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ORIGINAL ARTICLES

Monitoring nest box use by cavity-nesting ducks on acid-stressed lakes in Ontario, Canada

Donald K. McNicol, Russel A. Walton & Mark L. Mallory

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Nest boxes erected on 75 small lakes near Sudbury, Canada were monitored annually between 1987 and 1996 to measure the response of cavity-nesting waterfowl to changing chemical and biological conditions of their nesting habitat from the effects of acidification. Nest boxes were used mainly by common goldeneyes *Bucephala clangula* and hooded mergansers *Lophodytes cucullatus*, although a few were occupied by common mergansers *Mergus merganser* and wood ducks *Aix sponsa*. Use by hooded mergansers and wood ducks increased from 1987 to 1996, while use by goldeneyes remained stable. Patterns in nest box use reflected general population trends observed in the area. Interspecific nest parasitism also increased to 33% of all nests in 1996, probably a consequence of more hooded merganser nests. Clutch size, nesting and hatching success of goldeneye and hooded merganser eggs were similar to values reported for conspecifics in other studies. Overall, interspecific nest parasitism did not appear to affect the nesting success of either species. Although goldeneyes nested more often on fishless lakes early in the study, overall, fish presence, pH-value, lake area and connectivity were not related to nesting attempts or measures of nesting success for either species. Therefore, it is believed that for common goldeneyes and hooded mergansers currently breeding in the acid-stressed Sudbury area, habitat characteristics have little influence on nest site selection, particularly when compared to their documented effects on brood-rearing. However, monitoring of nest boxes may prove a less expensive method than aerial surveys to track population responses of cavity-nesting species to chemical improvements.

Key words: acid rain, biomonitoring, cavity-nesting waterfowl, nest boxes

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In response to widespread evidence of ecosystem damage caused by acid precipitation (reviewed in Schindler 1988, Longcore, Boyd, Brooks, Haramis, McNicol, Newman, Smith & Stearns 1993), chemical and biological monitoring programs have been initiated in eastern Canada to determine the rate and extent of recovery of aquatic ecosystems following reductions in emissions of acidifying pollutants (see Clair, Dillon, Ion, Jeffries, Papineau & Vet 1995). One such program, undertaken by the Canadian Wildlife Service (CWS), monitors waterfowl and their breeding habitats (mostly small lakes and wetlands) in Ontario, including the area around Sudbury (McNicol, Kerekes, Mallory, Ross & Scheuhammer 1995b). The Sudbury region has a history of degradation from acid precipitation due to historically high local emissions, but improvements in the water quality of area lakes have been observed following immense reductions in local sulphur emissions since the 1970s (e.g. Keller, Pitblado & Carbone 1992, McNicol & Mallory 1994). More importantly, recent evidence suggests that corresponding improvements have also occurred in species richness and abundance of aquatic biota at lower trophic levels in certain acid-damaged ecosystems (e.g. fish, Gunn & Keller 1990; macroinvertebrates, Griffiths & Keller 1992; phytoplankton, Nicholls, Nakamoto & Keller 1992; zooplankton, Locke, Sprules, Keller & Pitblado 1994). However, relatively little is known about responses among predators at higher trophic levels, especially wildlife.

Because waterfowl rely on components of the food chain affected by acid precipitation (McNicol, Bendell & Ross 1987a, McNicol & Wayland 1992, Longcore et al. 1993), they are useful indicators of biological responses to chemical recovery (McNicol et al. 1995b). Piscivorous waterfowl, such as common mergansers *Mergus merganser*, rely on fish populations for food, and thus as these populations return to or improve in lakes affected by acid precipitation, fish-eating species should benefit directly (McNicol, Mallory & Wedeles 1995c). Insectivorous waterfowl are also useful indicators, but the effects vary among species and lake types. In some situations, these species benefit from the return of acid-sensitive invertebrate prey (hence increased diversity and quality of prey) to lakes as chemical conditions improve. However, because fish also compete for these prey (McNicol & Wayland 1992), some insectivorous waterfowl, e.g. common goldeneye *Bucephala clangula* may find conditions less suitable as fish return to certain lakes following recovery (McNicol et al. 1995c, McNicol, Ross, Mallory & Brisebois 1995d).

As part of the biomonitoring program conducted in Ontario, CWS initiated a study in 1986 to monitor use of nest boxes by four species of cavity-nesting waterfowl, i.e. common goldeneyes, hooded mergansers *Lophodytes cucullatus*, common mergansers and wood ducks *Aix sponsa*, in the acid-stressed Wanapitei area northeast of Sudbury. We erected nest boxes on a variety of lakes to satisfy several objectives. In the short term, the nest box program supported research aimed at answering several discrete questions on brood movements and reproductive effort of females in relation to habitat quality (Mallory, Weatherhead, McNicol & Wayland 1993, Mallory, McNicol & Weatherhead 1994, Wayland & McNicol 1994). Our long-term goals were: a) to determine whether nest box occupancy patterns were similar to known trends in local waterfowl breeding populations, b) to establish baseline information on the nesting biologies of cavity-nesting waterfowl in the area, c) to determine habitat preferences for each cavity-nesting species, and d) to document whether changes in nest site selection occurred over this time period and whether these changes were related to changing lake chemistries. In this paper, we report results from the first nine years of the study, and we evaluate the effectiveness of using nest boxes as tools for monitoring biological recovery of lakes from the effects of acidification.

Study Area

The 460 km² Wanapitei study area, described by McNicol et al. (1987a, 1995d) and McNicol, Mallory & Kerekes (1996), is located 50 km northeast of Sudbury (46°45'N, 80°50'W). Many of the 378 small lakes and wetlands (<20 ha) in this area have been heavily affected by local smelting emissions from Sudbury, resulting in a high proportion of acidic lakes lacking fish and acid-sensitive invertebrates (Bendell & McNicol 1987, 1995a, McNicol et al. 1987a). This has created a broad range of breeding habitat for both piscivorous and insectivorous waterfowl (McNicol et al. 1996). Chemical recovery of damaged lakes is presently occurring in the Sudbury region (e.g. Keller et al. 1992), and specifically in the Wanapitei study area (Mallory, McNicol, Cluis & Laberge 1996) at a more accelerated rate than elsewhere in eastern Canada (McNicol et al. 1995d). Of the roughly 160 lakes

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monitored by CWS in the Wanapitei study area, which span a broad range of habitat and chemical characteristics, nest boxes were established on a subset of 75 primarily smaller lakes (81% < 8 ha) important as breeding habitat for waterfowl (McNicol et al. 1987a). Nest box lakes were selected to represent the range of existing fish status (presence/absence) and acidity (pH-value) categories (see Table 1 for distribution of pH and fish presence/absence; see also McNicol et al. 1996).

Methods

Nest boxes

All nest boxes were built from 1.3 cm thick plywood (dimensions 22 × 25 × 47 cm) with doors opening on the side. Interiors were painted black, with 0.5 cm wire mesh attached inside the box under the oval-shaped entrance hole (dimensions 13 × 10 cm). Roughly 2.5 cm of wood chips were placed in the bottom of each box; wood chips were not replaced annually. Exteriors were light brown initially, due to treatment with linseed oil preservative, but darkened over time. Boxes were 'highly visible' (Semel, Sherman & Byers 1988), situated along the shoreline and positioned facing open water on live conifers (red pine *Pinus resinosa* (31), jack pine *P. banksiana* (18), white pine *P. strobus* (16), white spruce *Picea glauca* (6), black spruce *P. mariana* (3), and eastern white cedar *Thuja occidentalis* (1)). We measured the direction boxes faced by taking compass bearings at the box entrance; overall, 13 boxes faced east (45° - 134°), 29 faced south (135° - 224°), 25 faced west (225° - 314°), and 8 faced north (315° - 44°). The distribution of nest boxes was also measured to control for possible interference effects among nesting females by calculating the number of lakes with boxes within 500 m. Table 2 summarizes the general characteristics of nest boxes (for a detailed description of each box, see McNicol et al. 1996).

In May 1986, 49 nest boxes were first erected, with additions of 22 boxes in July 1988, three boxes in August 1989, and one box in May 1993. Only one nest box was erected on each lake. Due to boxes falling down or box doors being open, between 46 and 71 boxes were available to ducks each year from 1987 to 1996 (see McNicol et al. 1996).

Box use and nest fate

Nest boxes were usually visited twice each year: during egg-laying or incubation in mid May, and after hatch in late June. In 1989 and 1990, visits were more frequent (as often as every five days) as part of other studies (Mallory et al. 1994, Wayland & McNicol 1994). No nest boxes were checked in 1991. A nest box containing ≥1 egg of any of the four species was considered a nesting attempt. In cases of interspecific nest parasitism, if the host species was unknown we assumed the species with the greater number of eggs was the occupant. We removed most egg shell fragments and down from boxes during the final visit each year.

We considered a nesting attempt successful if ≥1 egg hatched. Unsuccessful nesting attempts were apportioned into three loss categories: 1) dump nests, where eggs possibly from several females, were never incubated (usually no down was present); 2) abandoned nests, where females did not complete incubation; and 3) depredated nests which included three instances where female common goldeneyes were killed by predators while on the nest. Six goldeneye nests abandoned due to human interference in 1989 (1) and 1990 (5) were excluded from analyses of nesting success. No incidences of human-caused losses were reported for other species. Total numbers of eggs laid and hatched each year by a species included eggs laid in another species' nest. We defined hatching success as the percentage of eggs in a clutch that hatched, and we calculated it only for successful nests. We excluded nests with unknown fates from analyses of nesting success.

Habitat characteristics

With the exception of common mergansers, the other cavity-nesting species are primarily insectivores during the breeding season, although hooded mergansers often include fish in their diet (McNicol, Blancher & Bendell 1987b, Bendell & McNicol 1995b). Because fish compete with waterfowl for food, fish presence or absence is a reliable indicator of macroinvertebrate availability for insectivorous species (Eriksson 1983,

Table 1. Distribution of 75 nest box lakes according to pH-categories and fish status relative to all biomonitoring lakes in the Wanapitei area (N = 157, in parentheses).

pH-category	Lakes with fish	Lakes without fish
pH < 5.0	2 (2)	22 (37)
5.0 ≤ pH ≤ 6.3	21 (42)	11 (35)
pH > 6.3	15 (33)	4 (8)
Total	38 (77)	37 (80)

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Table 2. General characteristics of nest boxes and study lakes (N = 75) in the Wanapitei area.

Variable	Mean (SE)	Minimum	Maximum
Height of box entrance from ground (m)	4.24 (0.04)	2.74	4.82
Distance from box entrance to water (m)	4.06 (0.43)	0	21.00
Height of tree base from water (m)	1.10 (0.12)	0	5.00
Circumference of tree at breast height (m)	0.98 (0.03)	0.30	2.0
pH	5.61 (0.10)	4.25	7.31
Open water area (ha)	6.7 (1.2)	0.6	86.0
Lakes[1] within 500 m	2.6 (0.2)	0	9
Lakes with nest boxes within 500 m	1.0 (0.1)	0	5

[1] Waterbody with open water area ≥ 0.4 ha

Bendell & McNicol 1987, McNicol & Wayland 1992, McNicol, Bendell & Mallory 1995a). Fish presence was determined previously using baited minnow traps set in the littoral zone of each lake (see McNicol et al. 1996); results showed that 38 lakes contained fish, while 37 lakes were fishless (Table 1). Also, previous work suggested that lake area and connectivity might influence nest site selection (McNicol et al. 1987a, Mallory et al. 1993). As such, we measured open water area (ha) and the number of wetlands within 500 m of study lakes from aerial photographs (scale 1:15,840) (Table 2).

Because the nest box program was designed to monitor the biological response of waterfowl to changing lake acidity, we used pH as our main chemical variable (see Table 1). We collected mid-lake water samples, usually after fall turnover (see McNicol & Mallory (1994) for methodology). Although many local lakes are improving chemically (see Mallory et al. 1996), only eight of the 75 nest box lakes demonstrated significant pH change during the study, and no lakes changed fish status. To minimize the effect of yearly fluctuations in pH and to restrict our analyses to years in which nest boxes were present, we used a mean pH-value for each lake (see Table 2) from samples taken between 1987 and 1995 (range: 4 - 7 years).

We selected lakes to fall within specific categories of pH-value and fish status (presence/absence) for two reasons: previous research indicated that these characteristics should be important to the breeding biology of cavity-nesting waterfowl (McNicol et al. 1987a, Blancher, McNicol, Ross, Wedeles & Morrison 1992, McNicol & Wayland 1992), and, as reduced emissions lead to improvements in water quality (less acidity), we expect biological recovery to progress along a gradient defined by these categories (McNicol et al. 1995a).

To assess possible effects of weather on waterfowl nesting each year, we used meteorological records from the Sudbury airport (situated within 50 km of most study lakes) for May and June of each study year (Environment Canada, Atmospheric Environment Service, Sudbury Airport). For each month, we obtained data on maximum, minimum and mean temperature, mean wind speed, and total precipitation.

Statistical analyses

Because of repeated sampling and the unequal annual availability of nest boxes, we weighted each observation by the number of times a lake was sampled for most analyses, i.e. 1/n. For example, if a box on a lake was available in seven of the eight years, each year's record would get a weighting of $^1/_7$, thereby giving each lake an overall equal contribution in statistical analyses. Some independent variables were categorical, so we used multiple logistic regression (Hosmer & Lemeshow 1989) to determine whether nesting attempts (presence or absence) or nesting success (presence or absence) were related to nest box or lake characteristics. When examining individual species, boxes occupied by other species were considered unavailable to the focal species. To determine if local weather conditions influenced cavity-nesting ducks, we divided the nesting period into two broad stages: an egg-laying and early incubation period (May), and an advanced incubation and hatching period (June). We then used Spearman correlations to examine relationships of nesting attempts and nesting success with maximum, minimum, and mean temperature, mean wind speed, and total precipitation for these periods (1987-1995). We also used a variety of univariate tests where appropriate. All means are reported ± SE.

Results

Nest box characteristics

On average, nest boxes were first occupied within 2.5

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(±0.2) years of being established. There was no influence of the year a nest box was erected on average time to its first occupancy (1986, N = 43; after 1986, N = 23; Welch's approximate t = 0.98, df = 59, P = 0.33); hence, we pooled data for all boxes. We used multiple logistic regression to test whether the use of nest boxes, including nesting attempts or nesting success, by waterfowl was affected by the lake characteristics listed in Table 2. Observations were weighted by the number of years a lake was sampled. No variables were retained in regressions for either nesting attempts or nesting success for each species (all P > 0.50). Similarly, tree species had no influence on the proportion of boxes occupied or unoccupied by waterfowl ($\chi^2 = 2.98$, df = 3, P > 0.35), or on the proportion of successful or unsuccessful nests ($\chi^2 = 1.05$, df = 3, P > 0.79) (because of small sample sizes in the weighted analysis, we combined white spruce, black spruce and eastern white cedar into one category (N = 10)). Nesting attempts and nesting success were also unrelated to the directions boxes faced (Watson U^2 tests, Ps > 0.50).

Nest box use

Common goldeneyes were the most frequent occupant of nest boxes, using approximately 31% of available boxes each year (Table 3). For 114 successful nests, mean clutch size for goldeneyes was 9.0 (±0.2) eggs, and mean hatching success was 93% (±1). Total production for goldeneyes did not change over the study period (for all following comparison, N = 9 years); neither nesting attempts, total eggs laid, nor total eggs hatched increased or decreased significantly (r_S: all P > 0.10). Furthermore, average production per nest also did not change for goldeneyes, with mean number of eggs laid per nest (dump nests excluded) and mean number of eggs hatched per successful nest neither increasing nor decreasing over the study period (r_S: both P > 0.4). Approximately 31% of all goldeneye nests were unsuccessful; none of these losses increased or decreased significantly over the study period (r_S: all P > 0.20). Although we could not separate returning females from new females without a marked population, goldeneyes appeared to show some tendency towards using the same nest box in successive years, with 55% (67/122) of lakes with goldeneye nests one year being followed by nesting attempts by goldeneyes the next.

Hooded mergansers were the other main species using nest boxes in the Wanapitei area, occupying on average 12% of available boxes each year (Table 4). For 45 successful nests, mean clutch size for hooded mergansers was 9.1 (±0.4) eggs, and mean hatching success was 92% (±2). Total production for hooded mergansers changed over the nine year study period, with the number of nesting attempts ($r_S = 0.86$, P < 0.01), total eggs laid ($r_S = 0.97$, P < 0.001), and total eggs hatched ($r_S = 0.97$, P < 0.001) increasing significantly from 1987 to 1996. Although females laid similar numbers of eggs per nest (dump nests excluded; $r_S = 0.24$, P = 0.55) over these years, the mean number of eggs hatched per successful nest increased significantly ($r_S = 0.80$, P = 0.01). Approximately 32% of all hooded merganser nests were unsuccessful, but none of these losses increased or decreased significantly over the study period (r_S: all P > 0.20). Hooded mergansers showed less tendency to use the same box in successive years (30%; 12/40) than goldeneyes.

Common mergansers occupied about 2% of available nest boxes each year (total of 11 nesting attempts) with no noticeable change in use observed

Table 3. Nest box use by common goldeneyes (CG) at Wanapitei study lakes, 1987-1996 (no data available in 1991). Nest attempts and successful nests do not include nests where goldeneyes parasitized another species. Total number of goldeneye eggs is in parentheses.

Nesting parameter	1987	1988	1989	1990	1992	1993	1994	1995	1996
Number of boxes available	46	47	68	71	59	67	67	68	67
Nesting attempts (≤ 1 egg laid)	17 (141)	18 (151)	18 (157)	24 (192)	17 (138)	22 (143)	21 (183)	18 (151)	15 (123)
Nests parasitized by CG	0	3 (9)	2 (12)	4 (13)	6 (17)	4 (11)	3 (16)	4 (15)	3 (7)
Total number of eggs laid	141	160	169	205	155	154	199	166	130
Successful nests (≤ 1 egg hatched)	11 (96)	15 (103)	12 (95)	10 (79)	9 (82)	12 (94)	17 (162)	13 (104)	12 (104)
Successful parasitic nests with CG eggs	0	1 (4)	1 (8)	2 (4)	3 (6)	3 (9)	3 (14)	4 (14)	3 (6)
Total number of eggs hatched	96	107	103	83	88	103	176	118	110
Number of dump nests	2 (5)	0	1 (15)	3 (11)	4 (23)	2 (7)	1 (1)	0	1 (12)
Number of abandoned nests	3 (29)	3 (32)	2 (23)	4 (42)	2 (14)	1 (7)	0	2 (23)	0
Depredated nests (mininum known eggs)	1 (8)	0	2 (11)	2 (4)	2 (16)	5 (13)	2 (8)	2 (9)	2 (2)
Human-caused losses	0	0	1 (8)	5 (49)	0	0	0	0	0
Unknown fate for nest	0	0	0	0	0	2	1	1	0

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Table 4. Nest box use by hooded mergansers (HM) at Wanapitei study lakes, 1987-1996 (no data available from 1991). Nest attempts and successful nests do not include nests where hooded mergansers parasitized another species. Total number of hooded merganser eggs is given in parentheses.

Nesting parameter	1987	1988	1989	1990	1992	1993	1994	1995	1996
Number of boxes available	46	47	68	71	59	67	67	68	67
Nesting attempts (≥ 1 egg laid)	3 (11)	6 (39)	6 (44)	9 (68)	9 (62)	9 (64)	8 (72)	10 (77)	9 (71)
Nests parasitized by HM	0	1 (1)	2 (5)	9 (1)	4 (10)	4 (7)	3 (6)	6 (21)	4 (140)
Total number of eggs laid	11	40	49	69	72	71	78	98	81
Successful nests (≥ 1 egg hatched)	1 (7)	3 (20)	2 (13)	6 (47)	6 (52)	6 (50)	7 (62)	7 (67)	7 (60)
Successful parasitic nests with HM eggs	0	0	0	0	1 (1)	3 (6)	3 (6)	4 (12)	4 (10)
Total number of eggs hatched	7	20	13	47	53	56	68	79	70
Number of dump nests	1 (2)	2 (7)	0	1 (1)	1 (1)	1 (1)	0	1 (5)	0
Number of abandoned nests	0	1 (7)	0	0	1 (8)	0	0	0	1 (6)
Depredated nests (mininum known eggs)	0	0	3 (29)	2 (15)	0	1 (1)	1 (6)	2 (1)	0
Unknown fate for nest	1	0	1	0	1	1	0	0	0

over the years. Wood ducks used only 1% of available nest boxes each year (seven nesting attempts) although no wood ducks nested in boxes before 1990.

Because of small sample sizes for common mergansers and wood ducks, interspecific nest parasitism was analysed only for hooded mergansers and common goldeneyes. Interspecific nest parasitism (hereafter, nest parasitism) increased from no cases in 1987 to approximately 33% of all nesting attempts in 1996. Nest parasitism was more likely to occur in boxes occupied the previous year, occurring in 37 of 52 (71%) parasitized nests for which consecutive year data existed. Overall, of the 984 goldeneye eggs successfully hatched during the study, 65 (7%) were incubated by either hooded mergansers (63) or wood ducks (2); similarly, 35 (8%) of 413 successfully hatched hooded merganser eggs were incubated by common goldeneyes.

Parasitized nests were as likely as non-parasitized nests to be successful (parasitized nests: 38 successful vs 13 unsuccessful; non-parasitized nests: 162 successful vs 59 unsuccessful; Fisher's exact test: $P = 0.51$). Average hatching success of hooded merganser eggs decreased from 95% in 25 nests where no parasitism occurred to 89% in 20 nests parasitized by goldeneyes, but this difference was not significant (Welch's approximate $t = 1.71$, $df = 25$, $P = 0.10$). Surprisingly, goldeneye eggs had a significantly higher mean hatching success in 20 nests where they were parasitized by another species (97% eggs hatched) than in 94 nests where no nest parasitism occurred (92% eggs hatched; Welch's approximate $t = 2.91$, $df = 55$, $P = 0.005$).

We calculated mean hatch dates for each species from brood surveys conducted in the Wanapitei study area during 1983-1995. While hatch dates for hooded mergansers and common goldeneyes were virtually identical, significant differences among species were noted (ANOVA, $F = 5.040$, $P = 0.0023$), with hooded mergansers ($\bar{x}$ = 10 June ± 1 day, $N = 83$) and goldeneyes ($\bar{x}$ = 11 June ± 1 day, $N = 72$) hatching much earlier than wood ducks ($\bar{x}$ = 24 June ± 5 days, $N = 8$; $P < 0.05$), and hooded mergansers hatching earlier than common mergansers ($\bar{x}$ = 17 June ± 2 days, $N = 30$; $P < 0.05$).

Neither the proportion of boxes occupied nor the mean number of eggs laid per nest was correlated with monthly weather conditions in May (all $P > 0.40$). Similarly, the proportion of successful nests and mean number of eggs hatched per nest were unrelated to weather conditions for June (all $P > 0.12$).

Habitat relationships

The availability of boxes, their use and nesting success by common goldeneyes and hooded mergansers for all years pooled within each of the six pH/fish categories are presented in Table 5. Of 145 nesting attempts by common goldeneyes, 62% were on lakes without fish, whereas 66% of 56 hooded merganser nesting attempts were on lakes containing fish. Roughly similar numbers of attempts by each species occurred in each of the pH-categories (see Table 5). To determine whether goldeneye or merganser nesting attempts or success were related to habitat parameters, we entered mean pH-value, fish status, water area and the number of wetlands within 500 m into weighted multiple logistic stepwise regressions. No variables were retained as significant in regressions for either species (all $P > 0.16$). Furthermore, for both species, mean pH was not correlated with clutch size, number of eggs hatched, or hatching success (r_S: all $P > 0.15$).

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Table 5. Number of boxes available/nesting attempts/nesting success, respectively, for nests with known fates for common goldeneyes and hooded mergansers for 1987-1996, according to pH and fish status categories. Damaged boxes and boxes occupied by other species were considered unavailable.

Species	Fish status	pH < 5.0	5.0 ≤ pH ≤ 6.3	pH > 6.3	Total
Common goldeneye	Absent	148/56/32	72/23/18	32/16/12	252/95/62
	Present	14/5/3	112/40/29	83/20/17	209/65/49
	Total	162/61/35	184/63/47	115/36/29	461/160/111
Hooded merganser	Absent	104/12/9	57/8/4	17/1/1	178/21/14
	Present	11/2/1	93/21/15	84/21/15	188/45/31
	Total	115/14/10	150/29/19	101/22/6	366/66/45

For common goldeneyes and hooded mergansers, mean pH was not correlated with clutch size, number of eggs hatched, or hatching success (r_S: all P > 0.15), with the exception that hatching success tended to be higher for hooded mergansers with increasing pH (r_S = 0.28, N = 45, P = 0.06). To control for the effects of all habitat variables simultaneously, we entered mean pH-value, fish status, water area and number of wetlands within 500 m into weighted multiple logistic stepwise regressions on goldeneye and hooded merganser nesting attempts and nesting success. No variables were retained as significant in regressions for either species (all P > 0.5).

Because previous work at our study lakes (Mallory et al. 1993) suggested that nest site selection by insectivorous cavity-nesting waterfowl is affected by fish presence, we looked at the proportion of successful and unsuccessful nests on lakes with and without fish. Unsuccessful nests due to abandonment or predation happened with equal likelihood on lakes with and without fish (fishless lakes: 19 losses vs 15 lakes where no losses occurred; fish lakes: 18 losses vs 16 lakes where no losses occurred; Fisher's exact P = 1.0). As well, mean hatching success and number of eggs laid and hatched did not differ for goldeneyes or hooded mergansers on lakes with and without fish (Table 6), although there was a weak trend for hooded mergansers to hatch more eggs per nest on lakes with fish (Fisher's exact P = 0.09).

We used two approaches to determine if common goldeneyes or hooded mergansers changed their use of lakes over time. First, we used the same four habitat variables in the multiple logistic regression as above, except we ran the regression separately on the first (1987-1990) and last five (1992-1996) years of the study (with no data collected in 1991, our study fell naturally into two time periods). Consistent with our preliminary analyses, nesting attempts by goldeneyes from 1987-1990 were negatively correlated with fish presence (y = -0.10 - 1.12 (fish), concordance = 72.6%, sum of weights = 74), but no relationships were found for nesting success (P > 0.27). No significant habitat relationships were found from 1992-1996 for goldeneyes (P > 0.16), or in either time period for hooded mergansers (P > 0.17). In a second approach, we created a scaled variable that measured the difference between the number of nesting attempts on lakes without fish minus those on lakes with fish. Goldeneyes showed a significant decrease in the relative proportion of fishless lakes used (r_S = - 0.95, P < 0.001) over the study (Fig. 1). Hooded mergansers, however, showed no changes in nesting attempts on lakes with or without fish (r_S = - 0.54, P = 0.14).

Table 6. Mean (SE) clutch size, number of eggs hatched, and hatching success for successful common goldeneyes and hooded mergansers on lakes with and without fish (t-tests: all P > 0.20).

Species	Variable	Lakes with fish			Lakes without fish		
		Mean	(SE)	N	Mean	(SE)	N
Common goldeneye	Clutch size	8.7	(0.4)	42	9.0	(0.3)	57
	No of eggs hatched	8.1	(0.4)	42	8.3	(0.3)	57
	Hatching success	0.92	(0.02)	42	0.92	(0.02)	57
Hooded merganser	Clutch size	9.3	(0.5)	26	8.8	(0.6)	12
	No of eggs hatched	8.7	(0.6)	26	7.7	(0.5)	12
	Hatching success	0.94	(0.02)	26	0.89	(0.03)	12

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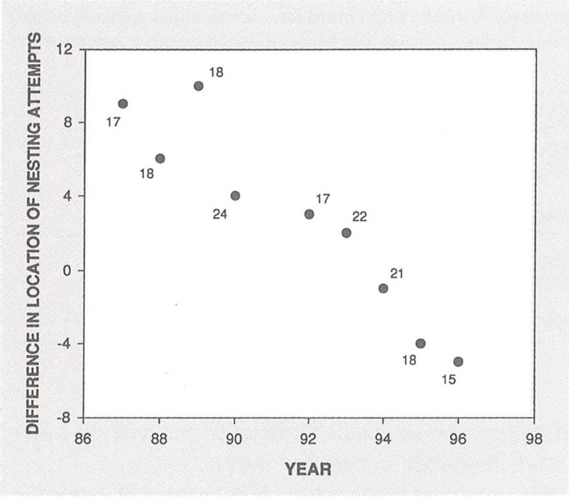

Figure 1. Shifts in relative use of lakes with and without fish by common goldeneyes. Each point represents the number of boxes occupied by common goldeneyes on lakes without fish minus the number of boxes occupied on lakes with fish in each year. The numbers by points represent total nesting attempts by common goldeneyes in that year.

To determine if habitat differences existed between lakes with boxes that were used 50% or more of the time (N = 34) and lakes with boxes that were never occupied or used less than half the time (N = 41), we used Wilcoxon tests to compare median values for mean pH, fish presence, water area and number of wetlands within 500 m for both groups. No significant differences were found for any habitat variable between frequently and less frequently used lakes (all $P > 0.20$).

Discussion

Nest box characteristics and use

The Wanapitei study area provides a unique opportunity to assess not only the responses of waterfowl to chemical recovery, but also to address questions of nest site choice by several species of cavity-nesting waterfowl when presented with a wide array of available habitat conditions. Although we did not measure the use of natural cavities by waterfowl in the area, our intent was to provide nesting alternatives that could be easily monitored, not to artificially increase the population. Unlike many other studies where higher densities of nest boxes invariably led to interference among nesting females (e.g. Grenquist 1963, Jones & Leopold 1967, Semel et al. 1988), we found no apparent female interference effect, probably attributable to our restriction of only one nest box per lake.

Considering the experimental design, one of the most interesting findings from this study is that very few of the potential causal factors that we measured were significantly correlated with nest box use. Specifically, we found no relationship between box use and the year boxes were erected, characteristics of the box (height, tree size or species, box direction, box density), weather (temperature, wind, precipitation), lake pH-value and most other habitat variables (lake area, connectivity). What makes these results even more compelling is that they were derived from an area where habitat characteristics vary dramatically and have been shown to influence habitat use by these species at other stages of the breeding season (McNicol et al. 1987a, McNicol & Wayland 1992, Mallory et al. 1993, Wayland & McNicol 1994). Our results are consistent with previous studies that have looked at some of these factors independently (Lumsden, Page & Gauthier 1980, Lumsden, Robinson & Hartford 1986, Dow & Fredga 1985, Dugger, Dugger & Fredrickson 1994), but we are aware of no other studies that have examined as many factors simultaneously.

Breeding pair surveys conducted from 1985 to 1996 in the general Sudbury area show that hooded merganser populations are increasing significantly, while common goldeneye populations are stable or possibly even declining (McNicol et al. 1995d). The Sudbury area is central to the breeding range of the hooded merganser but is at the southern limit of the goldeneye's range. Trends we observed in nest box use reflected overall population trends for hooded mergansers and goldeneyes, suggesting that our boxes did not artificially increase local waterfowl populations. While other studies have reported increased populations with the addition of nest boxes (e.g. Eriksson 1982, Savard 1988, Allen, Corr & Dorso 1990), this probably did not occur in our study because of our restriction of one nest box on each lake.

Clutch size, nesting success, and hatching success for common goldeneyes and hooded mergansers were similar to values reported in previous studies on cavity-nesting ducks (summarized in Dugger et al. 1994, Eadie, Mallory & Lumsden 1995). Mean hatching success for hooded merganser clutches increased significantly over the years, but this result should be interpreted cautiously due to the small number of hooded merganser nests early in the study. Although

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we did not use marked females, based on the number of boxes with consecutive years of occupancy and assuming that females occupying boxes in successive years were the same females, goldeneyes showed a maximum site fidelity incidence of approximately 54%. This is similar to other reports of site fidelity for this species (Eadie et al. 1995). Similarly, our maximum site fidelity measurement of approximately 30% for hooded mergansers is nearly identical to that reported by Zicus (1990; 29%) for marked hens nesting in northern Minnesota. Thus, despite the range of lake characteristics available in our study area, basic nesting biologies of hooded mergansers and common goldeneyes were similar to those of conspecifics in other geographic areas, even when nesting at extremes of their breeding ranges.

Behavioural interactions among species could affect the reliability of using waterfowl as indicators of biological recovery in two main ways: through interspecific nest parasitism, and through competition for nest boxes. Although we have no reliable measure of intraspecific nest parasitism, since it is very difficult to determine whether a nest represents the efforts of more than one female (Eadie et al. 1995), interspecific nest parasitism increased significantly over the study to approximately 33% of all nesting attempts in 1996. Nest parasitism is common in areas where common goldeneyes and hooded mergansers overlap (see Dugger et al. 1994, Eadie et al. 1995). The increase in nest parasitism observed in our study was probably linked to the relative increase in hooded merganser nests. In terms of total production, over 7% of successfully hatched goldeneye and hooded merganser eggs were incubated by another species, a proportion substantially higher than the 2% reported by Zicus (1990) for hooded mergansers.

Except for a tendency for hatching success of host hooded merganser eggs to be lower in parasitized (89%) than non-parasitized nests (95%), apparently no negative costs were associated with nest parasitism, a finding consistent with other studies where clutch sizes did not exceed 16-20 eggs (see Eadie et al. 1995). Our restriction of one nest box per lake probably reduced the 'behavioural pathologies' associated with nest parasitism in areas with high densities of boxes (Semel et al. 1988). Surprisingly, hatching success in parasitized goldeneye nests was 5% higher than in non-parasitized goldeneye nests. This may be explained by the tendency of both species to parasitize nests occupied the previous year; nest prospecting by failed breeders and immature females could lead to more experienced females being parasitized than first-time breeders (e.g. Eadie & Gauthier 1985).

Hatching chronologies were similar for common goldeneyes and hooded mergansers in the Wanapitei study area. Using observations of broods and allowing roughly 30 days for incubation and a laying rate of approximately two days per egg for each species (Dugger et al. 1994, Eadie et al. 1995), both species, on average, initiated nests around 23 April. Although we cannot address the possibility that either species competitively excludes the other from nest boxes, their similar nesting chronologies and the surplus of available, unused boxes suggest that hooded mergansers and goldeneyes have equal access to nest sites, thus allowing the potential for selection based on habitat characteristics, a critical factor for bioindicator species. Because common mergansers and wood ducks generally nest later, fewer unoccupied nest boxes will be available to them; habitat selection may be limited for these species if the surplus of available, unoccupied boxes diminishes.

Weather did not appear to influence nesting success during our study, although more subtle effects of weather on nesting biology that we did not measure (e.g. incubation duration, hen condition) may be significant. Nonetheless, our results suggest that weather conditions in our study area are probably not limiting production during nesting; weather effects are more likely to be critical at the brood stage when young are directly exposed to environmental conditions (Eadie et al. 1995).

Habitat relationships

Because fish can seriously reduce the abundance of macroinvertebrates available to insectivorous waterfowl, numerous studies have shown that insectivores, especially common goldeneyes, prefer to feed and to raise their broods on lakes without fish (Eriksson 1979b, 1983, Eadie & Keast 1982, Wayland & McNicol 1994), and, to a lesser extent, on lakes with non-competing fish species (McNicol & Wayland 1992). Conversely, piscivorous species such as common mergansers prefer to raise their broods on lakes containing fish (McNicol, Ross & Blancher 1990). In the Wanapitei area, most fishless lakes have resulted from acidification. As lakes recover, we expect fish species to recolonize their former habitats, changing the relative availability of food for both insectivorous and piscivorous waterfowl. Proportionally, goldeneyes tended to nest more often on fishless lakes

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(62%), while hooded mergansers (which can effectively feed on fish; Dugger et al. 1994), nested more often on lakes containing fish (66%). All common merganser females nested on lakes with fish.

Neither common goldeneyes nor hooded mergansers appeared influenced by pH-value after we controlled for fish presence. For goldeneyes, this is consistent with an earlier study by Mallory et al. (1994) on a subset of these lakes that found no effects of pH-value on clutch size, number of eggs hatched, or hatching success. Similarly, Pöysä, Rask & Nummi (1994) also determined that pH-value had little effect on goldeneye densities after accounting for the effects of fish (and hence invertebrate food resources).

Unlike earlier studies on our lakes (Mallory et al. 1993, 1994), however, logistic regression analyses indicated that female goldeneyes and hooded mergansers did not preferentially nest or have larger clutches on fishless lakes. To understand this apparent contradiction, we divided the study into two periods (early and late). Consistent with earlier work on a subset of lakes (Mallory et al. 1993), common goldeneyes were more likely to nest on fishless lakes during 1987-1990; however, during 1992-1996 nesting attempts were not related to fish presence. This difference in nesting preference between studies is a result of a significant shift in goldeneye nesting attempts to lakes with fish (see Fig. 1). Given that nesting success did not differ on lakes with or without fish, and that the fish status of the study lakes remained unchanged during the study, the reasons for this shift are unclear. Our results, however, are consistent with those of Eriksson (1978, 1979a), who found that food availability had little influence on goldeneye nest site selection. No temporal shifts in nesting preference were found for hooded mergansers.

Mean pH-value, fish presence, open water area and wetland connectivity were uncorrelated with either nesting attempts or nesting success for both species during the study. While this result is surprising considering the well-documented preference of common goldeneyes, especially, to feed on fishless lakes, our results suggest that habitat characteristics of the nesting lake itself may be unimportant for both nesting goldeneyes and hooded mergansers. Our inability to discern habitat differences between frequently used lakes and seldom or never used lakes supports this interpretation. Similarly, studies in Ontario and Scandinavia have shown that female goldeneyes often move their broods to new lakes shortly after hatch (Eriksson 1978, Pöysä & Virtanen 1994, Wayland & McNicol 1994; note that similar information is lacking for the hooded merganser). These movements are usually to lakes with abundant food resources, and duckling mortality appears to be unassociated with the length of the move (Pöysä & Virtanen 1994, Wayland & McNicol 1994). Hence, the importance of habitat features for nesting lakes is probably minimal for both goldeneyes and hooded mergansers, and therefore habitat suitability is likely to be more important at the brood-rearing stage for both species, a conclusion also reached by Pöysä et al. (1994).

Implications for biomonitoring

For a species to be an effective bioindicator, its habitat requirements must be thoroughly understood. This study establishes some important baseline information on the nesting biologies and interactions of hooded mergansers and common goldeneyes in our study area, and it reports on the limited use of nest boxes by common mergansers and wood ducks. With improvements in water quality expected following reduced local emissions of acidic pollutants, fish species are expected to recolonize many lakes where they were formerly present. As a result, hooded merganser and common merganser populations are expected to increase, whereas goldeneye populations are expected to decline (McNicol et al. 1995d). Because nest box use in our study reflected general population trends observed using more costly aerial surveys, monitoring boxes may prove an effective, inexpensive way to track population changes expected as biological recovery occurs in the Sudbury area and elsewhere.

Monitoring use of nest boxes should also allow us to track more subtle responses of cavity-nesting waterfowl to improving chemical conditions. For species like common goldeneyes, for instance, with a well-known preference for feeding on fishless, often acidic lakes, clutch size and nesting success of females in this area may decrease as the number of fishless lakes declines, causing females to begin egg laying or to finish incubation in poorer physical condition, and possibly affecting their ability to care for broods. Although high densities of available, acidic lakes and high brood mobility may reduce the current importance of nest site selection by goldeneyes, selection should become more important for goldeneyes as fewer appropriate brood-rearing lakes remain, placing an increased value on nesting on or near a good brood-rearing lake. Changes in nesting

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behaviour for common and hooded mergansers should be more subtle.

Biomonitoring programs should identify the limiting step in a species' breeding biology. Our results indicate that common goldeneyes and hooded mergansers are not limited at the nesting stage in our lakes, and that changes in productivity will more likely occur at the brood-rearing stage. Knowing the availability of boxes and the success of nests on roughly half the lakes in our study area, we can control for the nesting stage in years in which the number of young that survive to fledge varies. We can then identify crucial factors which affect overall production, and thereby predict more reliably how these species will respond to future changes in lake conditions.

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