BEHAVIOURAL RESPONSES OF HOST WOOD DUCKS (AIX SPONSA) TO BROOD PARASITISM AND ITS THREAT

by

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Behavioural responses of host Wood Ducks (*Aix sponsa*) to brood parasitism and its threat.

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ABSTRACT

The behavioural responses of host Wood Ducks to intraspecific brood parasitism, and to the threat of brood parasitism, were studied from 1988 to 1990 on the Creston Valley Wildlife Management Area, B. C. I placed small chicken eggs in nests to simulate brood parasitism by Wood Ducks and floated model Wood Ducks near nests to simulate the presence of brood parasites. Nest box occupancy by Wood Ducks was less than 25% in all three years of the study, and the spatial pattern of nests changed between years. Brood parasitism and nest failures increased in 1989, when most nests were initiated within 100 m of one another. Wood Ducks parasitized 3 of 24 nest boxes in 1989 that both contained chicken eggs and had Wood Duck models floating in front of the nest boxes, but never parasitized control boxes or those containing only chicken eggs. Wood Ducks did not parasitize experimental nest boxes in 1990. Wood Duck pairs did not change the proportion of time they spent performing different behaviours in the area of the nest box during the egg-laying period when potential parasites were nearby, although these data were difficult to collect and sample sizes were small. Females increased the time they spent in their nest box during the egg-laying period when potential parasites were nearby, but not after foreign eggs were added to their nests. The proportion of eggs that hatched in a clutch decreased with increasing clutch size, and parasitized clutches were larger than unparasitized clutches (12.6 ±0.7 vs. 8.0 ±0.6). Despite lower host egg hatchability and other potential costs of brood parasitism, anti-parasite strategies do not seem to be well-developed among Wood Ducks. The frequency of brood parasitism in natural situations was probably much lower due to the low density and inconspicuousness of tree cavities as compared to nest boxes, and the cost of defending nests against parasites was apparently higher than the moderate and infrequent costs of brood parasitism.

DEDICATION

For Harold Dennis Foster

1909-1990

ACKNOWLEDGEMENTS

Although this thesis is a source of personal pride, there are many people who have influenced what follows on these pages. To them I am grateful for their time and friendship during my years at SFU.

My supervisor, Nico Verbeek let me do my own thing throughout my extended stay at the university and was very helpful in my last fall while I was trying to finish things from a distance. Larry Dill was a supportive supervisor during a critical year of my studies; his ideas and criticisms greatly improved the final product. Discussions with Ron Ydenberg, both at school and in the field, kept me on track. Alton Harestad also served on my committee and provided excellent suggestions. Thanks to Jean-Pierre Savard for serving as my external examiner.

Ray Holland in the Science Electronics Shop at SFU worked very hard through most of late 1988 and early 1989 on a project that started from a few sketches but ended up providing me with most of the data for this thesis.

The Creston Valley Wildlife Management Area provided me not only with a study site, but with a place to live, equipment, coffee, and lots of keys. In the end, they also provided me with a job, and allowed me the time off during 1990 to finish my fieldwork and to disappear to Vancouver

once in a while. Brian Stushnoff, the area manager, was very tolerant, and was also an important source of information on the biology of the management area. Special thanks must go to Lawrence Schalla: my neighbour, endless source of B-movies, clam chowder and automotive advice. The rest of the management area staff provided, as they still do, many smiles.

Assistants were an important part of my field experience, and I was lucky to work with two who not only collected good data, but provided hours of companionship through days of less-than-exciting fieldwork. Sue Holroyd maintained her good humour through my early work in 1988, and Chantal Pineau brought her own unique flair to my project in April and May 1989.

Many students worked in Creston during my summers there, and they have left me with a lifetime of memories. I relied a great deal on Dave Wiggins and Barb Beasley for entertainment during April and May each spring before the arrival of other students through science fairs, Roy's nights, and evenings of warm sunsets, cool jazz, and refreshments. Joanne Siderius, my other lab-mate, inspired me with her good cheer through the worst of the field seasons. Brent Charland never let the conversation lag. Summers would not have been the same without the barbecues and company of the other researchers, assistants, and Wildlife Centre staff, particularly Adriane Lewin, who's company kept me sane through the chicken pox and other crazy events of the summers of 1989 and 1990.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

1. INTRODUCTION

The Wood Duck (Aix sponsa) is a cavity-nesting species that exhibits a variety of egg-laying strategies (Clawson *et al*. 1979). Some Wood Duck hens are brood parasites; they lay eggs in conspecifics' nests (Yom-Tov 1980). Parasitic behaviour in this species does not appear to be age-related (Heusmann 1975), nor is it an alternative life history strategy to normal nesting (Clawson *et al*. 1979). Parasitic behaviour can occur where nest sites are abundant, suggesting that it is not a response to a shortage of nest sites (Morse and Wight 1969, Heusmann *et al*. 1980, Semel and Sherman 1986, Semel *et al*. 1988). Studies of other cavity-nesting waterfowl that exhibit brood parasitic behaviour have reached similar conclusions (McCamant and Bolen 1979, Andersson and Eriksson 1982, Andersson 1984, Eadie 1989). Brood parasitism may simply be an opportunistic behaviour that allows Wood Duck hens to increase their reproductive success when host nests are available. In any given breeding season, most hens lay and incubate a normal clutch whether they lay parasitically or not (Clawson *et al*. 1979).

Among bird species with little post-hatching parental care, such as waterfowl, researchers have had difficulty demonstrating a clear cost of brood parasitism to hosts (Morse and Wight 1969, Clawson *et al*. 1979, Amat 1985, Eadie and Lumsden 1985, Eadie et al. 1988, Eadie 1989, Rohwer and Freeman 1989 but see Jones and Leopold 1967, Andersson and Eriksson 1982, Amat 1987). Some researchers have suggested that brood parasitism may be beneficial to hosts by reducing the predation risk to host young in larger broods (Andersson 1984, Eadie and Lumsden 1985, Eadie et al. 1988). Observations by Semel and Sherman (1986) of Wood Duck hens behaving surreptitiously in the vicinity of their nest boxes, and of hens aggressively excluding parasitic females from entering their boxes, suggest that Wood Ducks do suffer some cost. The most obvious cost is incurred when parasitic eggs in the nest adversely affect the hatchability of the host's own eggs, sometimes causing the abandonment of the nesting attempt (Semel et al. 1988, Eadie 1989).

The scant available data suggest that the time Wood Duck hens spend in the nest box during the egg-laying period cannot be explained simply by the minimum physiological time required to lay an egg. Reported egg-laying times range from 0.3 minutes to more than three hours (Breckenridge 1956, Stewart 1962, Clawson et al. 1979).

Energetic requirements of parents, thermal requirements of the clutch, and perhaps predation risk are thought to be responsible for nest attentiveness patterns observed among anatids during the egg-laying and incubation periods (Caldwell and Cornwell 1975, Korschgen 1977, Afton 1980, Ringleman et al. 1982, Hohman 1986, Brown and Fredrickson

1987, Thompson and Raveling 1987). Snow Geese (*Chen caerulescens*) arrive on their breeding grounds with sufficient endogenous reserves to lay eggs and incubate clutches without foraging (Ankney and MacInnes 1978) and, consequently, nest attentiveness of incubating geese (Canada Goose, *Branta canadensis*; Emperor Goose, *Chen canagica*) is very high (Raveling 1979, Thompson and Raveling 1987, respectively).

Ducks lay larger clutches and disproportionately larger eggs than geese and rely more heavily on food available on their breeding grounds (Lack 1967). Energy requirements of ducks peak during early egg-laying (Drobney 1980, 1982) which might necessitate long periods of absence from the nest in order to forage. Among species like Wood Ducks, in which males do not share nest duties, nests are vulnerable when left unattended by females.

Since unincubated eggs are tolerant to temperature fluctuations (Webb 1987), females are probably not increasing the time they spend in the nest box during the egg-laying period to protect the eggs from temperature extremes. Once incubation begins, the thermal requirements of the developing embryos and the fasting ability of hens regulate nest attentiveness (Caldwell and Cornwell 1975, Korschgen 1977, Afton 1980, Ringleman *et al*. 1982, Hohman 1986, Brown and Fredrickson 1987).

Predation risk has been implicated as an influence on nest attentiveness among those species with exceptionally high rates of predation such as arctic-nesting geese and eiders (Korschgen 1977, Thompson and Raveling 1987). Building nests in cavities may offer species better protection from predators (von Haartman 1957) and provide a more favourable microclimate for eggs than building open nests. This should allow Wood Ducks to be less attentive during incubation than ground-nesting species of similar size; however, Wood Ducks are more attentive than such species (Breckenridge 1956, Afton 1980).

I hypothesize that nest attentiveness during the egg-laying period is related to the immediate social environment of a nesting hen, specifically, the risk that the nest will be parasitized by other Wood Ducks. Since Wood Ducks lay eggs within a few hours after sunrise (Grice and Rogers 1965, this study), a hen can reduce the likelihood of her nest being parasitized by increasing the time she spends on the nest in the morning after laying her own egg.

I studied the relationship between the threat of intraspecific brood parasitism and the behaviour of breeding pairs in the vicinity of nests during the egg-laying period, and between brood parasitism and the nest attentiveness of hens, in a box-nesting population of Wood Ducks in the Creston Valley, B. C. The objective of my study was to examine how host Wood Duck pairs change their behaviour in response to the threat of brood parasitism, and in response to the presence of extra eggs in the nest.

2. STUDY POPULATION

Study area

Fieldwork was conducted from April to July 1988 and 1989, and in April and May 1990, at the Creston Valley Wildlife Management Area (CVWMA) in southeastern British Columbia (Figure 1). For details of the study area see Butler *et al*. (1986). A nest box program was initiated in the late 1960's to enhance populations of cavity-nesting ducks. A total of 440 boxes were erected on trees and posts throughout the Management Area from 1972 to 1976. Although four different box designs were used, their dimensions were similar to the wooden nest box design suggested by Bellrose (1953). Yearly checks and routine maintenance of the boxes by Management Area staff continued until 1981.

I repaired and monitored the use of nest boxes in Corn Creek Marsh, Leach Lake, Six Mile Slough, Duck Creek, Kootenay Channel, and the Dale Marsh in 1988. In 1989, I monitored existing boxes in Corn Creek Marsh, Duck Creek, and Dale Marsh, as well as 60 new boxes that were erected during the winter and early spring of 1989 in the Corn Creek and Dale Marshes. I monitored the same boxes in 1990, except some of the new boxes in Corn Creek Marsh that were removed to alleviate nesting interference problems in areas of high nesting density (see "Results").

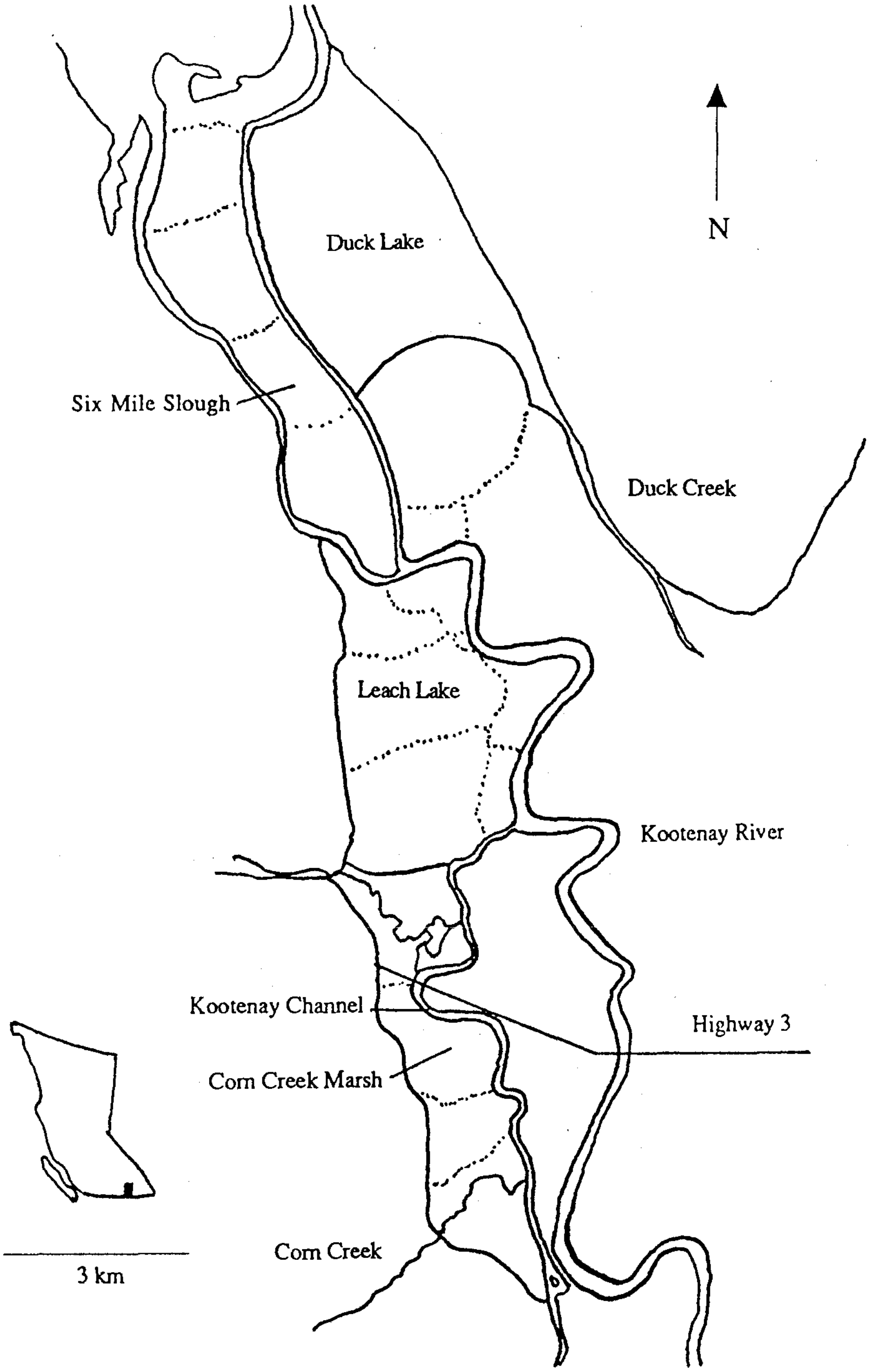

Figure 1. Major pond units and features of the Creston Valley Wildlife Management Area, B. C. The Dale Marsh (DM) is a 23 ha unit located 10 km south of Corn Creek.

Methods

I removed all previous nesting material, added a layer of 5-10 cm of coarse sawdust, and made general repairs to all nest boxes before ducks began looking for nest sites in late March and early April each year. I placed a small piece of grass across the entrance hole of each box to indicate which boxes had been entered since my previous visit. Prospected boxes were checked for nesting activity every four to seven days from 10 April to 19 June 1988, 30 March to 30 May 1989, and 11 April to 7 May 1990. When duck eggs were found, they were numbered at each end with a black felt marker and the length and width at the widest point were measured to the nearest 0.5 mm with Vernier callipers. Egg volumes were calculated according to the formula used by Harris (1964) for gull eggs. A nest was defined as any box in which one or more eggs were laid. Nests were checked daily after their discovery and new eggs were marked and measured on the day they were laid. If more than one egg was laid in a nest during one day, the nest was considered to be parasitized. Daily visits in 1988 and 1989 continued until a hen was present on the nest, or was flushed from the box, when checked. The female was then presumed to be spending the night in the nest box.

Nests were subsequently left undisturbed for 21 days. This was to ensure that birds were not disturbed until late in the incubation period, when they would be less likely to abandon the nest (Grice and Rogers 1965). During the 1990 season, nests were checked until the eighth egg was laid, then left undisturbed until hatching. This was to avoid disturbance to birds that were beginning to spend time in the box during the day.

I attempted to trap most incubating Wood Duck hens in 1988 and 1989 after approximately three weeks of incubation (see Appendix). Trapping procedures were similar to those used by Grice and Rogers (1965). When a female was suspected to be in a nest box, the box's hole was covered with a burlap plug tied to an aluminum extension pole and the bird was taken directly off the nest. New eggs were marked and measured. Faeces were cleaned off eggs. I weighed hens with a 1500 g Pesola scale to the nearest 5 g. I also measured culmen and tarsus length to the nearest 0.5 mm with Vernier callipers, and measured wing chord length to the nearest mm with a wing board. Each hen was banded with a U. S. Fish and Wildlife aluminum leg band. In 1988, I fitted all captured Wood Ducks with unique colour and shape combinations of nylon nasal pieces (Bartonek and Dane 1964, Lokemoen and Sharp 1985). After processing, birds were returned to the nest and the nest box's hole was uncovered after three to five minutes.

Nests in 1988 and 1989 were left undisturbed for a further 14-20 days after females were trapped before they were checked for evidence of hatching. A nest was considered successful if at least one embryo sac or egg cap was present in the box. All unhatched eggs, dead ducklings, egg caps, and embryo sacs were noted, and nesting material was cleared from the box. Incubation periods were calculated as the number of days from when a hen started to spend the night on the nest to the day all activity in the box ended. I then subtracted one day for each egg the host was known to have laid after her first night in the box (considered part of the egg-laying period), and subtracted one additional day to compensate for the period after hatching of the ducklings and before they left the nest box, assumed to be about 24 hours (Bellrose 1976).

I used the Number Cruncher Statistical System version 5.0 (J. L. Hintze, Kaysville UT) for most statistical analyses. All means were expressed ± one standard error except where noted.

Results

The proportion of nest boxes used by Wood Ducks was low in all three years of the study, and differed between areas of the CVWMA (Table 1). Within Corn Creek Marsh, the distribution of nests also differed between years. In 1988, only four of 12 nests had nearest neighbours closer than 100 m ("close" nests). In 1989, 12 of 16 were "close" nests, and in 1990, two of six were "close" nests.

Table 1. Nest box use by Wood Ducks on the Creston Valley Wildlife Management Area. Pond units are: CC, Corn Creek Marsh; DC, Duck Creek; DM, Dale Marsh; LL, Leach Lake; SM, Six Mile Slough; KC, Kootenay Channel.

Year	Nest Boxes	CC	DC	DM	LL	SM	KC
1988	available	87	31	23	23	16	15
	used	12	4	3	0	0	1
	% used	14	13	13	0	0	7
1989	available	165	11	14			
	used	16	4	1			
	% used	10	36	7			
1990	available	130	11	12			
	used	6	1	1			
	% used	5	9	8			

The first Wood Duck eggs were detected in the nest boxes during the second week of April in all three years. Egg-laying continued until the first week of June, although about 66% of the nests were initiated during the last week of April and the first week of May in both 1988 and 1989. No nests were initiated in the nest boxes after 27 April in 1990. The modal dates of clutch initiation were 1 May 1988 (based on 11 nests for which clutch initiation dates are known), 28 April 1989 (n=21), and 15 April 1990 (n=7). The mean clutch size of Wood Duck nests was 9.0 ±1.2 (n=20) in 1988 and 11.2 ±0.8 (n=21) in 1989. This difference was not significant (Mann-Whitney U-test: n=41, P=0.16). These clutch sizes included eggs that were laid parasitically. Final clutch size data were not available for 1990 nests because I avoided flushing hens after the eighth egg had been laid.

I detected no intraspecific brood parasitism among Wood Ducks in 1988, although three Wood Duck nests had mixed clutches of Wood Duck and Common Goldeneye (<u>Bucephala clangula</u>) eggs (Table 2). Because many nests were not discovered until after hens had begun incubating, the number of parasitic Wood Duck eggs was probably underestimated. In contrast, 10 nests were parasitized intraspecifically in 1989 (eight during the egg-laying period and two after incubation began) and one nest was a mixed clutch of Wood

Table 2. Summary of nest box use by Wood Ducks on the CVWMA.

	1988	1989	1990
Total number of boxes monitored	95	190	153
Wood Duck nests initiated	20	21	8
Wood Duck parasitism detected	0	10	1
Artificially parasitized nests	0	3	0
Mixed clutches with Goldeneye eggs	3	1	0
Number of nests incubated	17	15	7
Number of successful nests	10	11	4

Duck and Common Goldeneye eggs (Table 2). Of the nests parasitized intraspecifically in 1989, seven were "close" nests. One nest was parasitized with one Wood Duck egg in 1990.

Three nests in 1988, six in 1989, and one in 1990 were not incubated (Table 2). Ten nests were successful in 1988, 11 in 1989, and four in 1990 (Table 2). The modal date broods left monitored nest boxes was 4 June 1989 (n=9). All but one brood left in the morning and the mean departure time was 7:51 am ±69 minutes Pacific Daylight Time (n=9).

All eggs hatched in 15 of 25 successful nests. Eggs added late in the egg-laying period or during incubation were less likely to hatch than the first eight eggs in the nest (G-test: n=206, $P<0.005$; Table 3). This includes eggs laid parasitically. Of the 24 unsuccessful nests, 17 had been abandoned prior to the disappearance of eggs due to predation. Of the remaining seven, only two had lost all eggs before the first time I checked the nest boxes following the hens' abandonment.

Discussion

Nest initiation in boxes was low during the three seasons of the study, despite improvements made to existing nest boxes and the addition of new boxes in 1989. The use of the nest boxes was limited, probably because of an abundance of natural nest sites on the CVWMA. The perimeters of ponds

Table 3. Unhatched eggs in 1988 and 1989 successful nests. "Early eggs" were the first eight found in each box. "Late eggs" were all other eggs. "Late eggs" were significantly less likely to hatch than "early eggs" (G-test: $P<0.005$).

eggs	early eggs	late eggs	total
unhatched	11	9	20
hatched	151	35	186
total	162	44	206

used by Wood Ducks are lined with mature Black Cottonwood (Populus trichocarpa) trees and snags. These trees provide natural cavities suitable for Wood Duck nesting, but were inaccessible to me for nest checking purposes. Most hens from successful nests in nest boxes were marked in 1988, yet most hens sighted with broods were unmarked. This suggests that most Wood Ducks nested in natural cavities. Nest box programs in Wisconsin suffered from low rates of use and the problem was attributed to the indiscriminant placement of nest boxes where natural nest sites were not limiting, or where other critical features of the habitat were unsuitable for Wood Ducks (Soulliere 1986). However, Strange et al. (1971) found that Wood Duck production increased with the introduction of nest boxes despite an abundance of natural cavities at Yazoo National Wildlife Refuge in Mississippi.

Nesting by waterfowl on the CVWMA in general appeared to be low during the three years of the study (Brian Stushnoff, pers. comm.). Many populations of waterfowl species across the continent are currently at their lowest levels ever recorded (Kelly et al. 1989), and although the Creston Valley has not experienced the drought conditions of many prairie nesting areas, CVWMA Wood Ducks may be suffering problems similar to those of other species at other times in their annual cycle (e. g. loss of staging and wintering habitat).

Weather may have played a role in the extremely low rate of nest initiation recorded in 1990. April 1990 was drier and warmer than normal, but May had 2.5 times greater than normal precipitation and temperatures below normal (Province of British Columbia 1990a, 1990b). Females that would have begun nesting in early May could have been delayed by poor weather. Rains did not stop until after the first week of June, after all but the latest nest initiation dates recorded during previous years. Wood Ducks may be particularly susceptible to inclement weather in the Creston valley as it is near the northern limit of the species' breeding range in the Pacific flyway (Bellrose 1976).

The increase in the density of Wood Duck nests in Corn Creek Marsh in 1989 was the result of a group of nest boxes installed close together on posts over water. Nest boxes were erected in that area because I had noted large concentrations of Wood Ducks feeding and loafing in that pond in 1988. Use of these boxes was high in 1989, but the rate of parasitism was also high and the rate of success of the nests was low. Other researchers have noted density-related problems of high parasitism and low nesting success (Jones and Leopold 1967, Strange et al. 1971, Haramis and Thompson 1985, Gauthier 1986, Semel and Sherman 1986, Semel et al. 1988, Eadie 1989). If close, highly visible nest sites encourage parasitism among Wood

Ducks it is not clear why females initiated nests in such situations when more concealed nest sites were available. There may have been some habitat characteristics that were superior to other areas, leading to the high rates of nest initiation (Lacki et al. 1987). Sousa and Farmer (1983) considered the maximum density of successful Wood Duck nests to be 12.5 per ha. Nest density in Corn Creek Marsh in 1989 was in excess of this figure.

Because most unsuccessful nests were abandoned before any eggs disappeared, and because many abandoned clutches could be left for many days without the eggs being disturbed, I concluded that predation on unattended eggs was low in this population and, therefore, hens would seem to have little to gain by increasing their nest attentiveness to deter egg predators such as raccoons and squirrels from the nest.

3. NEST ATTENTIVENESS

Methods

The nest attentiveness of female Wood Ducks was monitored in 1989 and 1990 with electronic temperature recorders (Figure 2). The recorders were designed and assembled specifically for this project by the Simon Fraser University Electronics Shop. Each recorder was self-contained and consisted of a temperature transducer probe and a waterproof plexiglass box that housed a printed circuit board and two 6 V lantern batteries. Each recorder's central processing unit was programmed to take a reading once every three minutes from the transducer and to emit a quiet "beep" every time a temperature was recorded. The "beep" ensured that the recorders were operating properly. A three minute interval allowed continuous monitoring of nests for up to 48 days without downloading data to a computer. Data were stored on-board as hexadecimal values in a zero-power random access memory chip. I calibrated each probe in an ice bath to compensate for variation in the temperature response of individual transducers. Each probe was placed in ice until the recorder reading no longer changed. This reading was assumed to equal 0° C.

When a Wood Duck nest was discovered, a temperature recorder was usually installed within 24 hours. Sawdust and

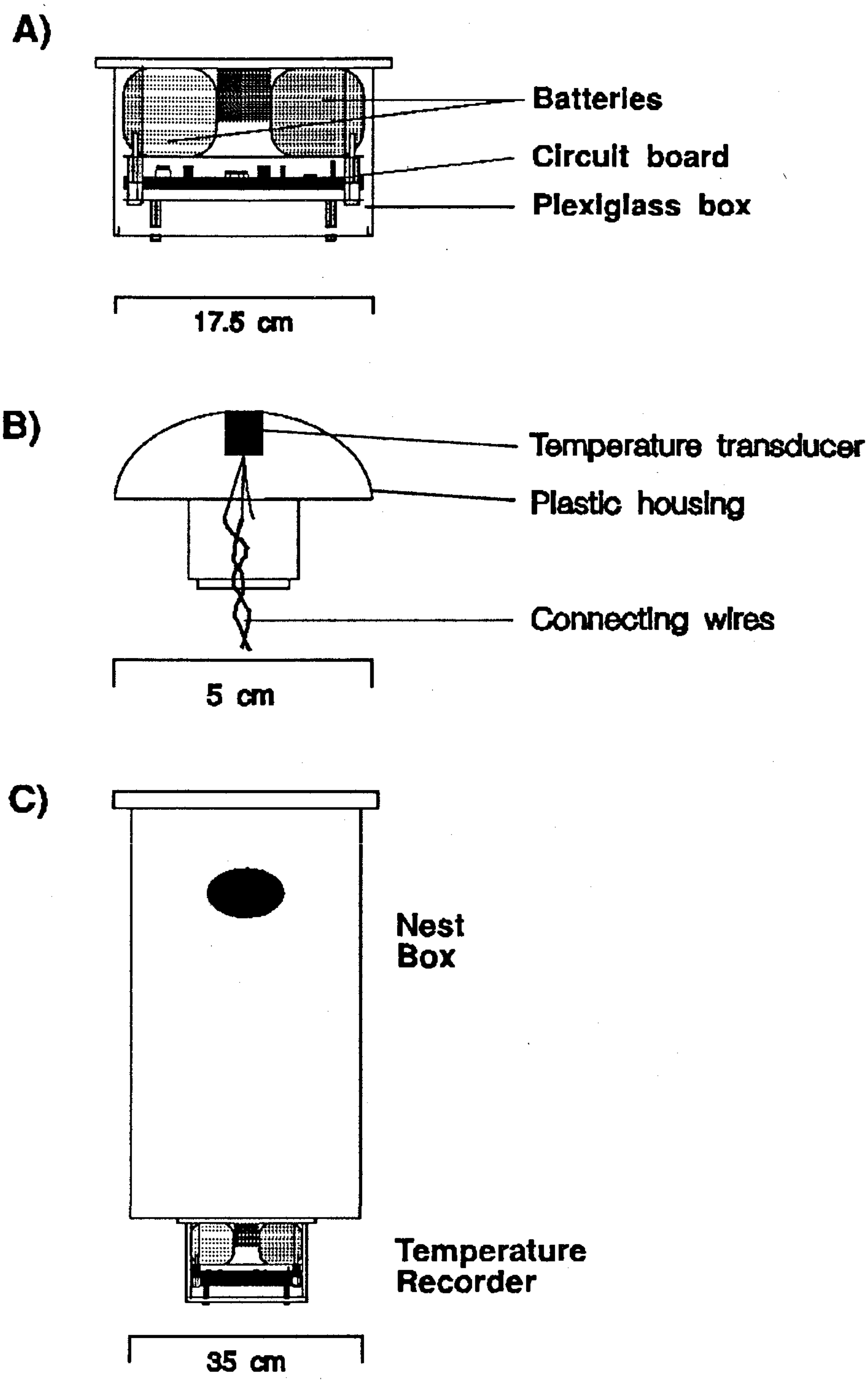

Figure 2. Electronic temperature recorders used in monitoring nest attentiveness data: A) temperature recorder; B) temperature probe; C) nest box with temperature recorder installed. Connector and connector wire for (A) and (B) are not shown.

eggs were removed from the box and a 2.5 cm hole was drilled through the centre of the nest box's bottom. The temperature transducer probe was placed into the hole and secured in place with a plywood plate. The recorder was covered with burlap, to make it less conspicuous to the birds and the public, and fastened to the underside of the box with four wood screws. The times the recorder was installed and started were recorded. The sawdust and eggs were returned to the nest box such that the temperature transducer was at the bottom of the nest bowl and touching the eggs.

Recorders were removed from nests 35-40 days after the onset of incubation, or sooner during occasional nest checks if the nest had been abandoned. Data were downloaded to an "IBM compatible" personal computer using the terminal emulation program ZSTEMpc-VT100 version 2.2 (KEA Systems Ltd., Vancouver B. C.). Hexadecimal values were converted first to decimal values (y) and then to degrees celsius (x) based on the equation: $x=(y-b)/m$, where b represents the ice bath calibration data, and m represents standard voltage input data (V/°C) supplied by the electronics shop. Each temperature reading was then assigned a date and time based on the time the respective temperature recorder was started during installation.

Diel patterns of nest temperatures were examined graphically for each day. Sharp drops in nest temperature of more than 3° C were interpreted as periods spent off the nest by the hen. Rapid increases in temperature were interpreted as the hen returning to the nest. Time off (where the sharp drop began) and time on (where temperature began increasing) were noted and daily sums of attentive periods were calculated for each hen. As birds neared the end of incubation, inattentive bouts were difficult to determine from temperature data. Consequently, only nest attentiveness data from the egg-laying and early incubation periods were used in analyses.

Results

Monitored nests were as successful as unmonitored nests (chi-square test: n=49, P>0.05). Temperature recorders failed at three nests in 1989 and at one nest in 1990. Egg-laying data for one nest were omitted in 1990 because the nest was discovered after the hen had begun incubating. Figure 3 illustrates a typical temperature record. Figure 4 shows the pattern of attentiveness of the same Wood Duck hen over the entire period monitored. Figure 5 shows the mean daily temperature for the same nest during the entire period monitored. Since the temperature probe was at the bottom of the nest and rarely in direct contact with the brood patch of the hen, temperatures reported are lower than actual egg temperatures. For all monitored nests, the length of attentive bouts measured by the recorders and by observers were similar, although recorders underestimated attentive

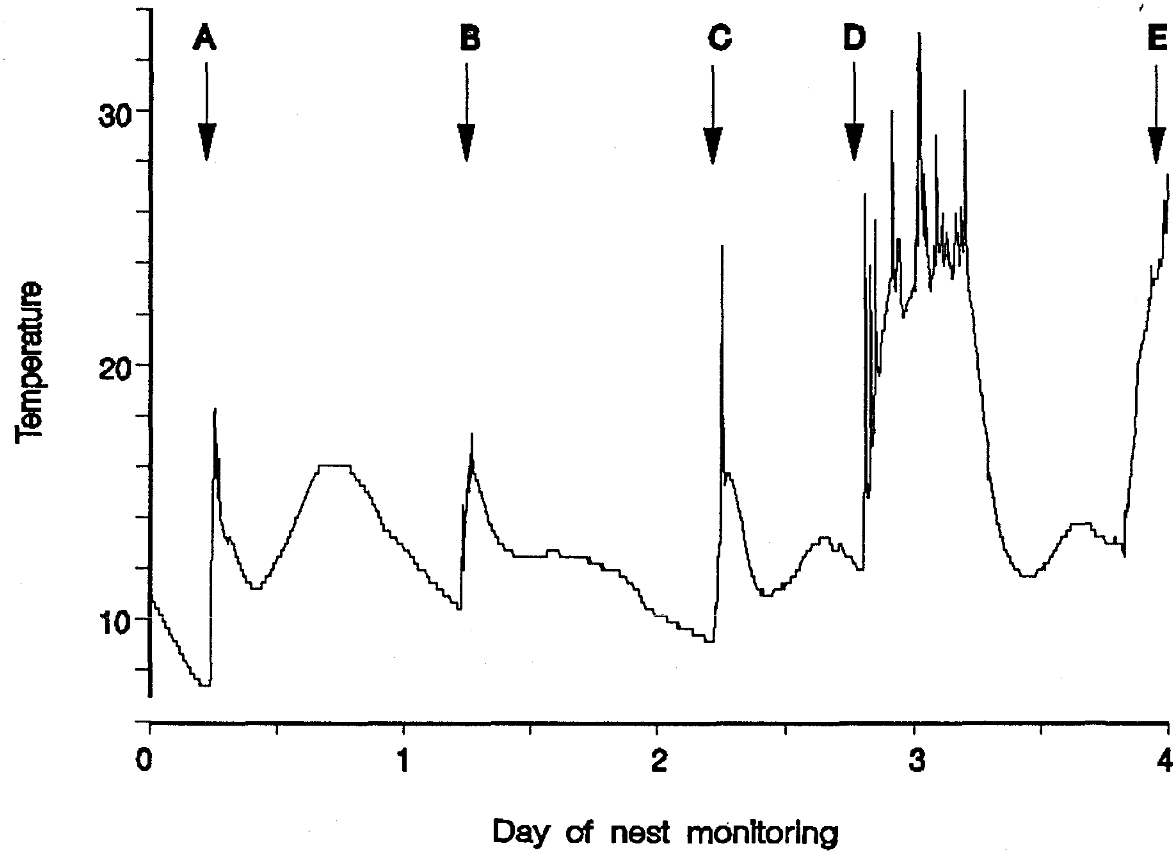

Figure 3. Sample recording of nest attentiveness by a Wood Duck hen over four days beginning at 12:00 am after a recorder was installed. Arrows indicate temperature increases associated with egg-laying (A, B, C) and nights spent in the nest box (D, E).

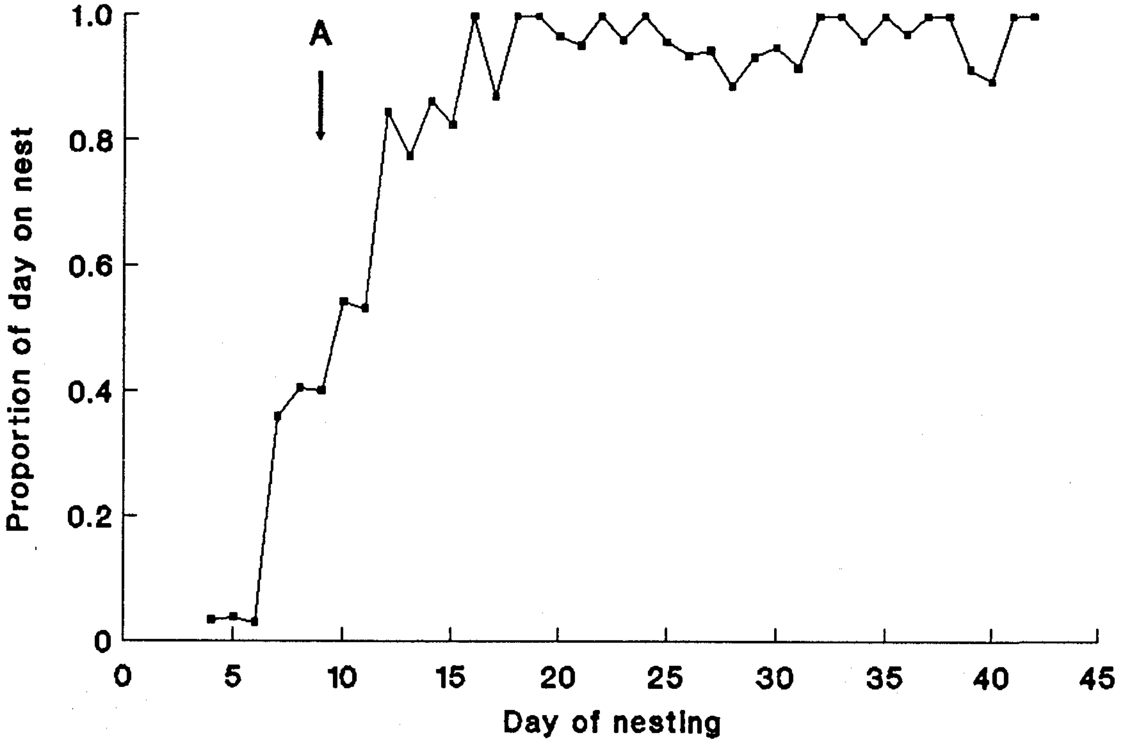

Figure 4. Sample recording of nest attentiveness by a Wood Duck hen. The temperature recorder was installed after three eggs were laid. The last day of egg-laying is shown at A.

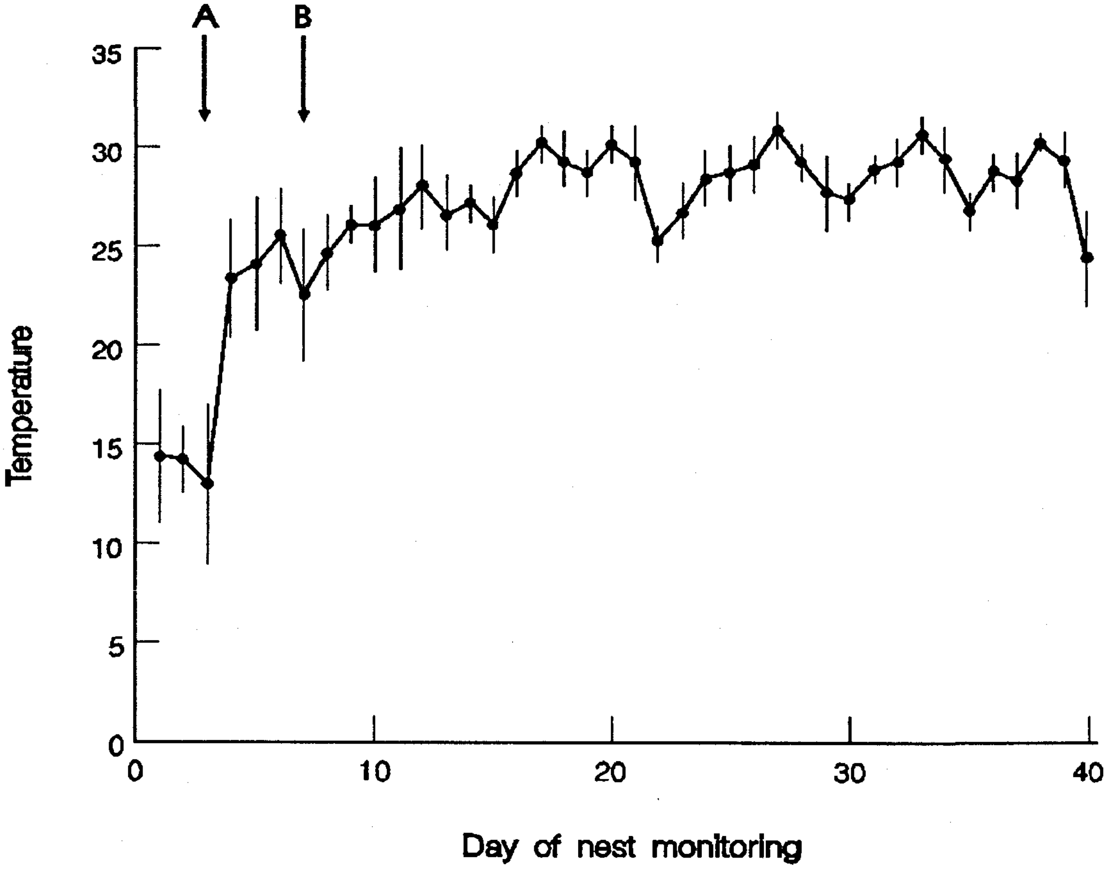

Figure 5. Daily mean temperatures (± 1 SD) recorded during the egg-laying and incubation periods of a Wood Duck hen. The hen began spending nights in the nest box at "A" and the final egg was laid at "B".

bouts by about 30 minutes (linear regression: $y=0.002+1.02x$, $n=12$, $r^2=0.96$, $P=0.0005$; see Chapter 5).

Females began spending the night in nest boxes and raising the temperature of eggs at various times towards the end of the egg-laying period. The modal date of the onset of this behaviour was 6 May 1989 and 1990 (n=22) for nests checked late in egg-laying (see Chapter 2) and nests monitored electronically. Among the 18 nests electronically monitored during 1989 and 1990, females began spending the night in the nest box when there were as few as four eggs in the nest. Only one hen waited until her clutch was complete before spending the night on the nest. On average, hens began spending the night in the nest box when there were 7.4 ±0.6 (n=22) eggs in the nest.

The mean incubation period of the nine successful nests that were successfully monitored with temperature recorders in 1989 was 31.0 ±0.6 days.

Discussion

Temperature recorders underestimated the time spent on the nest by egg-laying females. The discrepancy was probably due to the time spent in the nest box after a hen had entered, but before she had settled on the eggs. Also, the heat applied to eggs takes time to warm the temperature probe. When a hen leaves the nest, the probe is insulated by the eggs and down feathers and therefore takes time to respond to the hen's absence.

Wood Ducks have been reported spending nights in nest boxes late in the egg-laying period. Breckenridge (1956) monitored the attentiveness pattern of a female and found that she spent the last three nights of the egg-laying period on the nest. Stewart (1962) reported a Wood Duck laying an egg the morning after incubation began. Although the incubation period of ducks has generally been assumed to begin after the egg-laying period (Afton 1979), quantitative studies have indicated that incubation begins gradually during egg-laying (Caldwell and Cornwell 1975, Cooper 1978, Afton 1979, this study). Kennamer et al. (1990) found that incubation late in the egg-laying period by Wood Ducks led to developmental asynchronies within clutches of up to five days by the end of the egg-laying period. Larger clutches exhibited the greatest degree of asynchrony and the lowest hatching success. The purpose of incubation during the egg-laying period is not known. Arnold et al. (1987) hypothesized that the declining viability with time of the first few eggs laid in the clutch could be offset by early, partial incubation; however, eggs left unhatched would then tend to be the first laid and this was not the case in this study.

4. BROOD PARASITE BEHAVIOUR

Introduction

The stimuli parasitic females use to find nest sites in which to lay eggs influence the behavioural strategies available to host pairs to avoid the costs associated with brood parasitism. A parasite may simply enter nest boxes (or cavities) at random and lay eggs, or she may search a number of boxes until she finds a duck nest containing eggs, and then lay an egg. Alternatively, she may use the behaviour of host pairs in the vicinity of nest boxes to locate nests. If parasites use one of the first two strategies, then increasing nest attentiveness would be a host's only defence against brood parasitism. A female that spends a greater proportion of time on her nest would be more likely to prevent a parasite from entering her box than a female that did not spend as much time in the nest box. If, however, parasites use the third strategy, then the behaviour of host pairs outside the nest box may also be important; the probability of being parasitized could be influenced by the time hosts spend in the vicinity of their nests, and by the behaviour of males while their mates are on nests.

Before examining the behaviour of host birds, I conducted an experiment to determine what stimuli parasitic females used when choosing sites to lay eggs: the presence of suitable nest sites, the presence of duck eggs, or the presence of duck eggs and nearby duck pairs.

Methods

The experiment was first conducted in Corn Creek Marsh from 15 April to 15 May 1989, then repeated from 17 April to 4 May 1990. The timing and duration of the experiment were chosen to coincide with the peak of nest initiation and egg-laying by Wood Ducks. Each test day, three nest boxes in 1989, and five in 1990, were selected randomly from the subset of Corn Creek Marsh boxes that were located less than 10 m from water, and were not being used by nesting ducks at that time. Each nest box was assigned randomly to one of three groups: (1) control, (2) eggs, or (3) models and eggs (three boxes were assigned to the latter group per test day in 1990). Control boxes were not manipulated. "Eggs" boxes were provided with six hard-boiled, small chicken eggs arranged in the bottom of the nest box and covered with sawdust as Wood Ducks do during early egg-laying. Eggs were put in the "models and eggs" boxes in the same manner, and male and female Wood Duck decoys were floated 5-10 m in front of each box. I used life-size hunting decoys (Cabela's Inc., Sidney NE) that I had touched-up with red and white acrylic paint. If a box was being used by a duck, the manipulation was moved to the closest available nest box that had not been used previously in the experiment.

Experimental boxes were left undisturbed for three days and then checked for duck eggs. Models and eggs were then moved to new boxes. Boxes were used only once during the experiment. I marked and measured any eggs laid and then monitored the nest, using the same procedure I used to follow nests found during regular nest box checks.

Results

Several observations were excluded from the analyses because some decoys and some eggs disappeared before the three day experimental period had ended. Eggs were not laid in control boxes or in "eggs" boxes in 1989, but eggs were laid in four "eggs and models" boxes (Table 4). This difference was significant (Kolmogorov-Smirnov test: $n=77$, $P<0.01$). One of the four "eggs and model" boxes was parasitized by a Common Goldeneye; however, "eggs and model" boxes were still parasitized significantly more often than "eggs" and control boxes when this observation was excluded. In total, eight Wood Duck eggs were added to three boxes (two sets of two eggs and one of four eggs) during the treatment period. After models and chicken eggs were removed, egg-laying continued in two of these boxes, and the eggs were eventually incubated. In the third box, and in the box parasitized by the Common Goldeneye (one additional Goldeneye egg was added) the clutches were not incubated.

Table 4. Results of the 1989 parasite behaviour experiment. Eggs were laid significantly more often in boxes which contained eggs and had a pair of Wood Duck models floating in front of them (Kolmogorov-Smirnov test: n=77, P<0.01).

treatment	n	boxes used	# eggs laid	incubated
control	27	0	0	0
"eggs"	26	0	0	0
"eggs and models"	24	4*	10*	2

*2 eggs were laid in one box by a Common Goldeneye; however, the result is still significant when this observation is deleted (P<0.01)

In 1990, among 18 control, 28 "eggs" and 28 "eggs and models" boxes, no eggs were laid parasitically by any species.

Discussion

Although only eight parasitic Wood Duck eggs were laid in three nest boxes over the two years of the study, I believe that this experiment provides some evidence that parasitic females observe other pairs to find host nests. Only 16 Wood Duck nests were initiated in nest boxes in Corn Creek Marsh in 1989 (Table 1). The density of Wood Ducks, therefore, was very low and the probability of an "eggs and models" box being parasitized during a three day treatment period was also very low. In addition, the density of Wood Ducks may have reflected the quality of nest sites provided by nest boxes. If a large number of "eggs and models" boxes were in poor locations, the presence of models may not have been an adequate stimulus to induce parasitic females to lay eggs. In fact, some boxes may have been in areas that were only rarely used by Wood Ducks, further lowering the probability of parasitism. I think that a more important result than the frequency of egg-laying in "eggs and models" boxes was the complete absence of egg-laying among control and "eggs" boxes.

In 1990, the density of Wood Duck nests was even lower than in 1989: only six nests were initiated in Corn Creek

Marsh and, consequently, the probability of any experimental nest boxes being parasitized was also lower.

Results from the 1989 trial agree with evidence from previous waterfowl work. Heusmann _et_ _al_. (1980) reported that Wood Ducks had a "strong decoying effect" on one another (p. 911). Also, nest initiation rates were not higher in boxes that contained eggs than in empty boxes. Semel and Sherman (1986) found that when a hen entered a clearly visible nest box to lay an egg, pairs from 0.5-1.0 km away flew to the nest box area and many females attempted to enter the box. Clawson _et_ _al_. (1979) found that parasites usually laid eggs when hosts were absent, but did not report the time of parasitic egg-laying with respect to host egg-laying. Clawson _et_ _al_. (1979) report that 96% of 312 parasitic Wood Duck eggs in their study were laid in boxes that already contained eggs. Since their study did not use experimental nests, one can assume that most of the boxes that contained eggs were active nests. Haramis _et_ _al_. (1983) located eggs laid by parasitic females injected with tetracycline and found tetracycline-marked eggs only in boxes containing other Wood Duck eggs. Redheads (_Aythya americana_) find host nests by searching nesting cover and by observing the nest building and egg-laying behaviour of other ducks (Weller 1959). Weller (1959) also found that Redheads did not lay eggs in artificial nests that did not already contain eggs. Eadie (1989) found that goldeneyes used both control (empty) nest sites and nest sites that contained goldeneye eggs, however, females that laid eggs in the sites that already contained eggs rarely incubated the clutches.

The nest-searching behaviour of parasitic hens explains an interesting nesting pattern described by Morse and Wight (1969), Semel and Sherman (1986) and other studies: often many nest boxes on a study area are not used although brood parasitism occurs at a high rate. Since parasites follow hosts, hens may be opportunistically laying eggs in other nests where the nests are clearly available, rather than initiating their own nests.

Many parasitizing species observe other birds to find host nests (see review by Payne 1977) including obligate brood parasites such as the Brown-headed Cowbird (Molothrus ater; Thompson and Gottfried 1976). Parasites that lay eggs in nesting colonies may not need to observe other birds to find nests since nests are close together and most likely very visible. Cliff Swallows (Hirundo pyrrhonota) parasitize close neighbours and lay their eggs early in, or even before, the hosts' egg-laying period (Brown and Brown 1989). Also, the rate of parasitism varies with the size of nesting colonies. Parasitism is rare, or absent, among solitary nesters or in small colonies (Brown and Brown 1989). In contrast, Barn Swallows (Hirundo rustica) tend to parasitize nests that contain eggs and are farther away from, rather than closer to, active neighbouring nests (Møller 1989). The arrangement of host nests seem to be more important than host behaviour in determining the behaviour of parasites in these species. No data are available that describe the spatial arrangement of parasitic egg-laying relative to the parasites' own nests among Wood Ducks, a species in which hens also initiate their own nests.

That two Wood Duck parasites continued to lay eggs after the removal of chicken eggs and eventually incubated the clutches appears to be very unusual. Eadie (1987) found that Barrow's Goldeneye brood parasites continued to lay eggs in hosts' nests after removal of host birds, however, the parasites never incubated the clutches. With a surplus of nest sites available, I do not know why Wood Duck females would incubate the nests they parasitize. Perhaps they sensed the abandonment of the nest by the host and continuing to lay eggs and to incubate the clutch was less costly than finding another site and initiating a nest.

Using the behaviour of Wood Duck pairs to find nests appears to be a good strategy for parasites. Where nesting is restricted to tree cavities, nest sites are well concealed. Randomly or systematically searching for nest sites and eggs is probably less efficient than simply following egg-laying pairs to their nests; therefore, host pairs could influence their likelihood of being parasitized by altering their behaviour in the area of their nests.

5. HOST RESPONSES TO THE THREAT OF BROOD PARASITISM

Introduction

If brood parasitism is in some way costly, then Wood Ducks should show various behaviours that reduce the chance of incubating eggs that are not their own. These behaviours could be associated with the nest box itself, or with the area surrounding it. The behaviours Wood Ducks use should depend on the behaviour of parasites. I have provided evidence that parasites find host nests by observing the presence of potential Wood Duck hosts neat their nests. A female could avoid being parasitized by staying in the nest box (after laying her own egg) until after the time of day when parasitic individuals in the population normally lay their eggs. Other Wood Ducks would then not see her fly from the box until after they had laid their eggs for the day. Also, if a parasite did try to enter, a host could repel her; Semel and Sherman (1986) observed hosts repelling intruding hens. There is a cost to hosts associated with staying in the nest box in that a hen reduces her available foraging time just when a great deal of energy is required for egg formation (Drobney 1980, 1982). There is evidence of a tradeoff between foraging and nest attentiveness in some species (European Starling, *Sturnus vulgaris*, Drent *et al*. 1985; Junglefowl, *Gallus gallus*, Hogan 1989).

In addition, males could perform behaviours that are intended to distract or harass nearby Wood Ducks and perhaps other hole-nesting ducks, while ignoring other species which do not normally parasitize Wood Duck nests.

I conducted two experiments with egg-laying Wood Duck pairs to determine whether they changed their behaviour when other pairs were nearby. Wood Duck decoys were used to simulate potential parasites (see Chapter 4) and life-sized Mallard decoys (Cabela's Inc., Sidney NE) were used to simulate ducks that do not parasitize Wood Duck nests.

Methods

(1) time budgets

Observations of Wood Duck pairs were conducted in Corn Creek Marsh during April and May 1989. Each nest was observed for two mornings as soon as possible after the discovery of the nest. When only one nest was available for observation, my assistant and I observed the same nest, otherwise we each observed different nests. Observations began at first light and ended after the female left the nest box and the pair left the area. The birds were observed through a spotting scope from a portable blind located 50 to 100 m from the nest. The blind was pitched the evening before observations were made to minimize disturbance to the birds' morning behaviour.

Activities of the male and female were recorded, when visible, at 30 sec intervals and classified as "feeding", "preening", "displaying", "swimming", "loafing", or "alert". An individual was classified as "feeding" if it skimmed the surface of the water with its bill or appeared to be searching for food. When birds used their bill to smooth feathers, the activity was classified as "preening". I defined "displaying" as those behaviours described as "sexual behaviours" by Johnsgard (1965). If a bird was moving in the water, and did not appear to be searching for food, I classified the behaviour as "swimming". When birds floated, or stood, very still and tucked their bill under their wing, or closed their eyes periodically, the behaviour was classified as "loafing". If a bird was still but holding its head high and actively looking around, I recorded the behaviour as "alert".

The times when pairs arrived and left the areas of their nest boxes were recorded. The nest box area was defined as the area within approximately 100 m of the nest box. The times when hens entered and left nest boxes were noted when observed, or were extrapolated from temperature recorder data (see Chapter 3). Nests were checked immediately after observation periods to confirm that eggs had been laid, except where such checks would disturb the behaviour of nearby ducks. If the first day of observations was successful (a female was observed entering and leaving the box and an egg was laid), the nest was left undisturbed for a day and then a second day of observations was carried out.

Nests were assigned alternately to one of two treatments for the second day of observations: a pair of Mallard or a pair of Wood Duck models were floated 5-10 m in front of the nest box. The models were anchored in place the afternoon before the observation period to avoid disturbing the pair's behaviour the next morning. Data collected were the same as on control days.

Time budgets were compiled for each bird every morning they were observed. Based on the time each duck was visible, the percent time they spent performing the different behaviour categories was calculated. Comparisons were made first, between observers, and second, between control and treatment days.

(2) female nest attentiveness

To further examine the possible influence of the threat of brood parasitism on the attentiveness of host females, I conducted an additional experiment using models in 1990. Prior to manipulation, egg depositions in experimental nests were closely monitored and I removed extra eggs if more than one egg was laid in a nest per day. Nests were presented with a model Wood Duck pair on day five of egg-laying. Models were floated 5 m to 10 m in front of nests during the early afternoon to ensure that hens were not in the box (thereby minimizing disturbance) and remained in place for approximately 24 hours. Nest attentiveness data were extrapolated from the nest temperature recorders (see Chapter 3) and were compared, for each nest, between the day of treatment and the days prior to and following the treatment.

Results

(1) time budgets

Behavioural observations were attempted on 26 nest-mornings. I had several problems collecting these data. First, the majority of monitored nests were close together (see Chapter 2) and during an observation period, Wood Ducks or other cavity-nesting ducks were often in the area of the focal pair's nest. Second, the time of day that hens returned to the nest to lay eggs was inconsistent. Pairs often returned before sunrise, or even returned the previous evening and did not leave the box until mid- to late-morning (see Chapter 3). During these long attentive bouts, males did not spend all their time around the nest box. Therefore, it was difficult to determine whether or not a hen was in the box, and whether a nearby lone male(s) was the mate of the egg-laying female. As a result, I was unable to collect two complete mornings of data for most nests that were observed and sample sizes for statistical tests are small. Because of the difficulties I had collecting behavioural data, I abandoned Mallard model presentations and concentrated on collecting a larger sample of Wood Duck presentations. Hereafter all reference to "models" refers to Wood Duck models.

There was no difference between the proportion of time Wood Ducks spent performing different behaviours when visible to both observers on four of five morning when we observed the same nests (chi-square tests: $P>0.05$).

Data were inadequate to test for possible differences between male behaviours when models were present at the nest and when they were absent. Males were often absent from the nest box area and I collected time budget data for only one male on both control and treatment days. There was no difference in the proportion of time males were visible to observers when models or live potential parasites were near by and when they were absent (Wilcoxon matched pairs test: $n=12$, $P=0.11$).

According to temperature recorder data and observations, egg-laying females spent more time on nests as the egg-laying period progressed (linear regression: $y=0.72 +11.57x$, $r^2=0.48$, $n=21$, $P=0.0003$; Figure 6). There was no difference between the nest attentiveness of hosts ($P=0.18$), nor between the time of day females entered ($P=0.59$) or left ($P=0.59$) the nest box, when models were present compared to when they were absent (all Wilcoxon matched pairs tests:

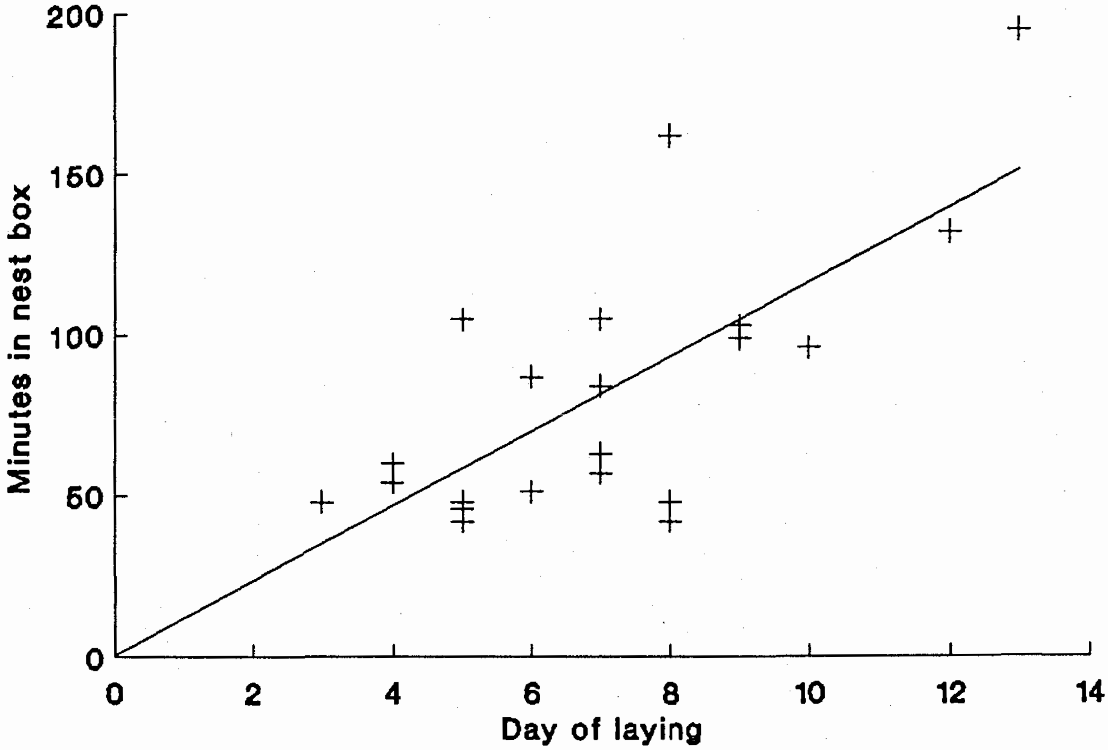

Figure 6. Change in the nest attentiveness of Wood Duck hens as the egg laying period advances ($y=0.72+11.57x$, $r^2=0.48$, $n=21$, $P=0.0003$).

n=6; Table 5). I also compared the nest attentiveness of hens when either models or live cavity-nesting birds were in the area to the nest attentiveness of hens when no potential parasites were in the area. Again, there was no difference in attentiveness (Wilcoxon matched pairs test: n=8, P=0.14; Table 5), but hens did leave the nest box later in the morning when potential parasites were nearby (Mann-Whitney U-test: n=8, P=0.04; Table 5). Most females spent time in the area of the nest box before entering to lay an egg (13.4 ±3.3 minutes in 6 of 10 observation periods) but usually left the area immediately after egg-laying (remained in area twice in 11 observed departures for 6.2 ±4.1 minutes). Data were inadequate to test for differences in arrival and departure times between days when potential parasites were present and when they were absent.

(2) female nest attentiveness

Hens were significantly more attentive on the day of a model presentation than on the day before (Wilcoxon matched pairs test: n=10, P=0.04; Figure 7) and more attentive on the day after than on the day before a presentation (Wilcoxon Matched Pairs test: n=10, P=0.04). Nest attentiveness did not differ between the day of the presentation and the day following (Wilcoxon matched pairs test: n=10, P=0.46; Figure 7). I also examined the nest attentiveness of 1989 females on days seven, eight, and nine of egg-laying. These days corresponded to the days before,

Table 5. The time of day females entered ("time in") and left ("time out") their nest boxes, and the time in hours they spent in the box ("time on") during control and treatment days.

		Control	Treatment	
Models	Time in	5:51 ±0:18	10:09 ±4:34	P=0.59[1]
	Time out	6:58 ±0:32	6:28 ±0:55	P=0.59[1]
	Time on	1:07 ±2:40	4:20 ±2:34	P=0.18[1]
Models and live ducks[4]	Time out	6:11 ±0:11	7:28 ±0:22	P=0.04[2]
	Time on	1:06 ±0:11	3:30 ±1:59	P=0.14[3]

[1] Wilcoxon matched pairs test: n=6

[2] Mann-Whitney U-test: n=8

[3] Wilcoxon matched pairs test: n=8

[4] "live ducks" were nearby cavity-nesting waterfowl, no additional "time in" data were collected when "live ducks" were nearby

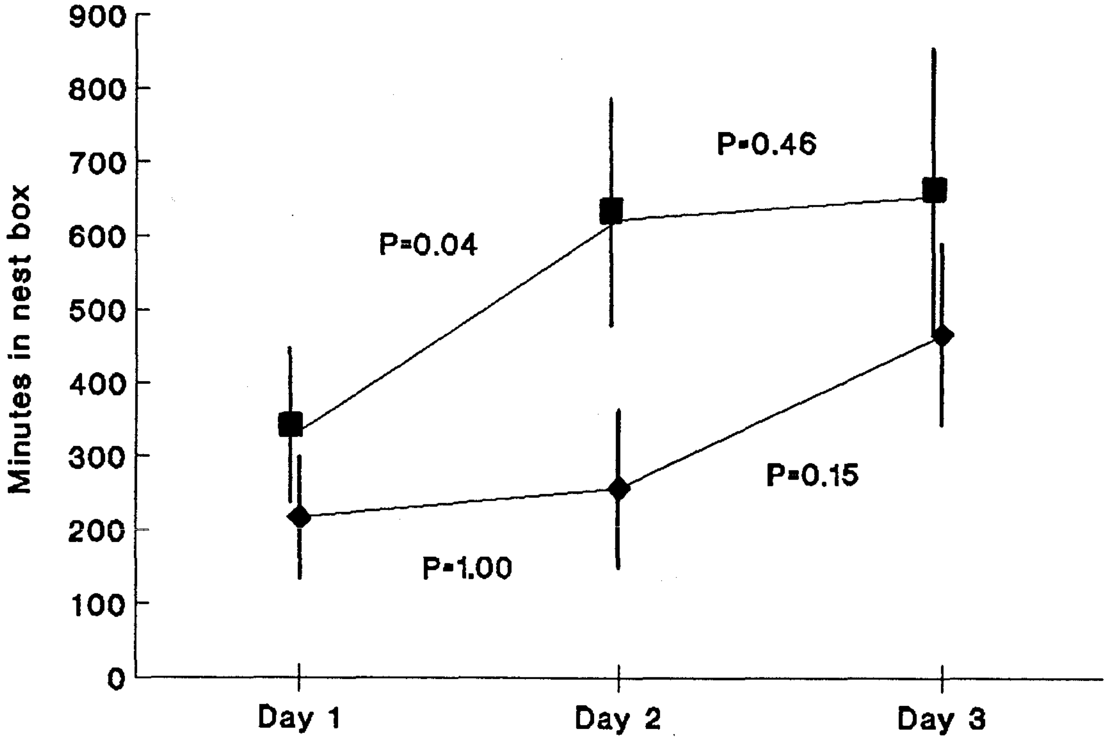

Figure 7. Attentiveness of Wood Duck hens on the day before (Day 1), during (Day 2), and after (Day 3) model presentations (squares, n=10). Data from unmanipulated 1989 nests are also presented (diamonds, n=12) for equivalent days in the egg-laying period.

during, and following models presentations for 1990 birds. Nest attentiveness did not differ between day seven and day eight of egg-laying (Mann-Whitney U-test: n=12, P=1.00; Figure 7), nor between day eight and day nine of egg-laying (Mann-Whitney U-test: n=12, p=0.15; Figure 7). Hens were significantly more attentive on day nine than on day seven (Mann-Whitney U-test: n=12, P=0.04).

Discussion

Due to the difficulties I had collecting behavioural data, the power of my statistical tests was probably inadequate to test for differences in the behaviour of egg-laying pairs between days when potential parasites (as represented by models) were present and when they were absent. When I examined the nest attentiveness patterns of hens more closely in 1990, I found that females increased the time they spent in the nest box on the day they were presented with models. The increase in nest attentiveness of unmanipulated females was not significant on the same days of egg-laying. In addition, I made three observations.

First, males appeared to play no role in nest defence against conspecifics. Aggression by mates of egg-laying hens towards nearby birds or models occurred rarely, and males often strayed from the nest box area when the hen was on the nest. If brood parasitism among Wood Ducks depresses the success of nesting attempts only moderately, or if there are extra females and there is enough time available to re-pair, then the cost to males of performing defensive behaviours exceeds the benefit of defending the nest against brood parasitism. Straying from the nest site while the hen is on the nest may allow the male to seek extra-pair copulations at a time when he is least likely to be cuckolded.

Second, females usually spent time in the area of the nest box before laying an egg but rarely afterwards. This may indicate a tactic used by hens to minimize the opportunity parasites had to locate their nest sites. Hosts may have spent time in the area prior to nest entry to ensure that no other Wood Ducks were using that area. Leaving immediately after egg-laying minimizes the time that the hosts were conspicuous around the nest.

Third, leaving the nest later in the morning may also reduce the risk of brood parasitism. Wood Ducks lay eggs early in the day (Grice and Rogers 1965, this study), and hens that stay on the nest until later in the morning are more likely to avoid exposing their nest during the few hours when parasites are egg-laying.

Few studies, particularly those concerned with waterfowl species, have examined the response of hosts to the threat of brood parasitism. Semel and Sherman (1986) found that females were reluctant to approach or enter the nest box when other Wood Ducks were nearby. In contrast, Clawson _et_ _al_. (1979) found that hens were usually tolerant of nest intruders during the egg-laying period. Fuller and Bolen (1963) found two Wood Duck females using the same nest box and even incubating simultaneously. Weller (1959) observed a brooding female Canvasback (Aythya valisineria) aggressively excluding a Redhead parasite from her nest. However, among goldeneyes, which are site-specific territorial species, territoriality does not serve to guard the nest from brood parasites (Eadie 1989).

Hosts of some other species are capable of driving potential parasites away (see review by Payne 1977). Barn Swallows nest guard vigorously prior to incubation (Møller 1989) and individuals that nest guard less are parasitized more often (Møller 1987). The intensity of nest guarding is greater during the pre-laying period than during the egg-laying period. This is likely due to the foraging requirements of egg-laying females. White-fronted Bee-eaters (Merops bullockoides) also appear to defend nest sites against parasites (Emlen and Wrege 1986). Nest guarding in this colonial species also has its costs: females are exposed to harassment by assemblages of males when they leave the nest cavity, and the female and her mate suffer an increased energetic stress by the restriction of male foraging to over-exploited areas near the nest. Wood Duck hens may also pay an energetic price by increasing nest attentiveness, particularly during early egg-laying. The energetic demands of breeding hens peak during the first six days of egg-laying (Drobney 1980, 1982). Responding to the threat of parasitism by increasing nest attentiveness during this time may stress hens to such a degree that they are likely to abandon the nesting attempt, or to a degree that their nest attentiveness patterns later in nesting are disrupted, reducing the efficiency of incubation.

The species that appear to respond most vigorously to brood parasitism are altricial, and the intensity of the response probably reflects the costliness to the host of being parasitized (Andersson 1984). Among Wood Ducks, the costliness of brood parasitism may be insufficient to warrant changes in behaviour that put the nesting attempt at risk.

6. HOST RESPONSES TO BROOD PARASITISM

Introduction

In this chapter I consider the possibility that a Wood Duck female changes certain aspects of her behaviour to avoid further parasitism after a parasite's egg has been added to the nest bowl. If a female is able to detect the presence of an extra egg or eggs in her nest she could increase her nest attentiveness during the remainder of the egg-laying period to prevent, or make it more difficult for brood parasites to return to her nest. Brood parasites are known to return to nests to lay additional eggs (Chapter 4), even after the removal of host hens (Eadie 1987). The increase in nest attentiveness by hosts could be costly in terms of lost foraging time during an energetically expensive period in the breeding season (Drobney 1980, 1982).

A female could also increase her nest attentiveness during incubation to compensate for the greater thermal requirements of the parasitically enlarged clutch. Nests that contain more eggs than are normally laid by a hen are probably more difficult to incubate; Mandarin Ducks (_Aix galericulata_) rarely abandon large clutches, but large clutches take longer to incubate than small clutches (Davies and Baggott 1989). Also, the addition of parasitic eggs probably reduces the proportion of hosts' eggs that hatch. Alternatively, the hen could abandon the nest if the added eggs resulted in a clutch size too costly to incubate (Jones and Leopold 1967, Clawson et al. 1979, Andersson and Eriksson 1982, Semel and Sherman 1986).

To test these possibilities experimentally, I added eggs to a number of nests to determine whether host hens changed their nest attentiveness during the egg-laying and incubation periods after foreign eggs were added to the nest.

Methods

Hard-boiled, small chicken eggs were added to nests in 1989 to simulate brood parasitism. Small chicken eggs are nearly identical in size and shape to Wood Duck eggs. Wood Duck eggs are light brown but the chicken eggs were not painted to match this colour. Eggs were added to nests at least 48 hours after egg-laying observations (see Chapter 5) were completed but before the incubation period began. Unfortunately, unlike 1988, brood parasitism was frequent in 1989 and several of my planned control nests were parasitized naturally. As a result, I stopped adding chicken eggs to nests early in the egg-laying season and examined the nest attentiveness of hens that had been parasitized naturally, as well as experimentally. Parasitic eggs added before I had discovered the nest (usually one to four days after nest initiation), could not be detected. Nests were followed like other nests through incubation and hatching (Chapter 2). The presence or absence of the chicken eggs was noted during post-hatch and post-abandonment checks. Nest attentiveness data were extrapolated from temperature recorder data (see Chapter 3).

Results

During daily nest checks, I detected 13 Wood Duck eggs laid by parasites in eight nests during the egg-laying period. I added a total of seven chicken eggs to four nests. Three of these nests received two eggs placed in nests two days apart. The fourth nest received only one egg because the hen was incubating when I returned to add the second egg. Two of the nests I added eggs to were nests that earlier had been presented models. For these nests there might have been a confounding effect between experiments.

Not all naturally parasitic eggs were included in the analysis because I was unable to recover data from two temperature recorders (see Chapter 3). I examined the response of hens to the first parasitic egg. The nest attentiveness of hens did not differ between the day of parasitism and the day after (Wilcoxon matched pairs test: n=10, P=0.10). Among successful nests, parasitized clutches were larger than unparasitized clutches (12.6 ±0.7 vs. 8.0 ±0.6; Mann-Whitney U-test: n=11, P=0.01).

Among successful nests, the hatchability of eggs decreased with increasing clutch size (linear regression: $y=1.24-0.03x$ where $x>7$, $r^2=0.36$, $n=11$, $P<0.03$; Figure 8). None of the added chicken eggs were found buried in the nesting material or pushed outside the nest scrape during incubation and post-hatch checks. One chicken egg was ejected from a nest and was found on the ground below the box's entrance.

Discussion

I added eggs after the hosts had left the nest for the day and the next day would have been the first time that hosts would have had the opportunity to sense the chicken eggs. I found no evidence that females increased their nest attentiveness on the day after chicken eggs were added to the nest; however, the sample size was small and, consequently, the power of the test was low.

Either my data were inadequate to reject the null hypothesis although it was false, or else the hens did not react to the chicken eggs because they did not recognize the eggs as foreign or, alternatively, they recognized the eggs as foreign but did not react to them because doing so would have been more costly than the benefit of increasing their nest attentiveness.

Heusmann et al. (1980) found that Wood Ducks accepted hard-boiled, dyed chicken eggs without incidence of

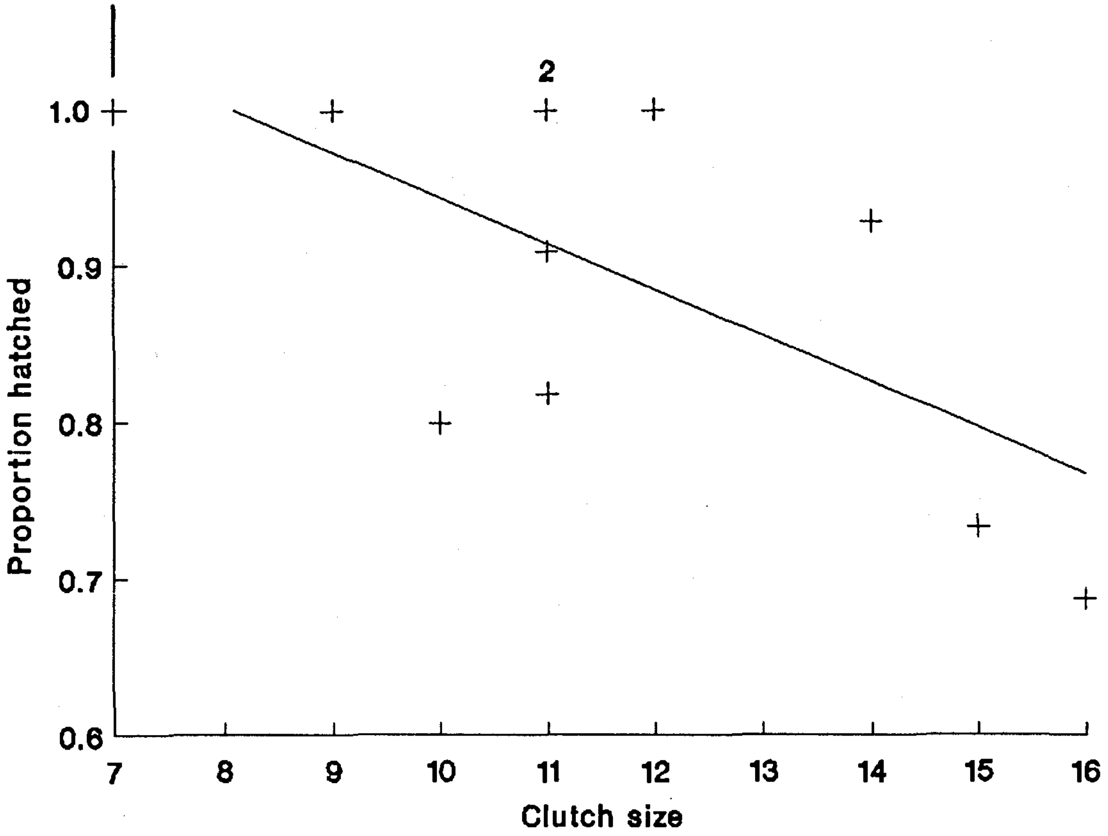

Figure 8. Hatchability of Wood Duck eggs as a function of clutch size among successful nests in 1989 (linear regression: $y=1.24-0.03x$, $r^2=0.36$, $n=11$, $P<0.03$).

abandonment. Weller (1959) added a variety of eggs to different ground-nesting waterfowl species' nests. He found that eggs similar to the hosts' were accepted during the egg-laying period. Hens ejected, buried, or pushed spotted chicken eggs to the side of the nest bowl. He tested the discrimination abilities of Canvasbacks, a species of duck that is frequently parasitized by Redhead ducks, and found that they rejected a spotted chicken egg (n=1) but always accepted Redhead eggs (n=3) which are very similar to Canvasback eggs. This species seems to have some egg discrimination abilities, but is unable to detect the eggs of its most frequent parasite. Eadie (1989) found that goldeneye females deserted only extremely large clutches and did not adjust their clutch size in response to the addition of parasitic eggs.

Hens that accept eggs similar to their own may be mistaking them for eggs that they laid. If so, they should reduce the number of eggs they lay themselves. Andersson and Eriksson (1982) found that during early egg-laying, Common Goldeneyes reduced their clutch by the number of eggs added by parasites (c. f. Eadie 1989), but did not adjust their clutch size when eggs were added late in egg-laying. Parasitic eggs added late in egg-laying are unlikely to cause adjustments in host clutch size because egg formation takes several days after follicles have ruptured (Welty 1962), and it would be too late to stop the laying of the last few eggs. Wood Ducks are also known to reduce their clutch size in response to brood parasitism (Weller 1959, Clawson *et al*. 1979) although they did not appear to do so in this study, as naturally parasitized clutches were significantly larger than unparasitized ones.

Perhaps Wood Ducks also have some rudimentary ability to recognize eggs (although Andersson and Eriksson [1982] suggest that this may be hampered in cavity-nesters by deep, dark nest sites), but the low cost of brood parasitism has resulted in a selection pressure too weak for hens to evolve the fine discriminatory ability necessary to identify the eggs of conspecifics, or even chicken eggs.

Among altricial species, where the costs associated with brood parasitism are assumed to be greater than among precocial species (Andersson 1984), the evolution of conspecific egg discrimination is not common. Among European Starlings, intraspecific brood parasitism is frequent (Andersson 1984), but hosts seem unable to distinguish parasitic starling eggs from their own, although they know when parasitic eggs have been added to the clutch. Stouffer *et al*. (1987) found that parasitic Starling eggs were removed from the nest if present before the host started to lay eggs, but they were rarely removed if added after egg-laying had started, and then only along with all the other (host) eggs in the clutch. Similarly, Groove-billed Anis (*Crotophaga sulcirostris*; Vehrencamp 1978) and Acorn

Woodpeckers (Melanerpes formicivorus; Mumme et al. 1983) removed parasitic eggs before, but not after, the beginning of egg-laying. Power et al. (1989) suggested that European Starlings actually leave room in their clutches for parasitic eggs. Their argument was based on the fact that the most productive clutch size was one egg larger than the clutch size most often laid by Starlings.

Hatching success declines with clutch size (Weller 1959, Heusmann 1972, this study), although the number of young hatching still increased slightly with increasing clutch size in this study. Whether hens compensate for larger clutches by increasing their nest attentiveness is not known. Unfortunately, some nest attentiveness data I collected late in the incubation period is suspect (see Chapter 3) and I had too few unparasitized clutches to adequately test whether the nest attentiveness of hens with parasitized clutches was higher than that of hens with unparasitized clutches during incubation, or if nest attentiveness changed with increasing clutch size. No studies are available to support the suggestion that females with larger clutches increase nest attentiveness to increase the hatchability of eggs. Harvey (1971) and Inglis (1977) found that more attentive Snow Goose and Pink-footed Goose (Anser brachyrhynchus) hens, respectively, were more successful (due to lower predation) than less attentive geese, but the authors did not report clutch size data.

7. CONCLUSIONS

The distribution of box-nesting Wood Ducks changed dramatically between 1988 and 1989, then the rate of nest initiation declined in 1990, particularly in Corn Creek Marsh. In 1988, one third of the nests had nearest neighbours closer than 100 m. In 1989, this proportion rose to three quarters. This was due primarily to the addition of a large number of nest boxes in an area frequented by feeding and loafing Wood Ducks. The frequency of brood parasitism detected also changed, increasing substantially in 1989. The majority of parasitism that year occurred in this area of concentrated Wood Duck nesting. I demonstrated that Wood Duck parasites observed host pairs to find nests in which to lay eggs; therefore, high rates of brood parasitism in areas of significant nesting concentrations are to be expected. However, why Wood Ducks chose to initiate nests in such an area when other boxes were available is less clear. Perhaps birds were reacting to advantages of other habitat characteristics regardless of the increased risks of brood parasitism.

The manner in which Wood Ducks should respond to parasitism presumably depends on the costliness of parasitic behaviour in terms of their reproductive success. From the literature, the principle cost of brood parasitism to hosts among precocial species is the lower hatchability of eggs in larger clutches than in smaller clutches, which could result in fewer host ducklings in a brood. Higher rates of parasitism result in abandonment of the nesting attempt. My results agree with this: the hatchability of eggs in larger clutches was lower, and areas where nests were frequently parasitized suffered high rates of abandonment. However, Wood Ducks did not respond to this cost of parasitism and its threat as expected.

Since parasites observed hosts to find nests, I expected hosts to react to the presence of other Wood Ducks near their nests. However, I failed to detect any changes in the behaviour of host pairs during the egg-laying period in the nest box area when potential parasites were nearby, although I found some evidence that females may have increased their nest attentiveness. Similarly, I believed that hens would discourage further brood parasitism after an egg was laid in their nest by increasing nest attentiveness. Wood Duck hens did not increase their nest attentiveness the day after parasitic eggs were added to their nests.

Clearly, anti-parasite behaviours are poorly developed among Wood Ducks, as they are in other waterfowl species that are regularly parasitized. The cost associated with brood parasitism is lower in Wood Ducks than in species with altricial young since the post-hatching cost of foreign eggs is likely negligible among precocial species. Brood parasitism may even be beneficial (Eadie et al. 1988); however, brood parasitism can have an impact through the lower hatchability of host eggs.

The appropriate response of hosts to brood parasitism depends not only on the costliness of brood parasitism when it occurs, but also on the frequency with which it occurs. Unfortunately, no data are available that describe rates of parasitism in "natural" situations (i. e., no nest boxes). Although Rohwer and Freeman (1989) claim that nest boxes and natural cavities are equally easy for birds to find, Semel et al. (1988) found that nests in boxes placed in a manner which resembled natural cavities (isolated and visually occluded) were parasitized less frequently and were more successful than nests in highly visible boxes erected close together.

Wood Ducks probably did not evolve the behavioural responses to cope with the moderate costs associated with parasitism because hosts of this traditionally solitary species infrequently encountered other Wood Ducks near their nest cavities. In most box-nesting situations, including this study, suitable nest site densities are far greater than those provided by natural sites (Prince 1968, Gilmer et al. 1978, Peterson and Gauthier 1985, Soulliere 1988, Lowney and Hill 1989) and higher rates of parasitism result. Although no response to brood parasitism, or to its threat, is the best strategy for hosts when the frequency of parasitism is low, it is not the best strategy in unnatural situations where parasitism is frequent, and it leads to low nesting success.

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APPENDIX. Morphometrics of Wood Duck hens and their eggs trapped on the nest in 1988 and 1989. Mass is expressed in grams. Culmen, tarsus, and wing lengths are expressed in mm. N is the number of eggs used to calculate mean egg volume. Volume is expressed in ml.

Date	Mass	Culmen	Tarsus	Wing	N	Volume	SD
28/5/88	525	32.0	32.9	220	8	34.6	2.0
02/6/88	565	33.1	32.8	226	10	36.5	1.8
26/5/88	645	32.8	34.4	231	7	35.8	1.5
02/6/88	505	31.8	33.3	221	12	32.2	2.3
23/5/88	520	34.4	33.5	219	7	31.6	1.0
13/6/88	565	33.0	34.0	219	10	34.5	2.3
30/5/88	540	31.8	34.8	222	10	32.8	1.6
20/6/88	585	32.0	34.8	222	4	34.1	1.3
15/5/89	620	32.4	32.9	256	12	36.5	1.3
25/5/89	540	31.4	33.6	215	9	30.3	1.5
25/5/89	650	33.1	34.8	228	10	33.6	2.9
03/6/89	600	33.6	34.0	228	9	37.0	9.7
07/6/89	580	34.4	30.9	---	10	33.5	1.1
14/6/89	560	33.4	32.4	221	11	36.2	1.8