × 18 × 20	11.5	360	8 × 8
	21	28 × 18 × 18	9.1	324	8 × 8

Females were captured on the nest or wetland, banded, and marked with plastic nasal tags of different shapes and colors for individual identification (Savard 1986). Known multiple observations for the same female in successive years were excluded from the analysis, although some birds remained unmarked (fewer than 20% each year) and may have been included more than once.

NATURAL CAVITIES

Two techniques were used to locate natural cavity nest sites in April and May of each year. First, thorough searches were conducted through forest stands surrounding lakes that contained paired birds. Searches were performed along ad hoc transects with 2–4 persons spread out at ca. 10-m distances, walking perpendicular from the water's edge for ca. 500 m. Second, natural cavity nests were located by following females returning to nest sites to incubate after feeding. This method proved to be more effective in locating cavity nests ($n = 31$ of 41 goldeneyes, and 65 of 100 Bufflehead cavity nests) and had the advantage of being unbiased with respect to our choice of habitat types in which to conduct transect searches. However, it must be acknowledged that this search technique can be biased toward successful females. Since most box-nesting females carried individual nasal tags, we directed our efforts at females known not to be incubating in boxes. Although some deserted and early-failing nests may have gone undetected, we feel confident that we located the nest sites (boxes or cavities) of over 90% of the breeding pairs for both species each year because few broods of unknown origin appeared on ponds at hatching.

Cavities were accessed using ladders, tree spikes, and climbing ropes, and were inspected using mirrors and flashlights. Two of the 41 goldeneye cavity nests had "open-top" entrances located in trees with broken tops, and were included in the analysis. No Bufflehead nests were found in open-top cavities.

PHYSICAL CHARACTERISTICS OF NEST SITES

We measured the following characteristics of each nest box and natural cavity: tree species, tree height, box or cavity height in tree, entrance hole dimensions (height and width), and distance of nest to the nearest water. We also measured the distances of nest sites from forest edge. Internal cavity measurements (depth, length, and width of floor) were measured to the nearest cm with measuring tapes, and cavity vol-

TABLE 2. Physical characteristics (means 6 SE) of active Barrow's Goldeneye and Bufflehead nest sites in nest boxes and cavities, 1997–1999. Available but unused nest sites were not included in the analysis. Nest sites used more than once were included only once.

	Barrow's Goldeneye		Bufflehead	
	Cavity	Nest box	Cavity	Nest box
n	41	174	100	46
Tree species used (%)				
Aspen	72	66	81	91
Douglas-fir	23	9	12	2
Lodgepole pine	5	22	7	7
White spruce	0	3	0	0
Tree height (m)	26.2 6 1.2	13.3 6 0.3	14.6 6 0.8	13.6 6 0.7
Nest height (m)	12.0 6 0.8	3.8 6 0.9	6.6 6 0.4	3.9 6 0.2
Distance from water (m)	89.7 6 13.0	41.3 6 3.4	37.1 6 5.5	24.5 6 4.5
Distance from edge (m)	36.3 6 24.9	3.4 6 0.5	3.5 6 1.0	2.6 6 0.7
Entrance size (cm)	14 3 12	11 3 12	9 3 9	8 3 8
Nest site volume (L)	16.0 6 0.1	28.6 6 0.4	5.5 6 0.1	8.7 6 0.1
Nest floor area (cm^2)	299 6 16	641 6 6	189 6 4	293 6 4

tion on daily egg-laying rates in each nest site was not collected in this study, and therefore, we were unable to calculate accurate nest parasitism rates. However, since females of both species typically lay 8–10 eggs (Gauthier 1985, Eadie 1989), we considered nests containing more than 10 eggs to have been parasitized. Although this technique likely produced conservative estimates of nest parasitism, it allowed us to compare minimum estimates between nest types.

STATISTICAL ANALYSES

Average values of physical characteristics of nest sites did not differ significantly between years, so data were pooled. Two-tailed independent *t*-tests were used to compare the physical characteristics of box nests to cavity nests. Within a species, and nest type, there was no annual variation in clutch sizes, so data were pooled across years for analysis of each nest type. Hatching dates did not differ between box nests and cavity nests among the three years, and these data were also pooled across years for subsequent analysis. Multiway contingency data analysis (PROC CATMOD, SAS 2000) was used to examine associations among nest fate, nest type, and year. Backward elimination techniques were used to select the best log-linear model during this analysis. Within-year comparisons of nest fates between nest types were made using chi-square tests with Bonferroni adjustments (*P* 5 0.05/*n* comparisons). Values reported are means 6 SE. A significance level of *P* , 0.05 was used throughout the analyses.

RESULTS

PHYSICAL CHARACTERISTICS OF NEST SITES

Physical attributes of box nests and cavity nests are presented in Table 2. Natural nest cavities used by goldeneyes were twice as far from water (t_{191} 5 25.1, *P* , 0.001), farther from forest edge (t_{191} 5 27.9, *P* , 0.001), and located higher in trees (t_{191} 5 218.1, *P* , 0.001) than box nests. The mean nest volume of goldeneye cavities was only about half the size of box nests (t_{312} 5 10.6, *P* , 0.001), as was the floor area (t_{312} 5 20.5, *P* , 0.001).

Nest cavities used by Bufflehead were also higher in trees (t_{200} 5 211.7, *P* , 0.001) than box nests (Table 2). Although Bufflehead cavity nests were located farther from water than box nests (t_{200} 5 22.8, *P* , 0.01), distances from the forest edge were similar (t_{200} 5 21.6, *P* , 0.1). Bufflehead cavity nests had a smaller nest site volume (t_{200} 5 16.3, *P* , 0.001) and floor area (t_{200} 5 16.9, *P* , 0.001) than box nests. For both species, active natural cavities were most commonly found in aspen and Douglas-fir trees. Both species most commonly used nest boxes on aspen trees.

CLUTCH SIZES

Mean clutch sizes of goldeneyes were significantly larger in box nests than in cavity nests (box nests: 10.5 6 0.2 eggs; cavity nests: 7.5 6 0.4; t_{239} 5 6.3, *P* , 0.001), but for Bufflehead, mean clutch sizes were similar in both nest types

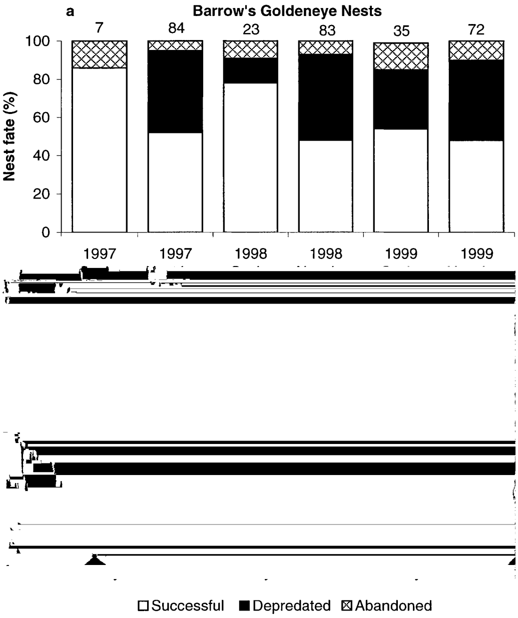

FIGURE 1. (a) Fates of Barrow's Goldeneye nests (successful, depredated, or abandoned) in boxes and natural cavities and (b) sources of nest predation from 1997–1999, at Riske Creek, British Columbia, Canada. Numbers above columns represent sample sizes.

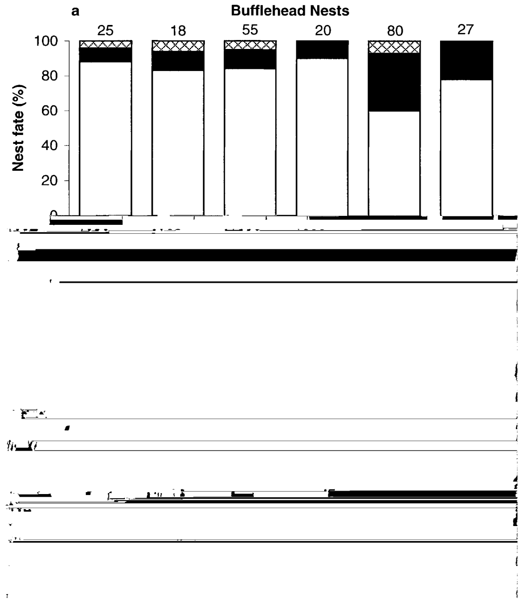

FIGURE 2. (a) Fates of Bufflehead nests (successful, depredated, or abandoned) in boxes and natural cavities and (b) sources of nest predation from 1997–1999, at Riske Creek, British Columbia, Canada. Numbers above columns represent sample sizes.

(box nests: 8.4 ± 0.3 eggs; cavity nests: 8.5 ± 0.2; $t_{179} = -0.6$, $P > 0.4$).

Twenty-five percent (60 of 234) of goldeneye box nests contained more than 10 eggs, compared to only 5% of cavity nests (2 of 41) indicating that nest parasitism was higher in box nests ($\chi^2_2 = 8.9$, $P < 0.02$). For Bufflehead, only 8% (9 of 118) of nests in boxes had more than 10 eggs, compared to 17% (17 of 100) of nests in cavities ($\chi^2_2 = 4.5$, $P < 0.03$).

HATCHING DATES

There were no differences between mean Julian hatching dates of nests in boxes compared to nests in cavities, for either species. The mean Julian hatching date for goldeneye eggs in box nests was 165.9 ± 1.4 (14 June) and 166.4 ± 2.4 (15 June) in cavity nests ($t_{191} = -0.3$, $P > 0.6$). Bufflehead had mean Julian hatching dates of 169.3 ± 0.6 (18 June) for eggs in box nests, and 169.5 ± 1.6 (18 June) for eggs in cavity nests ($t_{109} = -0.2$, $P > 0.7$).

NEST FATES

The log-linear model examining associations between Barrow's Goldeneye nest fate, nest type, and year showed interactions between nest fate and nest type ($\chi^2_2 = 7.3$, $P < 0.05$), and nest fate and year ($\chi^2_2 = 12.4$, $P < 0.01$). Further analysis indicated that nest fates did not differ significantly among box nests throughout the study, nor did they differ among cavity nests between 1997 and 1998 (Fig. 1a). However, nesting success in cavities dropped from 86% in 1997 and 78% in 1998 to 54% in 1999, as a result of higher levels of nest predation. Goldeneye nests in natural cavities had significantly higher nesting success rates than those in boxes in 1997 and 1998 (1997: $\chi^2_2 = 7.7$, $P < 0.02$; 1998: $\chi^2_2 = 8.6$, $P < 0.01$). However, no differences in nest fates were detected in 1999 ($\chi^2_2 = 1.2$, $P > 0.4$; Fig. 1a).

For Bufflehead, the log-linear model showed an interaction between nest fates and year ($\chi^2_2 = 14.8$, $P < 0.01$). This was a result of increased

0.2, $P > 0.8$; 1998: $\chi^2_2 = 1.1$, $P > 0.5$; 1999: $\chi^2_2 = 5.1$, $P = 0.07$).

Goldeneye nests in boxes were less successful than Bufflehead nests in boxes through all three years of the study, (1997: $\chi^2_2 = 6.5$, $P < 0.05$; 1998: $\chi^2_2 = 10.9$, $P < 0.01$; 1999: $\chi^2_2 = 7.6$, $P < 0.05$). There were no differences in cavity-nest fates between the two species over the three years (1997: $\chi^2_2 = 1.8$, $P > 0.3$; 1998: $\chi^2_2 = 0.4$, $P > 0.7$; 1999: $\chi^2_2 = 1.3$, $P > 0.4$) and both species experienced markedly higher levels of cavity predation in 1999 (Fig. 1a, 2a).

SOURCES OF PREDATION

The types of predators that preyed on goldeneye nests in boxes differed from those responsible select smaller holes may experience reduced predation risk and competition with larger species (Moeed and Dawson 1979, Peterson and Gauthier 1985).

Most comparative studies of box versus cavity nesters have found lower rates of predation and higher fledging success in box nests than in natural sites; examples include the European Starling, Great Tit, Blue Tit, Nuthatch (*Sitta europaea*; Nilsson 1975), and Tree Swallow (Rendell and Robertson 1993). These results are opposite to ours, which we suspect is due primarily to the presence of bears at our site, a major box predator in our study that has not been reported by others. Bears may be unusual nest-box predators and thus limit the generality of this result. An earlier study of Common and Barrow's Goldeneyes, located only 70 km southeast of our study, found little to no bear depredation of box nests (J. Eadie, pers. comm.).

CLUTCH SIZE

Clutches in Barrow's Goldeneye box nests were significantly larger than in cavity nests. Two plausible explanations exist for this result. First, our results suggest that increased levels of conspecific nest parasitism may occur in boxes (also see Eadie 1989), and this may be attributed to their increased degree of conspicuousness. Second, all natural cavities were smaller than boxes and thus the larger basal area of boxes may allow for larger clutches (Nilsson 1984a).

The more likely explanation is that larger clutch sizes in box nests resulted from increased levels of conspecific nest parasitism (Eadie 1989). Like predators, parasitic females can more easily detect artificial nest sites, and our conservative estimates indicated parasitism to be 20% higher in box nests. Previous studies of goldeneyes estimated nest parasitism to be 8% higher in box nests than in cavity nests, and 15–61% higher in Wood Duck box nests (Eadie et al. 1998). Other species that have been reported to experience higher conspecific brood parasitnest structures differs considerably from that in natural cavities. In contrast, we recorded few physical or biological differences for Bufflehead. Unnaturally low nest predation in nest boxes of other studies appears to be an artifact of nest box designs (Møller 1989). In our study the design and placement of goldeneye nest boxes contributed to artificially high predation rates.

Nest boxes are an important management tool for species experiencing drastic population declines, particularly in areas under intensive forest harvesting, where the availability of natural cavities is limited (Eadie et al. 1998). Nest-box programs are normally considered an effective

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