

BEHAVIORAL INTERACTIONS AMONG BROOD PARASITES WITH PRECOICIAL YOUNG: CANVASBACKS AND REDHEADS ON THE DELTA MARSH¹

RODNEY D. SAYLER

Department of Natural Resource Sciences, Washington State University, Pullman, WA 99164-6410

Abstract. I studied brood parasitism among 110 *Aythya* nests and filmed 125 interactions at 14 Canvasback (*A. valisineria*) and 5 Redhead (*A. americana*) nests to describe host-parasite behavior. Redheads outnumbered breeding Canvasbacks by about 5.4 to 1 on the Delta Marsh, Manitoba, and heavily parasitized Canvasback nests ($\bar{x} \pm SE = 7.6 \pm 2.8$ eggs/nest). High rates of parasitism resulted in delayed host embryo development, up to 23% longer incubation periods, and extended brooding behavior at nests containing unhatched or late-hatching eggs. Females followed potential hosts to locate nests, made pre-laying nest visits, and selected active rather than deserted nests to parasitize. Parasitic laying was not markedly deterred by host resistance and occurred at all stages of host laying and incubation, resulting in only 34% of parasitic Redhead eggs hatching in successful Canvasback nests. Laying females aggressively displaced incubating hosts, causing eggs to be accidentally displaced from nests. Host Canvasback eggs were five times as likely to be cracked and twice as likely to be dislodged from nests than were parasitic Redhead eggs. Hosts limited defensive actions to pushing against intruders or pecking at the heads of parasitic females, resulting in some parasitic eggs being deposited outside nest bowls. Incubating females may be constrained from using highly aggressive behavior to deter brood parasites partly because of fitness costs of fighting and breaking or displacing their own eggs. The existence of host defensive behavior suggests that brood parasitism may present significant fitness costs, even among species with nidifugous precocial young, by affecting the critical processes of synchronous hatching and nest exodus.

Key words: brood parasitism; Canvasback; *Aythya valisineria*; Redhead; *A. americana*; host-parasite behavior.

INTRODUCTION

Brood parasitism is common among waterfowl (Anatidae) which have precocial young that generally are not fed by parents (Sayler 1992). Brood parasitism potentially can impose severe fitness costs on waterfowl hosts because of reduced egg success and higher nest desertion rates (Weller 1959, Andersson and Eriksson 1982, Sayler 1992). If brood parasitism is detrimental, there should be strong selection pressures for hosts to evolve defensive measures. Rothstein (1975) estimated that avian species exposed to Brown-headed Cowbird (*Molothrus ater*) parasitism could change from parasitic "egg acceptor" species to "rejectors" in as little as 20-100 years. Why then do high rates of brood parasitism occur among waterfowl and yet the group appears to be characterized by relatively unsophisticated host-parasite interactions?

After observing a Canvasback female apparently tolerate parasitic intrusion by a Redhead,

Nudds (1980) hypothesized that such tolerance was a way that hosts might recoup any fitness losses through enhanced post-hatch survival of young in larger mixed broods. Due to various "selfish herd" effects (Hamilton 1971), a female's progeny might be buffered from predation by the additional precocial young, which require little or no extra parental care. The fitness costs of post-hatch brood amalgamation appear to be minimal among waterfowl (Eadie et al. 1988, Afton and Paulus 1992). McKinney (1954), however, photographed a Canvasback female defending her nest against laying by a parasitic Redhead female. Redhead and Canvasback nests often have dislodged eggs that have fallen into the water beneath parasitized nests (Sayler 1992). Thus, it is unclear whether waterfowl hosts normally tolerate or defend against brood parasitism and at what fitness cost or benefit.

Many hypotheses have been offered to explain potential adaptive benefits of waterfowl brood parasitism (Sayler 1992), but there are few descriptions of how hosts actually respond to brood parasites (Sayler 1985, 1992, Sorenson 1991). I

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filmed nesting Canvasbacks and Redheads to describe host-parasite encounters, document the effects of parasitism, and evaluate the apparent adaptive basis for host behavior.

STUDY AREA AND METHODS

I conducted this study on the 27,000 ha Delta Marsh in Manitoba, Canada, from 1977–1980. The Delta Marsh is an extensive shallow marsh extending for over 20 km along the south shore of Lake Manitoba (Hochbaum 1944). Dominant emergent plants include giant reed (*Phragmites australis*), cattail (*Typha* spp.), and bulrush (*Scirpus* spp.), with whitetop rivergrass (*Scolochloa festucacea*) in extensive surrounding wet meadows. The physiognomy and flora and fauna have been described in detail elsewhere (Hochbaum 1944, Sowls 1955, Anderson and Jones 1976).

I studied breeding Redheads and Canvasbacks about 8 km east of the Delta Waterfowl and Wetlands Research Station on several smaller bays projecting north from Clair Lake (Sayler 1985). Six blinds on 4 m high towers were erected at wetland edges, allowing observers to enter and leave without disturbing birds on the water. I captured Redheads of both sexes in decoy traps from May 1 to June 15 each year using live Canvasback or Redhead females as "bait" (Anderson et al. 1979). Birds were individually identified with nasal markers (Sugden and Poston 1968) and aged by plumage characteristics (Dane and Johnson 1975, Sayler 1995).

I used time-lapse photography at nests to monitor behavior of incubating females and interactions with parasitic females. Super-8 movie cameras, fitted with intervalometers and night shutoff switches, exposed film at 1 frame/min, recording diurnal activities for about three days between film changes. Visible photographic images were registered from about 05:00–21:00 CST. Cameras were mounted on 2 m high poles 2–3 m from nests and the 4–6x lens adjusted to allow a clear view of the nest bowl from this elevated position. Cameras photographed a variable area (0.5–1 m) around each side of the nest, depending upon surrounding vegetation. Incubating females adjusted to the presence of movie cameras within about 15–30 min after returning to a monitored nest for the first time, and thereafter, appeared to ignore the camera. Minimal durations for encounters at nests were calculated assuming

1 frame/min and by using battery-operated clocks set in the background behind nests.

Photographed nests were visited every 3–4 days to change film and monitor egg fate and deposition of parasitic eggs. Other nests were visited every 7–10 days. Parasitic eggs deposited intraspecifically could usually be identified by differences in size, shape, and color from the host clutch (Sorenson 1991) or by the occurrence of fresh eggs during the incubation period. All eggs were individually marked with waterproof ink. The sediment underneath and vegetation around nests were carefully searched when nests were found, when marked eggs disappeared from clutches, and at nest termination to locate eggs displaced into the water. I candled live eggs and examined the contents of failed eggs to determine embryo age (Weller 1957, Caldwell and Snart 1974). I determined that parasitic eggs were laid during filmed encounters at nests by either observing the egg on the edge of the clutch after a female left or by confirming the presence of new eggs during subsequent nest visits.

To evaluate the hypothesis that host presence would increase the occurrence of parasitic laying, I repeated Weller's (1959) experiment in which he attempted to solicit parasitic laying by Redheads in artificial nests. I modified his experiment by placing live Canvasback females in 1.75 m diam holding cages adjacent to five artificial nests containing three chicken eggs. These decoy nests were placed in areas of emergent cover used for nesting and were inspected like natural nests from 15 May to 15 June, 1978.

Statistical analyses were conducted using version 3.1 of JMP® (SAS Institute 1995). Factors predicting the duration of nest encounters were compared using analysis of variance (ANOVA) models and *t*-tests. The proportion of laying and nest visits occurring before vs. after 12:00 was compared with an expected even distribution using a likelihood ratio test (*G* test). For purposes of exploratory analysis, I treated egg location (interior vs. outer ring of clutch) as an independent observation each time I visited a nest because females turn and reposition eggs frequently during the day (Afton and Paulus 1992). Furthermore, I never observed an incubated clutch in which eggs had not clearly shifted positions or in which the ratio of interior to exterior eggs did not change among host and parasitic eggs between nest visits. Means are reported \pm SE.

RESULTS

PARASITISM RATES

Redhead females outnumbered nesting Canvasback females on the Delta Marsh by about 5.4 to 1, based upon repeated pair counts (total: 527 Redhead pairs, 97 Canvasback pairs) during April and May. Redheads parasitized 95% of 60 Canvasback nests, laying an average of 7.6 ± 2.8 eggs per nest (range = 0–30). About 52% of 846 eggs found in and underneath Canvasback nests were Redhead eggs. The only Canvasback nests to escape Redhead parasitism were those deserted early in laying before they received any parasitic eggs. At least 21% of 405 Redhead eggs in Redhead nests also resulted from intraspecific parasitism, using differing color, size, and laying date as conservative criteria of parasitic eggs.

NEST SELECTION

Parasitic females typically located host nests by watching nesting activities and following potential hosts or other parasitic females to nest sites. All Canvasback females ($n = 17$) observed from blinds while nesting were followed at times by Redhead females as they fed in open water or undertook nesting activities. Canvasbacks were relatively conspicuous when nesting in emergent cover near open water and such nests contained more Redhead eggs ($\bar{x} = 10.1 \pm 1.6$, $n = 23$) than nests ($\bar{x} = 5.9 \pm 0.97$, $n = 34$) located in the interior of large stands of emergent cover ($t = 2.4$, $df = 55$, $P = 0.02$).

Host presence influenced which nests were selected for parasitic laying by females. Deserted nests generally could be distinguished by human observers by having cold, exposed eggs, few fresh down feathers, and weathered and matted nesting materials. Redheads may readily have assessed nest status as well because they typically stood or sat briefly (≤ 3 min) on deserted clutches before leaving, although they sometimes removed nesting materials and pulled their bill through the clutch to turn the eggs. Redhead females had a lower proportion of laying events at deserted nests (16 visits, 3 laying events) compared to nests being actively incubated (21 visits, 74 laying events) ($\chi^2 = 27.9$, $df = 1$, $P < 0.001$). Two of three laying events in deserted nests happened within 24 h after Canvasback hosts had deserted and there was still activity at the nests from continuing visits by multiple Redhead fe-

TABLE 1. Percentage occurrence of events (n) during parasitic encounters at host nests.

Host species	Host present during laying	Parasitic egg was laid	Host pecked parasitic Redhead ¹
Canvasback	87.5 (88)	75.0 (88)	48.2 (54)
Redhead	70.6 (17)	88.2 (17)	91.7 (12)

¹ Comparing pecking by host species: $\chi^2 = 5.9$, $df = 1$, $P < 0.02$ with continuity correction.

males. The experiment with artificial nests supported these observations. One of five artificial nests with a caged decoy host received three parasitic Redhead eggs, unlike Weller's (1959) experiment in which artificial nests without hosts were not parasitized.

PARASITIC LAYING

Redheads encountered incubating hosts while parasitizing nests 88% of the time for Canvasback and 71% for Redhead hosts (Table 1). These estimates are possibly biased high because it was difficult to find and film nests during the early laying period when hosts would be on the nest less often. Even so, Redheads typically encounter incubating hosts while laying parasitically because waterfowl spend increasing amounts of time on the nest as laying progresses and Canvasbacks are attentive incubators (Afton and Paulus 1992). Redheads laid parasitic eggs in 75–88% of filmed encounters at host nests; the remaining interactions were nonlaying nest visits (Table 1).

Host presence did not markedly deter parasitic laying. Redheads spent similar amounts of time ($P > 0.57$) laying eggs at deserted nests, when hosts were absent during incubation recesses, and when Canvasback hosts pecked during an encounter vs. when they did not peck (Table 2, model 1). Parasitic Redheads physically removed hosts from their clutches to lay eggs. Females aggressively pushed and shoved hosts to the side or tunneled underneath them with their head and neck to lever them partially or completely off the clutch. Physical contact with the clutch appeared important because females often continued tunneling underneath or pushing hosts about the nest until they could sit on some host eggs. During two encounters, parasitizing Redheads did not displace the Canvasback host enough and laid eggs outside of the nest bowl. Canvasbacks parasitizing intraspecifically were equally as adept

TABLE 2. Analysis of variance models predicting time (log min) spent by Redheads and Canvasbacks visiting or laying parasitic eggs in host nests.

Model/Statistics	Variable/Level	LSM ¹	SE	F ratio	P
Model 1: Redhead laying events ($R^2 = 0.03, F = 0.68, df = 76, P > 0.57$)	Host presence			0.7	0.565
	Nest deserted	1.99	0.26		
	Host absent	2.09	0.15		
	Host not pecking	2.12	0.09		
	Host pecking	2.24	0.08		
Model 2: Redhead laying events; host present ($R^2 = 0.28, F = 4.6, df = 64, P < 0.002$)	Host incubation stage (A)			6.9	0.011
	Early (day 0-11)	2.3	0.07		
	Late (day 12-24)	2.1	0.08		
	No. of host pecks (B)			4.7	0.013
	None	2.0	0.08		
	One	2.2	0.10		
	≥ Two	2.4	0.09		
Model 3: Both species; laying and visiting ($R^2 = 0.72, F = 43.1, df = 88, P < 0.001$)	Interaction term (A × B)			4.8	0.012
	Host incubation stage			11.2	0.001
	Early (day 0-11)	2.0	0.12		
	Late (day 12-24)	1.6	0.10		
	No. of host pecks			4.8	0.012
	None	1.68	0.10		
	One	1.63	0.13		
	≥ Two	2.03	0.14		
	Species of parasite			18.1	0.001
	Canvasback	2.1	0.17		
	Redhead	1.4	0.07		
	Type of interaction			134.9	0.001
	Egg laying	2.5	0.09		
Nest visit	1.0	0.14			

¹ LSM = least squares means.

as Redheads at gaining access to host nests, using the same pushing and tunneling behavior.

Parasitic laying and nest visits occurred throughout the diurnal period, but were more common ($P < 0.02$) prior to 12:00 than later in the day (Fig. 1). Parasitic laying occurred at all stages of host egg laying and incubation, includ-

ing one Canvasback nest parasitized intraspecifically while it contained hatched ducklings

Nonlaying nest visits by Redheads at Canvasback nests were short ($\bar{x} = 2.1 \pm 0.2$ min) and females exhibited different behavior. Visiting females stood at the edge of the nest, walked over the host or around the nest, or briefly sat beside

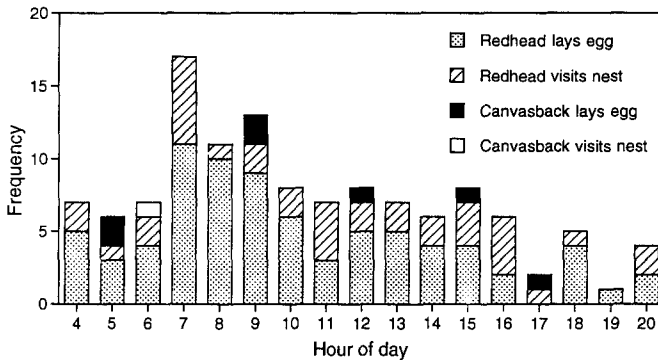


FIGURE 1. Frequency distribution for nest visits ($n = 38$) and egg-laying events ($n = 84$) by parasitic Redheads and Canvasbacks. The observed distribution of events in morning (prior to 12:00) vs. later in the day (84 vs. 38) varies significantly from an expected even distribution (65 vs. 57) ($\chi^2 = 6.3, df = 1, P < 0.02$).

the host without trying to displace them before leaving. A higher proportion of visits (22 visits, 12 laying episodes) occurred when the host was absent from the nest during an incubation recess than when hosts were present (15 visits, 64 laying episodes) ($\chi^2 = 22.6$, $df = 1$, $P < 0.001$), suggesting that parasitic females were more likely to investigate nests closely when hosts were gone.

Several factors were associated with how long parasitic females remained on host nests. Redheads spent more time laying eggs in nests from day 0–11 of the host incubation period than later and when hosts pecked intruders ≥ 2 times (Table 2, model 2). In a full model of all host-parasite interactions, Canvasbacks took longer to lay parasitic eggs than Redheads and nest visits were shorter in duration than egg-laying events (Table 2, model 3).

HOST RESPONSE TO PARASITISM

Incubating hosts typically remained sitting, vocalized, and resisted being pushed or lifted off the clutch by parasitizing females, sometimes with wings partly spread and braced against the nest. Hosts sometimes aggressively pecked or bit intruding Redheads on the head or neck (Table 1; also see McKinney 1954). Redheads responded passively to this aggression, stretching their heads and necks away from biting hosts or sat facing the opposite direction, undoubtedly to protect their eyes. Canvasbacks appeared as likely to peck other Canvasbacks (4 of 7 interactions) during laying encounters as they were parasitic Redheads (26 of 54 interactions). Pecking and biting by Canvasbacks increased from the first (31%, $n = 39$) to the last half of incubation (56%, $n = 39$) ($\chi^2 = 5.2$, $df = 1$, $P < 0.03$). Redhead hosts were more aggressive than Canvasback hosts in pecking other parasitic Redheads (Table 1).

EFFECTS OF PARASITISM ON HOSTS

Five times as many Canvasback eggs were cracked and twice as many were dislodged from nests during parasitic encounters than were Redhead eggs (Fig. 2). Redhead eggs are smaller than Canvasback eggs (Palmer 1976) and occupied the more protected interior of the clutch more often (33% of 480 egg observations) than Canvasback eggs (24% of 373) after females had adjusted the clutch into a uniform bowl for incubation ($\chi^2 = 7.9$, $df = 1$, $P < 0.01$). Detrimental effects of fighting on host eggs were vividly illustrated in

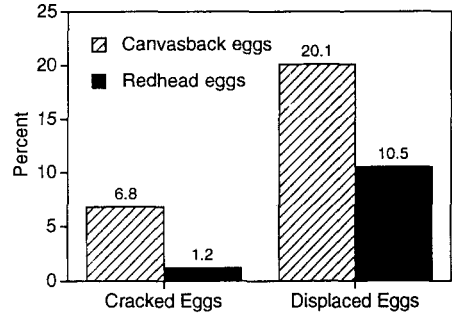


FIGURE 2. Percentage of eggs in Canvasback nests displaced into the water or cracked during encounters with parasitic Redheads (for cracked eggs, $\chi^2 = 13.7$, $df = 1$, $P < 0.001$, $n = 365$ Canvasback and 329 Redhead eggs; for displaced eggs, $\chi^2 = 12.6$, $df = 1$, $P < 0.001$, $n = 354$ Canvasback and 354 Redhead eggs).

photographic sequences. For example, one Canvasback aggressively pecked and pushed against a parasitic Redhead for four minutes as it tried to climb on the nest. While the Redhead was clawing with its feet to displace the host, it kicked all nine host eggs backwards out of the nest. The Redhead eventually pushed the host off the nest, then spent seven minutes laying its egg while the Canvasback continued to vigorously peck the intruder. The Canvasback intermittently tried to incubate the Redhead egg, but repeatedly left and finally deserted the nest completely later in the day.

No film evidence suggested that hosts discriminated between parasitic eggs and their own eggs or that eggs were purposely ejected from nests by either host or parasite. Canvasbacks tried to retrieve all dislodged eggs, including Redhead eggs, failing only when eggs rolled into the water or became stuck in nesting materials. During two encounters, Redheads momentarily stopped trying to dislodge Canvasbacks from their clutches and attempted to retrieve eggs that had rolled out of the nest bowl. All egg displacement occurred during fighting and pushing matches or when parasitized clutches became overly large for hosts to manage during nest building and normal movements on the clutch. Among Canvasback nests successful in producing at least one duckling, Canvasback egg success was 62% of 112 eggs compared to 34% of 114 parasitic Redhead eggs in the same nests.

Extended incubation and brooding behavior. Host nests containing large numbers of parasitic eggs at various stages of embryo development

had longer incubation periods and extended brooding behavior. A deserted Canvasback clutch, confirmed by the presence of down, contained 4 host embryos a maximum of 4–6 days old while the parasitic Redhead eggs had 3 day-4, 4 day-6, and 5 day-8 embryos, indicating that host eggs were receiving less effective incubation, possibly because of their isolated and more peripheral position in the clutch. In two Canvasback nests with 14 and 27 Redhead eggs, hatching did not occur on day 24 as expected (Barzen and Serie 1990), but on day 30 and 32 of incubation.

Film records revealed that females with dry and active young, but several unhatched eggs, often left with broods only to return to nests frequently and resume incubation. Ducklings sometimes left nests and entered the water alone for short periods while females continued incubating unhatched or late-hatching eggs. Unfortunately, I could not estimate how long host incubation and brooding on the nest typically may have been extended under these circumstances. Cameras were removed from some nests because I judged that females should have departed with broods one or two days earlier, only to discover from later film analysis, that they were still partially attentive to unhatched eggs. Two Redhead females continued incubating pipping or unhatched parasitic eggs for 48 hr after the first dry, active ducklings appeared until I unknowingly disturbed them.

DISCUSSION

BEHAVIOR OF PARASITIC FEMALES

Habitat conditions on the Delta Marsh were poor during three of four years of this study and most Redheads did not nest (Sayler 1985). During severe droughts, many Redhead females may lay parasitically to partially salvage a breeding attempt rather than not breed at all and many lay relatively indiscriminately in host nests whether by choice or by default (Sayler 1985). The high ratio of Redheads to Canvasbacks on the Delta Marsh further contributes to high parasitism rates and consequent low success of host Canvasback and parasitic Redhead eggs.

Neither species seems deterred from parasitic laying by host presence. Parasitic females are adept at physically displacing hosts trying to cover and protect their clutches, despite host ag-

gression by pecking and biting. Sorenson (1991) also filmed episodes of Redheads parasitizing Canvasback nests, confirming the results of this study that nest encounters fall into two relatively distinct categories (1) short visits in which females apparently evaluate host nests prior to laying and (2) longer encounters in which females aggressively displace hosts to lay eggs. I did not observe encounters in which parasitic females appeared to be unsuccessful in laying at the host nest, although host resistance increased the necessary time and effort and resulted in some eggs not making it into clutches.

Females limit their behavior while parasitizing nests, for although hosts pecked and bit, intruding females did not respond in kind. Relatively passive responses by parasitic females to host aggression may be adaptive in reducing the possibility of host nest desertion.

LIMITATIONS ON HOST DEFENSIVE BEHAVIOR AT NESTS

Among different species of waterfowl, hosts may attempt to avoid brood parasitism by (1) nest concealment or habitat selection, (2) surreptitious behavior near nests to avoid disclosing nest location to other females, (3) deserting some parasitized nests, and (4) aggressive behavior to deter parasitic females at nests (Sayler 1985, 1992). Canvasback and Redhead hosts clearly limit their defensive behavior at nests. Hosts do not use the same pushing and tunneling behavior of parasitic females to regain possession of the nest bowl once they have been pushed aside. Hosts undoubtedly possess the ability to do so because some Redhead hosts lay parasitically earlier in the nesting season and thus are themselves brood parasites (Sayler 1985, Sorenson 1991). Hosts may avoid using this same behavior to regain the nest because it would only increase loss of their own eggs.

If extreme defensive behavior increases egg loss, why then should hosts resist parasitizing females at all? Host defensive behavior may limit parasitism by preventing at least some females from laying directly in the clutch. Defensive behavior may be more successful for some species of waterfowl because of presence of pair males (Mineau 1978, Owen and Wells 1979) or limited access to nests through cavity openings (Grenquist 1963, Chronister 1985, Semel and Sherman 1986). Eggs laid outside cavity nests may result

TABLE 3. Summary of factors potentially affecting hosts parasitized by brood parasites in species with precocial young.

Factor	Potential effect
Host eggs on periphery of clutch	Lower average egg temperature Displacement from clutch more likely Synchronization of parasitic Redhead eggs more likely
Lower egg temperature	Extended incubation period
Host eggs separated by or in contact with younger parasitic eggs	Retarded development and extended incubation Altered hatching synchrony
Unhatched parasitic eggs left in clutch	Extended incubation Delayed nest departure
Late-hatching parasitic eggs	Distress vocalizations extend host incubation or delays nest departure with brood
Extended incubation or delayed nest departure	Increased chance of nest loss (e.g., predators, flooding, fire) Increased chance of female death by predation Lower female body condition

from parasitic females being repelled from entering nests by aggressive hosts (Clawson et al. 1979, Semel and Sherman 1986). Defensive behavior may be more constrained for species nesting over water because of higher probabilities of egg loss.

Host eggs may be more vulnerable to cracking and loss from nests than parasitic eggs for several reasons. First, some host eggs generally are in the nest first and are subjected to the effects of fighting and displacement before parasitic eggs are laid. Secondly, my preliminary analysis suggests that host Canvasback eggs are found on the perimeter of clutches more often, and therefore, may be more prone to displacement. The strength of this result, however, is limited by the assumption of independence among clutch observations, which may unrealistically inflate sample size. Differential positioning of eggs within waterfowl clutches apparently has not been reported previously. Additional, more detailed work is needed to determine the potential effects of egg size, shape, and number on egg location and fate within incubated clutches.

COSTS OF BEING PARASITIZED

Hosts resist intrusions of parasitic females at their nests, indicating there may be fitness costs to being parasitized, even among species with nidifugous precocial young (Table 3). I suggest brood parasitism potentially may affect incubation or early brood care for these species by (1) lower average host egg temperature in large clutches (Jones and Leopold 1967, Pienkowski

and Evans 1982, Saylor 1985), (2) developmental retardation resulting when host embryos are separated and in direct auditory contact with less-developed embryos in parasitic eggs (Vince 1964, 1968), and (3) extended incubation and brooding behavior by females responding to presence of unhatched eggs or vocalizations from late-hatching eggs (Gaioni 1982, Tuculescu and Griswold 1983, Evans et al. 1994). Thus, incubation and brooding periods may be longer when host clutches contain parasitic eggs with delayed embryos, a situation characterizing waterfowl brood parasitism (Saylor 1992). Because pipping embryos may increase vocalizations when their temperature drops (Evan et al. 1994), females with hatched broods essentially may be held behaviorally captive at nests by distress vocalizations of late-hatching parasitic eggs. If hatching and parental care is extended in parasitized nests, the fitness costs will be biologically significant by increasing female mortality and losses of nests and broods to predators, flooding, and fire.

Synchronous hatching and nest exodus are critical processes for species with precocial young. The rates of parasitism in this study are higher than in most other studies of Canvasback nesting biology and the effects of parasitism might be larger than would occur in lightly parasitized nests. At issue is the threshold number and timing of parasitic eggs at which these processes are affected. However, film records (Sorenson 1992, this study) now confirm the ubiquity of host/parasite encounters and defensive behavior among nesting Canvasback and Redhead hosts, as originally suggested by McKinney (1954). Un-

derstanding the potential adaptive basis for host behavior and consequences of brood parasitism among species with precocial young awaits experimentation.

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