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BROOD PARASITISM AMONG WATERFOWL NESTING ON ISLANDS AND PENINSULAS IN NORTH DAKOTA[1]

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Abstract. During 1985 and 1986 I studied interspecific brood parasitism among seven species of waterfowl nesting on 36 islands and 24 peninsulas in central North Dakota. On islands, 40% of 178 nests were parasitized with an average of 4.3 parasitic eggs, and on peninsulas 2% of 275 nests were parasitized with an average of 2.2 parasitic eggs. Redheads (*Aythya americana*) were the primary parasite, adding eggs to 92% of all parasitized nests. Species nesting in open cover were parasitized at a higher rate than species nesting in dense cover. Nests with parasitic eggs had fewer host eggs and there was a negative association between the number of parasitic eggs and the success of host eggs. Parasitized nests had lower success, but additional parasitic eggs had no added influence on nest success. Interspecific brood parasitism had significant negative effects on dabbling ducks on islands but Lesser Scaup (*Aythya affinis*) were little affected. Even so, the number of young hatched per nest was much higher on islands because of the high loss of eggs to predators on the mainland. Parasitic eggs were deposited during the middle of the nesting season, but the peak of parasitic laying occurred before the peak of normal nesting.

Key words: *Redhead;* Aythya americana; *brood parasitism; islands; nesting; peninsulas; waterfowl.*

INTRODUCTION

Brood parasitism occurs in five of the 170 families of birds and is found commonly among the Anatidae (Weller 1959). Weller (1959), in his classic paper on brood parasitism in waterfowl, reported that 21 species of North American Anatidae laid eggs in nests of other species. Parasitic laying can reduce the clutch size and the nest success rate of the host and increase the abandonment rate (Weller 1959, Joyner 1976). The Redhead (*Aythya americana*), a common brood parasite, normally nests over water in emergent vegetation, and usually parasitizes nests located in similar habitat (Weller 1959, Lokemoen 1966). Weller (1959:350) noted that "[T]he Redhead apparently makes no effort to stray from its preferred habitat to parasitize nests." However, Redheads have been observed nesting in uplands, although the average nest was only 2.1 m from open water (McKnight 1974).

In a study of islands in Canada, Giroux (1981) found that many duck nests situated in the uplands near water were parasitized by Redheads. He suggested that it would be valuable to learn the rate of brood parasitism in nests in the surrounding uplands. The purposes of this study were, first, to examine the incidence and effects of brood parasitism among seven duck species nesting on islands in central North Dakota, and second, to compare the rate of brood parasitism on islands with the rate on nearby peninsulas.

STUDY AREA AND METHODS

Data were collected from 36 islands and 24 peninsulas located in the prairie pothole region of central North Dakota during 1985 and 1986. This region has a moderately rolling topography and contains numerous natural wetlands. Most islands and peninsulas were located in the larger, more permanent wetlands. In general, the shorelines along the islands and peninsulas were bare with few tall emergent plants. Islands averaged 0.6 ha in size and ranged from 0.04–4.2 ha. The peninsulas averaged 10.2 ha and ranged from 1.6–31.6 ha. Egg predators were trapped and removed from half of the peninsulas but were not trapped on the islands, which contained few resident predators.

Any scrape with one or more eggs was considered a nest. The species of duck incubating the nest was determined by identifying the flushed hen and by characteristics of the down, eggs, and breast feathers (Klett et al. 1986). The identity of each parasitic egg was determined by color,

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size, shape, and texture (Harrison 1978). Analyses were restricted to interspecifically laid eggs because of the difficulty in detecting intraspecific parasitism. A nest was considered successful if at least one host or one parasitic egg hatched. Nest success was calculated from the modified Mayfield method (Johnson 1979).

Islands were searched once in May and once in June to locate nests. On islands, nests were located by two or more people who systematically searched all habitats by walking parallel transects. Peninsulas were searched twice in May and twice in June. On peninsulas, nests were located by pulling a 1.3 cm diameter rope weighted with chains or a 1.0 cm diameter chain over all nesting cover (Klett et al. 1986). All nests in this study were located on dry ground in the uplands. Nest locations were plotted on a map and flags were set 4 m north of each nest. All nests were revisited to determine nest fate.

The size of each island and peninsula was measured on aerial photographs. Vegetation on each island and peninsula was classified as low shrub, tall shrub, grass, or forb. Plant density was measured with a height-density pole as modified by Kirsch et al. (1978). Wetlands were classified using a system developed by Stewart and Kantrud (1971).

STATISTICAL TESTS

A Kolmogorov-Smirnov test was employed to compare the distributions of nest initiation dates for parasitized nests and unparasitized nests. We compared square root and arcsine transformed (Zar 1984:239–241) proportions of nests parasitized on islands and peninsulas using an analysis of variance (ANOVA). In these comparisons we used islands and peninsulas as the sample units.

ANOVA was used to compare clutch size and the number of host eggs that hatched in parasitized and unparasitized nests. In these comparisons we used the nest as the sample unit. As clutch size did not differ between islands and peninsulas, nests from both types of areas were used to compare clutch sizes. Only islands were used to examine the effects of parasitic eggs on the success of host eggs and on host clutch size because egg success was higher on islands and there were few parasitized nests on peninsulas. To examine the effect of the number of parasitic eggs on host clutch size, we used a linear regression analysis. The hypothesis that parasitized nests had lower nest success than unparasitized nests was tested as suggested by Johnson (1979). A logistic regression was used to determine if the number of parasitic eggs in a nest affected whether or not the clutch hatched.

ANOVA was used to compare the mean number of parasitic eggs laid in host nests on islands and peninsulas. Using only nests on islands, we compared the proportion of parasitized nests among host species following the methods of Fleiss (1973:92–96). Finding significant differences, we next compared the average rate of parasitism for open-cover nesters with closed-cover nesters. We used a Spearman rank correlation to relate the rate of brood parasitism by species with a ranking of cover openness at the nest. The cover-openness rankings were derived from data on 3,257 nests reported by Higgins et al. (in press). To quantify openness we summed the percentages of the categories tent, erect upon, and between clumps excluding cover categories under fallen vegetation, erect closed, and under dominant plant. Also, the rate of parasitism was plotted against variables for vegetative type, plant density, island size, and wetland class to locate possible relationships. Variables that showed trends in these plots were entered into a multiple regression procedure.

RESULTS

RATES AND TIMING OF PARASITISM ON ISLANDS AND PENINSULAS

Duck nests located on islands were parasitized more frequently than duck nests located on peninsulas. The differences were significant for all species studied except Mallards (*Anas platyrhynchos*) and Redheads (Table 1). For all species, 71 (40%) of the 178 nests found on islands were parasitized, compared to only six (2%) of the 275 nests located on peninsulas.

Redheads were the most important parasitic species. On islands, Redheads, Lesser Scaup, and Gadwalls (*Anas strepera*) laid eggs in 96%, 4%, and 3%, respectively, of the parasitized nests. On peninsulas, Redheads laid parasitic eggs in three nests, Lesser Scaup in two nests, and Gadwalls in one nest. Parasitized nests on islands received a mean of 4.5 parasitic eggs compared to a mean of 2.2 for nests on peninsulas (Table 2). Parasitic eggs were also more successful on islands, where 34% hatched compared to 15% that hatched on peninsulas.

TABLE 1. A comparison of the frequency of interspecific brood parasitism for seven duck species nesting on islands and peninsulas in central North Dakota, 1985 and 1986.

Host species	Islands			Peninsulas			ANOVA comparisons	
	No. of nests	No. parasitized	No. of islands	No. of nests	No. parasitized	No. of islands	F	P
Mallard	16	4	9	51	1	13	2.3	0.14
Gadwall	64	22	15	106	3	15	13.9	<0.01
B-w Teal	13	8	7	54	0	17	20.8	<0.01
N. Shoveler	9	5	7	13	0	8	8.1	0.01
N. Pintail	17	12	8	14	0	9	7.6	0.01
Redhead	17	0	5	1	0	1	—	—
L. scaup	42	20	15	36	2	8	7.7	0.01
Total or avg.	178	71	66	275	6	71	22.0	<0.01

Two nests on islands were parasitized by two species. One Gadwall nest contained eight host eggs along with four Lesser Scaup eggs and three Redhead eggs. In the other case a Mallard nest received two Redhead eggs and one Gadwall egg.

On islands, the seasonal distribution of nest initiations for parasitized nests was significantly different from that for unparasitized nests (Kolmogorov-Smirnov, $D = 0.325$, $n_1 = 92$, $n_2 = 48$, $P = 0.003$) (Fig. 1). In general, nests that were parasitized were initiated during the middle portion of the nesting season. Also, the peak nest initiation period for parasitized nests occurred about a week earlier than the peak for unparasitized nests.

EFFECT OF PARASITISM ON HOST CLUTCH SIZE AND NEST SUCCESS

Overall, the host clutch size was reduced by 2.5 eggs, with parasitized clutches averaging 7.4 eggs and unparasitized clutches averaging 9.9 eggs. Mean clutch sizes for parasitized Mallard, Gadwall, Blue-winged Teal (*Anas discors*), and Northern Pintail (*Anas acuta*) nests were significantly lower than mean clutch sizes for unparasitized nests (Table 3). Parasitized Northern Shoveler (*Anas clypeata*) clutches were not significantly different than unparasitized clutches. Lesser Scaup seemed unaffected by parasitic intrusions and parasitized nests contained no fewer host eggs than unparasitized nests. In dabblers, each parasitic egg reduced the clutch size of the host by 0.40 to 0.85 eggs.

On islands, nest success was significantly higher for unparasitized nests of Gadwall, Blue-winged Teal, and Northern Shoveler compared to parasitized nests (Table 4). The overall success of unparasitized dabbling duck nests was 82% compared to only 59% for parasitized nests. Nest success was not higher for unparasitized Lesser Scaup nests. Nests that were parasitized did not suffer further reductions in success with increasing numbers of parasitic eggs ($P > 0.08$). The number of host eggs that hatched was significantly reduced by the presence of parasitic eggs only for Gadwalls ($F = 4.63$, $P = 0.04$). There

TABLE 2. Frequency and intensity of brood parasitism by Gadwalls, Redheads, and Lesser Scaup on islands and peninsulas in central North Dakota, 1985 and 1986.

Parasitic species	Site	Parasitized nests	Parasitic eggs			
		n	n	$\bar{x}$	No. suc.	(%)
Gadwall	Island	2	4	2.0	3	75
	Penin.	1	4	4.0	0	0
Redhead	Island	68	309	4.5	102	33
	Penin.	3	4	1.3	2	50
L. Scaup	Island	3	8	2.7	3	37
	Penin.	2	5	2.5	0	0
Total or avg.	Island	71[a]	321	4.5	108	34
	Penin.	6	13	2.2	2	15

[a] Note that two nests were parasitized by two species.

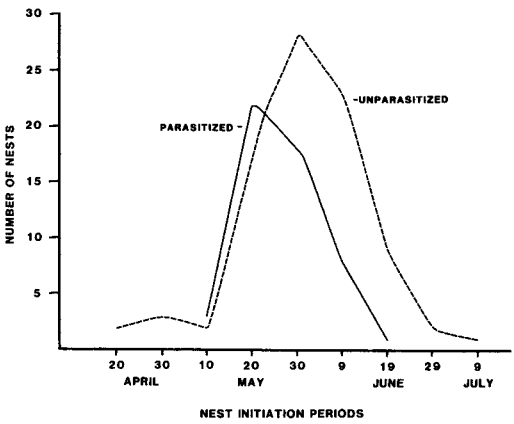

FIGURE 1. Comparison of nest initiation dates by 10-day periods for parasitized and unparasitized nests on islands.

were significant ($P < 0.04$) negative relations between the number of parasitic eggs (NP) in a nest and the number of successful host eggs (NS) for Gadwall [NS = 7.63 – 0.70(NP)], Northern Shoveler [NS = 10.0 – 1.0(NP)], and Northern Pintail [NS = 7.12 – 0.59(NP)].

HOST AND HABITAT PREFERENCES OF BROOD PARASITES

Redheads were the only species with a sufficient sample size to examine differences in the number of eggs added to nests of hosts. Redheads parasitized all of the other six species of ducks studied. Considering islands only, there was no difference among species in the number of Redhead eggs laid in parasitized nests (ANOVA, $F = 0.61$, $P = 0.718$). However, significant differences ($\chi^2 = 11.932$, 5 df, $P = 0.035$) were detected in the proportion of nests parasitized among the host species. The average proportion (64%) of nests parasitized for the three species nesting in open cover (Northern Pintail, Blue-winged Teal, and Northern Shoveler) was significantly higher ($\chi^2 = 8.354$, 1 df, $P = 0.004$) than the average proportion (38%) of the other three species.

Although the proportion of nests parasitized was related to cover openness at the nest, we found no such association with island vegetative type or density. Also, island size and wetland class explained little of the variation in the rates of parasitism. None of these variables, singularly or in combination, adequately modeled parasitism on islands.

DISCUSSION

RATES AND TIMING OF PARASITISM ON ISLANDS AND PENINSULAS

Other studies of parasitism found that Redheads were the most important brood parasite, Ruddy Ducks (*Oxyura jamaicensis*) were second most prevalent, with little parasitism by Gadwalls and Lesser Scaup (Weller 1959, Joyner 1976, Giroux 1981). No parasitic Ruddy Duck eggs were found in this study, probably because Ruddy Ducks would have difficulty walking in the uplands to locate host nests.

The 40% rate of interspecific parasitism recorded in this study exceeded the 19% and 8% noted respectively by Giroux (1981) and Hines

TABLE 3. Mean host clutch size for parasitized and unparasitized nests of six duck species and the relationship between the number of parasitic eggs and the number of host eggs in nests on islands and peninsulas in central North Dakota, 1985–1986.

Host species	Nest type	No. nests	Clutch comparisons		Clutch relationships[a]	
			Mean	*P*	Regression	*P*
Mallard	Para.	4	6.0	<0.01	CS = 9.51 – 0.40 (NP)	<0.01
	Unpara.	45	9.6			
Gadwall	Para.	24	8.6	<0.01	CS = 9.94 – 0.44 (NP)	<0.01
	Unpara.	119	9.9			
B-w Teal	Para.	8	6.0	<0.01	CS = 10.64 – 0.85 (NP)	<0.01
	Unpara.	44	10.8			
N. Shoveler	Para.	4	9.2	0.26	CS = 10.46 – 0.42 (NP)	<0.01
	Unpara.	14	10.4			
N. Pintail	Para.	11	5.4	0.02	CS = 8.16 – 0.51 (NP)	<0.01
	Unpara.	12	8.0			
L. Scaup	Para.	22	9.4	0.94	CS = 9.48 – 0.06 (NP)	0.55
	Unpara.	36	9.4			

[a] CS = host clutch size and NP = number of parasitic eggs.

TABLE 4. The effect of interspecific brood parasitism on nest success of the host, on islands in central North Dakota, 1985 and 1986.

Host species	Unparasitized nests			Parasitized nests			P
	Exposure days	Nest suc. (%)	(SE)	Exposure days	Nest suc. (%)	(SE)	
Mallard	148	79	0.7	0	—	—	—
Gadwall	706	82	0.2	250	66	0.7	<0.01
B-w Teal	59	57	1.7	84	45	1.7	<0.01
N. Shoveler	33	100	—	37	16	3.7	<0.01
N. Pintail	29	100	—	75	100	—	—
L. Scaup	360	75	0.5	374	76	0.5	0.90

and Mitchell (1984) on island and dike habitats. Also, the mean of 4.5 parasitic eggs per parasitized nest found in this study was higher than the 2.7 parasitic eggs found by Giroux (1981) and the 1.6 noted by Hines and Mitchell (1984). This high rate of parasitism was surprising as Redheads composed only 6.7% of the breeding ducks in North Dakota in 1985–1986 (U.S. Fish and Wildl. Serv. 1990). Also, Redheads normally nest over water and accomplish most parasitic activity in emergent vegetation. However, it is obvious from this study and that of Giroux (1981) that Redheads do focus parasitic nesting on islands.

The enhanced numbers of Redheads at islands may be the result of adult females and their progeny returning and nesting near previously successful nesting sites. Johnson (1978) noted that Redhead females have a strong tendency to home to breeding sites, and Lokemoen et al. (1990) reported that successful Mallard and Gadwall females home at a higher rate than unsuccessful ones. On my study area, several islands had large numbers of Redheads and high rates of parasitism, whereas other islands had no Redheads.

Islands probably had a higher incidence of parasitism than peninsulas because most parasitism was due to Redheads, which composed 9% of the nesting ducks on islands and less than 1% on peninsulas. Also, Redheads normally nest in emergent vegetation over water or near the shoreline (Bellrose 1976) and Redhead females usually locate host nests by searching near water or watching other females (Weller 1959, Heusmann et al. 1980). Host nests on islands were located closer to shorelines, where Redhead nesting activities are normally concentrated. Peninsulas were also located on wetlands, but they were larger than islands and the average nest was located farther from water. Reinecker and Anderson (1960) found that 2.9% of the duck nests on dikes or peninsula-like habitat were parasitized by Redheads or Ruddy Ducks, a figure similar to that found on peninsulas in this study.

Even though the rate of parasitism was lower on peninsulas than islands, it exceeded the rate normally found in prairie uplands. Upland nests are normally widely distributed, far from water, and brood parasitism is rare. In South Dakota, Duebbert and Lokemoen (1976), working in upland fields near numerous small wetlands, found no interspecific brood parasitism in 570 duck nests.

EFFECT OF PARASITISM ON HOST CLUTCH SIZE AND NEST SUCCESS

Weller (1959), Joyner (1976), and Talent et al. (1981) have reported that parasitized nests had smaller host clutch sizes than unparasitized nests. Weller (1959) noted that nest success of parasitized nests was lower than that of unparasitized nests and he suggested that increased numbers of parasitic eggs would further depress host nest success. I also noted lower nest success for parasitized nests but found no relationship between the number of added eggs and host nest success.

On islands, parasitism had little effect on Lesser Scaup, was not measured for Redheads, but negatively affected dabbling ducks. The impact of parasitism might best be estimated by comparing duckling production from unparasitized nests with parasitized nests. For unparasitized dabbling duck nests, the product of the average clutch size (9.9 eggs) and the average nest success (0.82) would yield an average production of 8.1 young. In contrast the average parasitized nest hatched only 4.3 young (7.3 eggs × 0.59 nest success). Because 43% of the dabbling duck nests were parasitized, the overall average number of young hatched per nesting attempt was 6.5. However, ducks benefit by nesting on islands because the reduction in clutch size caused by nest parasitism is much less than egg losses due to predation on the mainland. In this study, an average

of only 4.0 young hatched from nests on peninsulas.

HOST AND HABITAT PREFERENCES OF BROOD PARASITES

Joyner (1976) found that nests of the Northern Pintail (42%) and Cinnamon Teal (*Anas cyanoptera,* 41%) (the western counterpart of the Blue-winged Teal) were parasitized the most, and Mallards the least (28%). Giroux (1981) did not find this pattern and noted that Mallards had the highest percentage of nests parasitized. I found that species with open nest sites were parasitized at a higher rate. This suggests that brood parasites are not seeking specific hosts but are seeking the most accessible, albeit acceptable, host species.

In this study, much like work by Weller (1959) and Giroux (1981), there was no apparent relationship between cover type and the rate of parasitism. Wetland type probably influences use by Redhead pairs but there was no link between wetland type and the rate of parasitism in this study. Also, there was no relation between parasitism and island size, although I would expect few nests to be parasitized by Redheads or Lesser Scaup in the interior of large islands. Giroux (1981) noted that Mallard and Gadwall nests located close to water were most likely to be parasitized.

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