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Effects of intra- and interspecific brood parasitism on a precocial host, the canvasback, *Aythya valisineria*

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Canvasback ducks (*Aythya valisineria*) suffer both intra- and interspecific brood parasitism. During 3 years in Manitoba, 80% of canvasback nests (n = 179 nests with completed clutches) were parasitized by redheads (*A. americana*), other canvasbacks, or both, with an average of 4.7 parasitic eggs per parasitized nest. Parasitism had significant negative effects on the reproductive success of nesting canvasbacks, although the proximate mechanisms involved differed from those operating in altricial species. Accidental displacement of eggs when parasitic females forced their way onto host nests was the principal negative effect of parasitism, reducing the number of host eggs that were incubated and ultimately hatched. Parasitism by redheads was relatively more costly to canvasbacks than was intraspecific parasitism, with approximately 0.31 and 0.17 host eggs displaced per parasitic redhead and canvasback egg laid, respectively. No additional negative effects of parasitism on the hatchability of host eggs occurred subsequent to parasitic laying. Posthatch survival of canvasback ducklings was lower in broods from parasitized nests but was unrelated to the presence or absence of redhead ducklings. Canvasback hosts resisted intrusions by parasitic females but showed no evidence of discrimination against parasitic eggs or ducklings. Because most costs of parasitism in this system are inflicted at the time of parasitic laying, subsequent rejection of parasitic eggs or ducklings is probably of little benefit to canvasback hosts, while the evolution of behavior that might prevent parasitic laying in the first place, such as more vigorous nest defense, may be constrained by its high costs. *Key words: Aythya americana, Aythya valisineria,* canvasback, interspecific brood parasitism, intraspecific brood parasitism, redhead. *[Behav Ecol 8:153-161 (1997)]*

Almost all obligate brood parasites have altricial young that require extensive parental care provided by a host species. Because the parasitic nestling is genetically unrelated to its foster siblings, there is no selection for it to restrain efforts to obtain parental feedings. Nestlings of some cuckoos (Cuculidae) and honeyguides (Indicatoridae) kill their nest mates soon after hatch, while the offspring of cowbird (*Molothrus* spp.) hosts may starve as they are outcompeted by the larger, rapidly growing cowbird (Payne, 1977). Severe costs of parasitism result in strong selection on hosts to prevent parasitic eggs from hatching in their nests. This high-stakes interaction between host and parasite has led to some of the most fascinating adaptations and clearest examples of coevolution among birds (e.g., Davies and Brooke, 1988; Rothstein, 1990). In contrast, the black-headed duck (*Heteronetta atricapilla*), the only precocial obligate brood parasite, requires only incubation and a short period of brooding from its foster parents and appears to have little effect on host reproductive success (Weller, 1968). Extremely precocial, black-headed ducklings leave the host nest soon after hatching and apparently care for themselves during a secretive and solitary juvenile period.

Although only one obligate brood parasite is precocial, facultative parasitic egg laying (both intra- and interspecific) is more common among waterfowl (Anatidae) than among any other family of birds (Lyon and Eadie, 1991; Rohwer and Freeman, 1989; Weller, 1959). Because waterfowl have highly precocial young, hosts may suffer few costs when parasitized (Andersson, 1984; Eadie et al., 1988; Nudds, 1980; Rohwer and Freeman, 1989). Parasitic ducklings or goslings are reared along with the host's own young, and the forms of parental care required by precocial parasites are generally provided to the whole brood. A female duck, for example, may invest no more time and energy incubating 15 eggs and leading and protecting 15 ducklings than she would invest in 10 (see Rohwer, 1992). Rohwer and Freeman (1989) suggested that low costs for hosts and the resulting lack of antiparasite adaptations have been important factors allowing the extensive evolution of facultative parasitism in precocial species. Taking this reasoning a step farther, "parasitism" may actually be advantageous to precocial hosts (Eadie and Lumsden, 1985; Eadie et al., 1988; Nudds, 1980). The addition of parasitic eggs could improve the survival of the host's own young either because parasitic young are taken preferentially by predators or because parasitic young simply dilute the effects of predation.

Even among waterfowl, redhead ducks (*Aythya americana*) are unusual in their extensive use of interspecific hosts and high frequency of parasitic egg laying. Redheads typically parasitize 50%-80% of canvasback (*A. valisineria*) nests, where the two species are sympatric, laying an average of three or more redhead eggs per parasitized nest (e.g., Bouffard, 1983; Erickson, 1948; Stoudt, 1982; Weller, 1959). Intraspecific parasitism is also frequent among canvasbacks (Sorenson, 1993), although more difficult to detect and usually noted only when large clutches have been observed (e.g., Olson, 1964). Almost every canvasback female that survives to nest more than once will be parasitized by redheads, other canvasbacks, or both. Because the strength of selection for host defenses depends not only on the magnitude of effects on individual hosts but also on the frequency with which nests are parasitized (Kelly, 1987; Rothstein, 1975a), even small negative effects of parasitism could select for antiparasite behavior in canvasbacks. Here I analyze the effects of interspecific parasitism by red-

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heads and intraspecific parasitism by canvasbacks on the reproductive success of canvasback hosts and then consider the responses of canvasbacks to parasitic laying.

METHODS

I monitored nesting and parasitic egg laying by redheads and canvasbacks near Minnedosa, Manitoba, Canada, from April through August 1986–1988. Nests of both species are built over water in the residual emergent vegetation encircling small wetlands. Nesting females typically lay seven to nine eggs on consecutive days and then incubate for 25 days. Within 48 h after hatch, the female and brood permanently leave the nest. Redhead ($n = 69$) and canvasback ($n = 150$) females were trapped and fitted with colored nasal markers for individual identification (Doty and Greenwood, 1974; Lokemoen and Sharp, 1985). I searched the emergent vegetation in all wetlands on the study area every 8–10 days during May and June to find as many nests as possible in the laying stage and before parasitic eggs were laid. Additional information on the natural history of these species, the study area, and field methods is provided elsewhere (Sorenson, 1991, 1993; Stoudt, 1982).

Time-lapse photography

I monitored most canvasback nests (142 of 179 nests with completed clutches) with Super-8 movie cameras for several days (7.4 ± 3.6 SD, range 1–20), usually during the second half of the laying stage and the first week of incubation. Cameras were equipped with interval timers set to expose one frame per minute. Each roll of film covered 48 h and generally started and ended in the late afternoon or evening. See Sorenson (1991, 1993) for additional information on time-lapse photography and precautions taken to minimize disturbance of nesting females.

Each sequence of frames with a female canvasback or redhead other than the nest owner on the nest was assigned to one of two categories: "nest visits" were intrusions of relatively short duration in which the intruding female probably did not lay an egg; "egg-laying events" were intrusions of longer duration (> 5 min) in which the intruding female appeared to lay an egg (see Sorenson, 1991, for descriptions of intruding female behavior and additional criteria used to classify film events). The number of egg-laying events on a given 2-day film usually matched the number of new parasitic eggs found in the nest when film was changed, although newly laid eggs were sometimes displaced before the nest was revisited (see Results), and a few parasitic eggs were apparently laid before sunrise (Sorenson, 1991). During the 3-year study, I recorded 278 parasitic egg-laying events in 1159 nest-days of filming at 171 canvasback nests. This included 184 and 94 parasitic egg-laying events involving intruding redheads and canvasbacks, respectively, representing about 39% of all parasitic laying at canvasback nests on my study area.

Nest and egg data

In addition to filming, I used several standard criteria (e.g., Lyon, 1993; Yom-Tov, 1980) to identify intraspecific parasitism in canvasback nests. Eggs added at a rate of > 1 per day during the host's laying stage and eggs laid during the host's incubation stage were considered parasitic. Obvious differences in the color and size of eggs, large clutch size, and differences in incubation stage within a clutch were taken as indications of likely parasitic eggs (see Sorenson, 1993). Redhead eggs are easily distinguished from those of canvasbacks by their glossy, ivory-colored shell (Bellrose, 1980), and those laid in canvasback nests could be classified unambiguously as parasitic.

I checked nests every other day during laying and early incubation and then at 1-week intervals until hatch. During each visit, new eggs were measured and numbered on both ends with permanent ink. I noted the numbers of previously laid eggs remaining in the nest and diagrammed the position of each egg in the clutch. Individual eggs were scored as being in the center of the clutch if they were surrounded on all sides by other eggs. During the final check of each nest site, I thoroughly searched for eggs in the nesting material and on the bottom of the wetland within 1 m of the nest.

Nests from which one or more eggs hatched were classified as successful (including one canvasback nest in which only redhead eggs hatched). Estimates of the number of parasitic and host eggs that hatched in each nest were based on the number of caps and membranes left from hatched eggs, the number of unhatched eggs remaining in the nest, the number of eggs outside of the nest, and the contents of the nest just before hatch. For a portion of nests, uncertainty in these estimates resulted from a variety of sources (see Sorenson, 1993), the most problematic of which involved the identification of intraspecific parasitic eggs; even in nests in which the exact number of parasitic canvasback eggs was known, the status of individual eggs was not necessarily known (see Sorenson, 1993). Analyses presented here use maximum estimates of host egg success, minimum estimates of the number of host eggs displaced from nests, and include likely cases of intraspecific parasitism. As such, the analyses are conservative (except as noted) with respect to finding significant negative effects of parasitism on hosts.

Duckling survival

Marked brood hens and their ducklings were followed for as long as possible after hatch to record the survival of redhead and canvasback ducklings in canvasback broods. An attempt was made to sight each brood at least once per week until the adult female abandoned the brood and/or until the brood began to break up and mix with other broods. Most females stayed with their broods until 30 days and up to 60 days after hatch. The proportion of ducklings surviving to the first sighting of each brood at age class IIa (22–28 days; Weller, 1957) was taken as an estimate of fledging success. Before independence and flight (55–69 days; Smart, 1965), almost all duckling mortality takes place in the first week after hatch (e.g., Rotella and Ratti, 1992).

Statistical analyses

Statistical analyses were conducted using SYSTAT (Wilkinson et al., 1992). Potential effects of parasitism on four components of host reproductive success (number of eggs laid, nest success, proportion of eggs hatched, and proportion of ducklings surviving) were evaluated in separate analyses. I combined data from all 3 years of the study for analyses involving the dynamics of parasitism at individual nests. Effects of parasitism on host egg fate in successful canvasback nests ($n = 98$) were evaluated with the following regression model: number of hosts eggs hatched (or displaced) = $\beta_0 \times$ number of host eggs laid + $\beta_1 \times$ number of parasitic eggs laid, with values of β_1 significantly different from zero indicating an effect of parasitism. By including number of host eggs laid as a covariate, this model, in essence, evaluates the effect of parasitism on proportion of host eggs hatched or displaced while avoiding problems with proportional data. The data for each nest were weighted by the inverse square-root of the number of parasitic eggs laid + 1, thereby minimizing the influence of the few nests with large numbers of parasitic eggs. One nest in which four canvasback eggs hatched and five were displaced (see below) and for which there was no evidence of parasitism was an extreme outlier (studentized residual, t = 5.05, $p < .0001$) in analyses of host egg fate and was excluded.

Factors related to the proportion of ducklings surviving to age class IIa in each brood (n = 76 broods tended by marked females and with at least 1 duckling surviving) were evaluated in multivariate analyses using MGLH in SYSTAT (Wilkinson et al., 1992). Models included four main effects (including two continuous variables: hatch date and total number of eggs hatched, and two categorical variables: year and presence/absence of redhead ducklings) and all possible two-way interactions. Nonsignificant terms were sequentially deleted from the model, starting with the term with the largest p value, until only significant ($p < .05$) effects remained (main effects involved in significant interactions were retained in the model). Proportional data were arcsine transformed.

Analyses of duckling survival do not consider possible effects of the presence of parasitic canvasback ducklings because the offspring of intraspecific parasites could not be distinguished in brood observations. Because of the low hatching success of parasitic canvasback eggs (Sorenson, 1993), only 13 of the 76 broods with at least one duckling surviving may have had a parasitic canvasback duckling at hatch. These broods did not differ from those without parasitic canvasbacks in canvasback duckling survival ($F_{1,72}$ = 0.85, p = .36), and broods with possible parasitic canvasbacks were equally divided between broods with (n = 6) and without (n = 7) redhead ducklings. It is therefore unlikely that conspecific parasitism confounded analyses on the effects of redhead parasitism on host duckling survival.

The relationship between parasitism and fate of canvasback nests was evaluated with log-linear models controlling for annual variation in parasitism and predation rates. Categorical analyses used the G test for goodness of fit or G test for independence with William's correction for sample size (Sokal and Rohlf, 1981).

RESULTS

Frequency of parasitism

During the 3 years of this study, 80% of canvasback nests with completed clutches (n = 179) were parasitized by redheads, other canvasbacks, or both species. Redheads parasitized 65% of canvasback nests, laying 3.8 ± 3.1 (SD) eggs per parasitized nest (range 1–16). Evidence of intraspecific parasitism was found in 41% of canvasback nests, and 2.8 ± 2.1 (SD) parasitic canvasback eggs were laid in these nests (range 1–10). The occurrence of redhead and canvasback parasitism at canvasback nests was independent. Canvasbacks parasitized 40% (46/116) of nests parasitized by redheads and 43% (27/63) of nests not parasitized by redheads (G = 0.08, p = .99, df = 3, log-linear analysis controlling for variation in parasitism rates among years).

Effects on reproductive success of canvasback hosts

Number of eggs laid

Considering only canvasback nests found during the laying stage, the number of host eggs laid was unrelated to the number of parasitic redhead and canvasback eggs added during the host's laying stage ($F_{1,86}$ = 0.26, p = .61, ANCOVA controlling for the effects of initiation date, $F_{1,86}$ = 32.5, $p < .001$, and year, $F_{2,86}$ = 4.45, p = .015). Note that inclusion of all likely cases of intraspecific parasitism biases this analysis (if any host eggs were incorrectly identified as parasitic) toward finding an effect of parasitism on host clutch size.

Table 1

Fate of canvasback nests in relation to redhead parasitism

Year	Fate	% Parasitized (N)	% Unparasitized (N)	
1986	Hatched	63 (30)	50 (5)	G_{adj} = 5.01, df = 2, p = .082
	Destroyed	21 (10)	50 (5)	
	Deserted	17 (8)	0 (0)	
1987	Hatched	67 (29)	52 (16)	G_{adj} = 4.53, df = 2, p = .10
	Destroyed	14 (6)	35 (11)	
	Deserted	19 (8)	13 (4)	
1988	Hatched	33 (11)	23 (7)	G_{adj} = 3.70, df = 2, p = .16
	Destroyed	48 (16)	71 (22)	
	Deserted	18 (6)	6 (2)	
Combined	Hatched	56 (70)	39 (28)	G_{adj} = 14.1,[a] df = 6, p = .028
	Destroyed	26 (32)	52 (38)	
	Deserted	18 (22)	8 (6)	

Analysis excludes nests terminated early in the host laying stage (≤4 host eggs) and considers only redhead parasitism: intraspecific parasitism could not be reliably detected in incomplete clutches that were already destroyed or abandoned when found.

[a] Test for fate by parasitism interaction in log-linear analysis controlling for variation in parasitism and nest success among years.

Nest success

For the 3 years of the study combined, the success of canvasback nests parasitized by redheads (54%, n = 130) was actually higher than that of nests not parasitized by redheads (25%, n = 110). Covariation between the time a nest was active and the probability that it was parasitized, however, produces this result: unsuccessful nests were active for fewer days and were therefore less likely to be found by parasitizing females. Excluding nests that were abandoned or destroyed when they contained only one to four host eggs partially controls this effect (only 5% of these nests were parasitized, n = 43) but the fates of canvasback nests parasitized by redheads still differed significantly from those not parasitized by redheads (Table 1). The source of this difference was primarily in the fates of unsuccessful nests (parasitized nests were less likely to be destroyed but were more likely to be abandoned; G = 10.8, p = .013, df = 3) rather than in the proportion of parasitized and unparasitized nests that hatched (G = 3.3, p = .34, df = 3). Considering only nests with completed clutches and excluding deserted nests, nests parasitized by redheads still tended to be more successful than unparasitized nests (G = 6.76, p = .080, df = 3), suggesting that parasitism at least had no detrimental effect on the probability of predation at host nests.

Number of eggs incubated and hatched

Displacement of host eggs from parasitized nests significantly reduced the number that were incubated and hatched. A strong temporal association between egg displacement and parasitic egg-laying events (Table 2), suggests that most egg displacement was a direct effect of parasitism. Displaced eggs sank to the bottom of the wetland, where they could not be retrieved by the host female.

Redheads and canvasbacks almost always laid parasitic eggs while the host female was on the nest: 85% (n = 184) and 89% (n = 94) of egg-laying events involving intruding redhead and canvasback females, respectively, occurred with the host canvasback present (see also Sayler, 1985). Most of the remaining events occurred at nests recently abandoned by the host female; 12% and 7% of events involving parasitic red-

Table 2

Temporal association of parasitic egg laying and egg displacement

	2-Day films with		
	No parasitic egg-laying events	≥1 parasitic egg-laying event	
Number with no eggs displaced	320	118	
Number with ≥1 eggs displaced	9	59	$G_{adj} = 90.8$, $p \ll .001$
% With eggs displaced	2.7	33	

Analysis includes both host and parasitic eggs laid and numbered before the start of the 2-day interval. Additional eggs laid during the 2-day interval also may have been displaced.

heads and canvasbacks, respectively. An intruding parasitic female typically tunnels under the host female with her head and neck and aggressively pushes the host off the clutch to gain access to the nest bowl. Although parasitic females usually succeeded in displacing the host, struggles between the two females (evidenced on films by slightly blurred images indicating motion and by changes in the positions of the two birds) often continued for several minutes (i.e., frames). Nests sometimes became quite disheveled and flattened, and eggs momentarily appeared at the edge of nests (i.e., visible in one frame but not the next), presumably just before the eggs rolled into the water.

The proportion of host canvasback eggs displaced from nests was significantly related to the total number of parasitic eggs laid (Figure 1A; host eggs displaced = 0.067 × host eggs laid + 0.24 × parasitic eggs laid; effect of parasitism: $F_{1,96}$ = 20.7, $p < .0001$, $r^2 = .18$), although this effect was highly variable among nests and among individual egg-laying events. At the extremes, one female's entire clutch of seven eggs was displaced from the nest during a single parasitic intrusion, while another female endured the laying of nine parasitic eggs without losing any of her own (four of the nine parasitic eggs were displaced from this nest). At least 20.5% of host canvasback eggs were displaced from successful parasitized nests (n = 630 eggs in 80 nests). Previously laid redhead eggs, however, were equally likely to be displaced during subsequent parasitic intrusions (Table 3), and there was no indication in time-lapse films that host or parasitic females deliberately pushed eggs from nests.

Parasitism by both redheads and canvasbacks resulted in egg displacement but parasitic intrusions by canvasbacks were less damaging than those of redheads: considering only 2-day films during which only one parasitic egg-laying event occurred, at least one previously numbered egg was displaced from the nest during 32% (n = 73) of 2-day intervals with one intruding redhead but only 17% (n = 42) of those with one intruding canvasback (G_{adj} = 3.13, p = .077, df = 1). In addition, the number of host eggs displaced was more strongly related to the number of redhead eggs laid ($F_{1,94}$ = 33.1, $p <$ .0001, r^2 = .26) than to the number of parasitic canvasback eggs ($F_{1,94}$ = 3.16, p = .079, r^2 = .033), with averages of 0.31 and 0.17 host eggs displaced per parasitic redhead and canvasback egg laid, respectively (model: host eggs displaced = 0.027 × host eggs laid + 0.31 × redhead eggs + 0.17 × parasitic canvasback eggs). This analysis excludes host eggs that disappeared from nests late in the incubation stage presumably due to causes other than parasitism (n = 22 eggs in 15 nests), thereby providing the best possible estimate of the average cost of parasitism to hosts per parasitic egg laid.

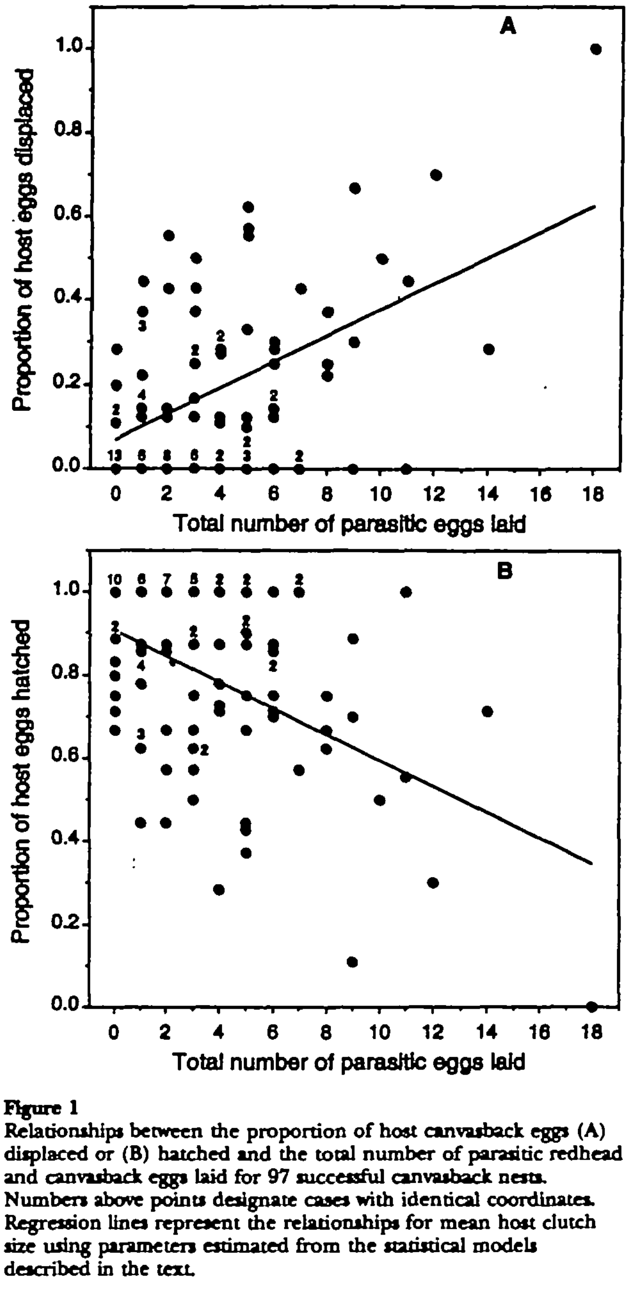

Figure 1

Relationships between the proportion of host canvasback eggs (A) displaced or (B) hatched and the total number of parasitic redhead and canvasback eggs laid for 97 successful canvasback nests. Numbers above points designate cases with identical coordinates. Regression lines represent the relationships for mean host clutch size using parameters estimated from the statistical models described in the text.

I eventually found 73% (n = 192) of previously numbered eggs that disappeared from parasitized nests. Although I almost certainly failed to locate some displaced eggs lost in the muck and vegetation beneath nests, some of the eggs that I scored as "displaced" in above analyses may actually have been cracked or broken during parasitic intrusions and then removed by the host female before my next visit to the nest. I noted cracked eggs in 20 of 116 nests parasitized by redheads compared with 3 of 63 nests not parasitized by redheads (G_{adj} = 6.37, $p <$ .025, df = 1). In nine cases, cracked eggs subsequently disappeared from nests during time intervals when no other eggs disappeared. A few eggs also may have been lost in the nest itself as host females repaired nests after parasitic intrusions. Cases of eggs temporarily buried in the

Table 3
Frequency of displacement of canvasback and redhead eggs

	Number of canvasback eggs displaced	Number of redhead eggs displaced	
Observed	44	22	$G_{adj} = 0.36$,
Expected	46.26	19.74	$p > .5$

Data from 37 two-day films at 26 nests during which egg displacement occurred and in which both canvasback and redhead eggs were in the nest at the beginning of the interval. The expected number of eggs displaced is the sum of the products for each 2-day interval of the total number of previously laid eggs displaced × the proportion of previously laid eggs belonging to each species. Analysis includes only eggs laid before the start of the 2-day interval. Additional eggs laid during the 2-day interval also may have been displaced.

nesting material and later recovered by the host female ($n = 5$ nests) or permanently lost in the nesting material ($n = 4$ nests) all occurred at parasitized nests.

As a result of egg displacement due to parasitic intrusions, fewer host canvasback eggs hatched as the total number of parasitic eggs increased (Figure 1B; host eggs hatched = 0.91 × host eggs laid − 0.24 × parasitic eggs laid; effect of parasitism: $F_{1,96} = 17.6$, $p < .0001$, $r^2 = .16$). On average, the addition of each parasitic egg laid resulted in a reduction of 0.24 host eggs hatched, although this effect was again highly variable among nests due to variability in egg displacement. Breaking down the effects of redhead and canvasback parasitism, only the number of redhead eggs was significantly related to host hatching success ($F_{1,94} = 24.7$, $p < .0001$, $r^2 = .21$; for parasitic canvasback eggs, $F_{1,94} = 1.77$, $p = .19$, $r^2 = .018$; model: host eggs hatched = 0.95 × host eggs laid − 0.31 × redhead eggs − 0.15 × parasitic canvasback eggs).

Parasitism had no additional negative effects on incubation efficiency. The hatching success of host canvasback eggs that were not displaced from nests was unaffected by the total number of parasitic eggs laid ($F_{1,96} = 0.12$; $p = .73$; host eggs hatched = 0.97 × host eggs remaining − 0.01 × parasitic eggs laid) or the total number of host and parasitic eggs remaining in the nest during the incubation stage ($F_{1,96} = 0.12$; $p = .73$; host eggs hatched = 0.99 × host eggs remaining − 0.01 × total eggs remaining).

Duckling survival

Hypothesized advantages of parasitism for precocial hosts assume that parasitism increases total brood size. Due to egg displacement and low hatching success of parasitic eggs (Sorenson, 1991,1993), however, the total number of eggs hatched increased by only 0.32 for each parasitic egg laid for nests with six or fewer parasitic eggs (total hatched = 0.87 × host eggs laid + 0.32 × parasitic eggs laid; effect of parasitism: $F_{1,80} = 10.1$, $p = .002$, $r^2 = .11$). Nests with more than six parasitic eggs achieved no further increase in brood size (Figure 2). In addition, total brood size (total number of host and parasitic young at hatch) was unrelated to duckling survival, either for all ducklings combined ($F_{1,74} = 0.44$, $p = .51$) or for canvasback ducklings only ($F_{1,73} = 0.15$, $p = .70$).

Contrary to the suggestion that predation might fall disproportionately on parasitic young, the survival of redhead and canvasback ducklings in mixed broods did not differ (0.71 ± 0.06 SE for redheads, 0.77 ± 0.04 for canvasbacks; $t = 0.30$, $p = .77$, $n = 35$ broods, paired t test). In addition, the presence of redhead ducklings in canvasback broods did not have a positive effect on the survival of canvasbacks ducklings (Figure 3A). Survival of canvasbacks in broods with and without redhead ducklings did not differ in 1986 ($F_{1,21} = 0.004$, $p = .95$) or in 1987 ($F_{1,34} = 1.33$, $p = .26$) and was lower in 1988 ($F_{1,14} = 7.38$, $p = .017$). Data for each year were analyzed separately because a significant year-by-redhead presence interaction ($F_{2,60} = 6.42$, $p = .003$) was found in the overall analysis due to the low survival of canvasbacks in the small sample of mixed broods in 1988. Effects of hatch date and total number of ducklings at hatch were insignificant in all analyses.

A comparison of canvasback duckling survival for broods from parasitized versus unparasitized nests suggested a negative relationship between parasitism and host duckling survival that did not depend on the presence of parasitic ducklings in the brood (Figure 3B). Survival of canvasbacks in broods from nests with no evidence of parasitism by either species (0.87 ± 0.04 SE, $n = 17$) was significantly higher than for broods from parasitized nests (0.73 ± 0.03, $n = 58$; effect of parasitism: $F_{1,71} = 6.63$, $p = .012$; effect of year: $F_{2,71} = 4.65$, $p = .013$; year by parasitism interaction nonsignificant). Apparent cases of total brood loss, which are not included in any of the above analyses, also were more frequent for parasitized nests (12 of 71) than for unparasitized nests (0 of 17, $G_{adj} = 5.19$, $p = .023$).

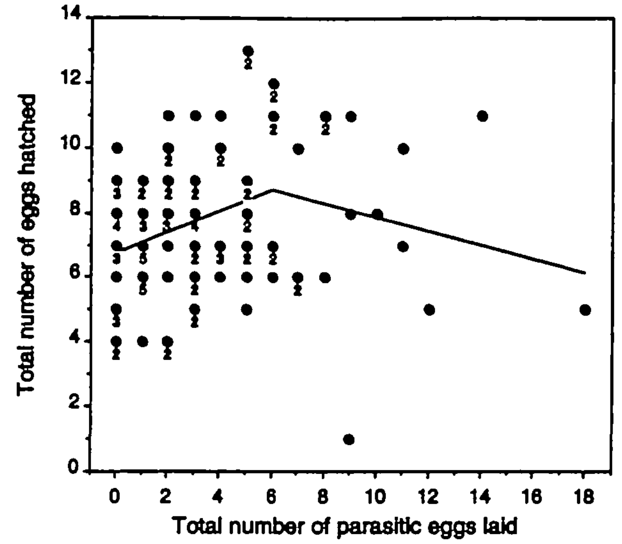

Figure 2
Relationship between the total number of eggs hatched (host and parasitic) and the total number of parasitic redhead and canvasback eggs laid for 97 successful canvasback nests. Piecewise regression with an unknown breakpoint (Wilkinson et al., 1992) suggested a negative relationship for nests with six or more parasitic eggs and provided a significantly better fit to the data than simple linear regression ($F_{2,92} = 3.23$, $p < .05$). Numbers below points designate cases with identical coordinates.

Responses of canvasbacks to parasitism

Responses to parasitic eggs

Although time-lapse photography provided an incomplete record of host behavior, I found no evidence for recognition or rejection of parasitic eggs by canvasback hosts. Canvasback and redhead eggs were equally likely to be displaced from parasitized nests during parasitic egg-laying events (Table 3), and an identical proportion (3.8%) of redhead and canvasback eggs disappeared or were displaced from nests during

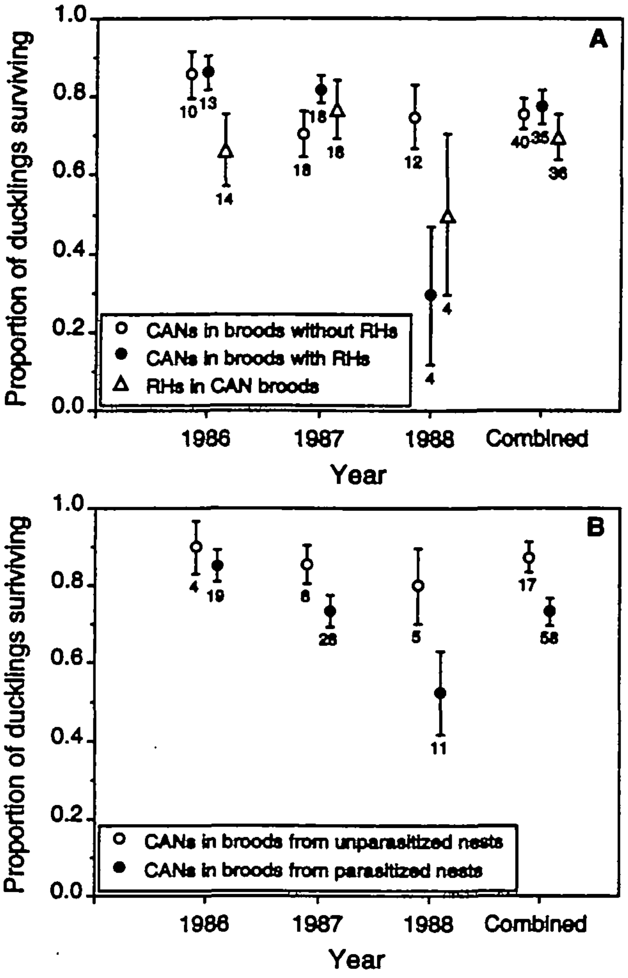

Figure 3

Survival of ducklings in canvasback broods to age class IIa (22–28 days old). The mean ± SE proportion of ducklings surviving per brood is plotted using untransformed data. (A) Survival of canvasbacks (CANs) from nests in which no redheads (RHs) hatched, canvasbacks in broods that included redhead ducklings at hatch, and redhead ducklings in canvasback broods. (B) Survival of canvasbacks from nests never parasitized by either species and canvasbacks from parasitized nests. Numbers below bars designate sample size (number of broods) for each category. In 1986, one "canvasback" brood included only redheads at hatch.

intervals with no parasitic laying (n = 186 and 442 redhead and canvasback eggs, respectively, that were not displaced in association with parasitic laying in successful nests parasitized by redheads). Canvasbacks also did not manipulate the position of redhead eggs within the clutch. The number of redhead eggs in the center and periphery of mixed clutches did not differ from that expected by chance (G_{adj} = 1.10, df = 1, $p > .2$; 332 of 1252 redhead eggs occupied the center of mixed clutches compared with a random expectation of 315.8, calculated as the sum over 459 observations at 105 nests of the number of redhead eggs in the nest × the proportion of all the eggs in the center of the clutch).

Nest defense

Nesting canvasbacks spend most of the day on their nests after the first few eggs have been laid (Sorenson MD, unpublished data). As a result, host females were at their nests during 97% of parasitic egg-laying events at active nests (n = 248), giving them an opportunity to deter parasitic females. In general, canvasbacks stayed on their nests and resisted being pushed off by the parasite. In only 15 events (6%) did host females get off nests <15 min before the appearance of the parasitic female on film, perhaps in response to a parasitic female approaching the nest. In only four events, however, did host and parasite arrive on the nest at the same time, suggesting interactions between the females away from the nest. In only three events (1%) is it conceivable that hosts ceded their nest to a parasite, leaving shortly before the parasite appeared and returning just after the parasite left. Male canvasbacks never defended the nest from parasitic females. Male canvasbacks were filmed on or near nests during seven egg-laying events involving intruding canvasback females (n = 86) but none involving redheads (n = 162), suggesting that these males were the mates of parasitic females.

Nest desertion

Nest desertion may be an effective response to parasitism, particularly when the costs of parasitism to hosts are high and hosts have the potential to renest (e.g., Moksnes and Røskaft, 1989). The fate of parasitized and unparasitized canvasback nests differed significantly (Table 1). This effect was due primarily to differences in the rates of desertion and predation between parasitized and unparasitized nests that were unsuccessful (see "Nest success," above). In 1986, desertion occurred at nests in which the effects of parasitism were relatively severe. All eight canvasback nests abandoned after the four-egg stage were either heavily parasitized (six or more parasitic eggs) and/or had suffered a reduction of three or more in the total number of eggs in the nest. Nests deserted in 1987 and 1988 were not so clearly distinguished. A higher proportion of younger females nesting in 1987 and poor environmental conditions in 1988 (Sorenson, 1991, 1993), may have resulted in more desertions in response to other causes. My activities also may have contributed to the overall frequency of nest desertion (Sorenson, 1993) but parasitized and unparasitized nests experienced a similar level of investigator disturbance.

Although more frequent for parasitized nests, nest desertion was not the usual response of canvasback hosts (Table 1). Most females continued to incubate even after tolerating repeated parasitic intrusions and substantial loss of their own eggs. In one extreme case, a female canvasback had all 7 of her own eggs displaced as a result of 18 parasitic intrusions (16 redhead and 2 canvasback) but continued to incubate the nest until 5 redhead eggs hatched.

DISCUSSION

Effects of parasitism

The most apparent effect of parasitism on canvasback hosts was the displacement of eggs from parasitized nests, which significantly reduced the number of host eggs hatching. A strong temporal association between parasitic laying and egg displacement, large variability in the number of eggs lost, and equal probabilities of displacement for host and parasitic eggs suggest that egg displacement was a direct, although accidental, consequence of parasitism. Although the cost per parasitic egg may be lower than for altricial species, high frequencies of multiple parasitism resulted in substantial negative effects on host reproductive success. This result bears on recent explanations for the high frequency of facultative parasitism among precocial species (Lyon and Eadie, 1991; Rohwer and Freeman, 1989; Sorenson, 1992). In particular, the assumption that precocial hosts will suffer few costs when parasitized

(Rohwer and Freeman, 1989) is not warranted, at least for canvasbacks.

The remarkable tunneling behavior exhibited by parasitic females as they push their way onto host nests and subsequent interactions between host and parasite during parasitic laying (McKinney, 1954) were probably responsible for most egg losses (see also Sayler, 1985). Parasitic laying by redheads resulted in a higher rate of egg displacement per parasitic egg laid than intraspecific parasitism, apparently because redheads were more aggressive and more successful in their attempts to dislodge the host female and gain access to the nest bowl (Sorenson MD, unpublished data). I found no evidence to support Sayler's (1985) suggestion that the slightly smaller eggs of redheads tend to occupy the center of mixed clutches, leading to a higher rate of displacement for canvasback eggs.

Nesting over water may make the costs of parasitism higher for canvasbacks than for other facultatively parasitic waterfowl. Cavity-nesting species are not subject to egg displacement, although egg breakage may be higher in parasitized nests (e.g., Eadie, 1989). Cavity nesters also appear better able to prevent parasitic females from entering nests, such that parasitic eggs are usually laid in unattended nests (Clawson et al., 1979; Semel and Sherman, 1986).

Presuming that waterfowl are indeterminate layers, Weller (1959) suggested that ovulation in canvasbacks may be suppressed by the addition of parasitic eggs. In contrast to several previous studies (Bouffard, 1983; Olson, 1964; Stoudt, 1982), including two that accounted for host eggs displaced into the water (Sugden, 1980; Weller, 1959), I found no effect of parasitism on the number of eggs laid by canvasback hosts. Previous analyses have not accounted for intraspecific parasitism or for the fact that only parasitic eggs laid before host clutch completion could suppress host egg laying. In addition, both canvasback clutch size and the frequency of intraspecific parasitism decline seasonally, while the frequency of redhead parasitism may increase (Erickson, 1948; Sorenson, 1991, unpublished data; Stoudt, 1982). Given that parasitic canvasback eggs were counted as host eggs in previous studies, all of these seasonal trends would contribute to an apparent negative effect of redhead parasitism on host clutch size (see Amat, 1987).

Andersson and Eriksson (1982) suggested that clutch-size reduction was an adaptive response to parasitism, allowing hosts to avoid negative effects of increased brood size (see also Power et al., 1989). Their finding that duckling survival declined with increasing brood size in goldeneyes (*Bucephala clangula*) is, however, unusual for waterfowl (Rohwer, 1992) and is inconsistent with the results of this study. The timing and dynamics of parasitism also make proximate effects on clutch size unlikely for canvasback hosts. First, many parasitic eggs are laid near the end of the host's laying stage or during the first few days of incubation (Sorenson MD, unpublished data), when the potential effect on host ovulation is little or none. Second, in many nests, the addition of parasitic eggs is completely offset by egg displacement: Erickson (1948) even suggested that parasitized canvasbacks laid additional eggs to compensate for egg displacement.

Amat (1985, 1993) suggested that parasitic eggs reduce incubation efficiency and result in higher prehatch mortality of host eggs in pochards (*Aythya ferina*) and red-crested pochards (*Netta rufina*). The high frequency of "dead embryos" recorded by Amat, however, may have included conspecific, nonterm parasitic eggs (i.e., eggs laid during host incubation) that died only after the host female and brood departed. I found no effect of parasitism on the hatchability of host eggs remaining in nests. Waterfowl can incubate more eggs than they lay (Rohwer, 1992), such that reduced hatchability of host eggs may become significant only when extreme rates of parasitism result in very large clutches (e.g., McCamant and Bolen, 1979; Weller, 1959).

In broods in which at least one duckling survived, the presence of redhead ducklings had no effect on the survival of canvasback ducklings, suggesting that mechanisms such as preferential predation of parasitic young or dilution of the effects of predation (Eadie and Lumsden, 1985; Nudds, 1980) did not increase the posthatch survival of host young. Evidence from several other waterfowl species also rejects the notion that hosts might receive posthatch benefits. Experimental manipulations of brood size suggested little relationship between brood size and offspring survival (Eadie, 1989; Lessells, 1986; Rohwer, 1985), and recruitment rates did not differ between broods from parasitized and unparasitized nests in wood ducks (*Aix sponsa*; Clawson et al., 1979; Heusmann, 1972) or snow geese (*Anser caerulescens*; Lank et al., 1990).

Possible covariation in host female quality and parasitism rate must be considered in interpreting the results of this study. Because my observational study provided no control for such confounding effects, correlations between parasitism and components of host reproductive success do not necessarily reflect direct causal relationships. For example, higher rates of desertion for parasitized nests may reflect higher rates of parasitism suffered by females that are inherently more likely to desert rather than a response to parasitism. Two results, however, independence of redhead and canvasback parasitism among nests and marginally higher success of parasitized nests, suggest that hosts were not an inferior subsample of the population of nesting females.

Sayler (1985) suggested that a suite of effects associated with the presence of nonterm parasitic eggs might impose additional costs on canvasback hosts at or near the time of hatch. Extended incubation, a longer hatching interval, delayed nest exodus, and reduced hatching synchrony might all increase mortality risks for eggs and ducklings. Consistent with this hypothesis, all apparent cases of total brood loss in this study involved broods from parasitized nests and, in 10 of 12 cases, the adult female was never sighted with ducklings, suggesting brood loss occurred shortly after hatch. In addition, ducklings hatched from nests with no evidence of parasitism by either species had higher survival than canvasbacks from parasitized nests. These apparent posthatch effects of parasitism are particularly difficult to evaluate, however, because duckling survival might be influenced by differences in parental effort in addition to inherent differences in female quality. Specifically, the low rate of total brood loss and higher duckling survival for unparasitized nests may reflect greater parental investment by females that have not lost eggs to parasitism in addition to higher quality of females that avoid parasitism. An experimental evaluation of the effects that parasitic eggs might have on hatching synchrony and the early posthatch survival of ducklings is needed to address these potentially important, additional negative effects of parasitism on canvasback hosts.

Host responses

The potential range of effective host responses to parasitism is determined by the nature and timing of its costs. Because the most significant costs of parasitism for altricial hosts of obligate parasites occur after hatch (but see Røskaft et al., 1990), there is strong selection for behaviors expressed after the parasitic egg is laid that prevent it from hatching. In contrast, because waterfowl provide incubation and posthatch care to the clutch or brood as a whole (Rohwer, 1992), the potential benefits of rejecting parasitic eggs or ducklings may be much fewer. It is not particularly surprising, therefore, that canvasbacks showed no evidence of recognition or discrimination against parasitic eggs, although canvasbacks do have the ability to remove eggs from nests: they reject chicken eggs painted with spots (Weller, 1959) and selectively remove cracked eggs. Even if ejecting parasitic eggs had benefits associated with hatching synchrony, discriminating among different shades of immaculate eggs would probably entail high costs of recognition errors (Davies and Brook, 1988; Rothstein, 1982). Intraspecific egg recognition has been demonstrated only in species with variation in egg markings (e.g. Arnold, 1987; Sorenson, 1995; Victoria, 1972).

Rather than reject parasitic eggs, canvasback hosts appeared to retrieve redhead (and canvasback) eggs that were pushed out of the nest bowl during parasitic intrusions but had not yet rolled into the water (see also Sayler, 1985). Lank et al. (1991) suggested that snow geese adopted parasitic eggs laid near their nests because the small cost of adding a parasitic egg would be offset by a lower probability of nest predation. Such a trade-off probably does not apply to canvasbacks because displaced eggs sank to the bottom of the wetland, where they would have little influence on rates of nest predation. Retrieval of parasitic eggs may simply represent a generalized response to any egg near the nest, a response that results in adaptive retrieval of the female's own eggs in the absence of parasitism.

Canvasbacks also do not discriminate against parasitic ducklings. Mattson (1973) observed all members of mixed broods initiating and responding to mutual neck-stretch displays and found no evidence of discrimination by canvasback females or ducklings against the redheads in their broods. Mattson also found that canvasback females aggressively defended mixed broods from outsiders, including canvasback ducklings from other broods. Although rejection of ducklings is not expected if there are no posthatch costs of parasitism, canvasbacks should at least abandon broods composed entirely of redheads. Two females in my study tended single redhead ducklings for 32 and 33 days after hatch, respectively, and similar observations have been made by others (Amat, 1985; Erickson, 1948; Giroux, 1981; Mattson, 1973; Weller, 1959). The failure of canvasbacks to discriminate against redhead ducklings parallels the failure of cuckoo and cowbird hosts to abandon parasitic young (Dawkins and Krebs, 1979; Lotem, 1993) and also argues against the suggestion that parasitized females are able to modify their level of parental investment in response to parasitism.

Nest desertion may be an effective response to parasitism depending on a variety of factors, including the number of host eggs remaining in the nest, the costs of incubation and brood care, the potential for successful renesting, and the probability that a second nest is parasitized. Although canvasbacks were more likely to abandon parasitized nests, the benefits of nest desertion are questionable. Hosts typically experienced only a partial loss of their own eggs and second clutches are smaller (Doty et al., 1984) and likely to be parasitized (Stoudt, 1982). That most females tolerated parasitism and continued to incubate even if most or all of the remaining eggs were parasitic suggests that desertion may be a generalized response to partial clutch reduction (Rothstein, 1986) or disturbance at the nest site (Eadie, 1989) rather than to parasitism, per se. Nonetheless, particularly severe parasitic intrusions accompanied by egg displacement and/or damage to the nest may lead directly to desertion.

Given the nature of costs for canvasbacks, perhaps the only effective host defense would be to prevent the act of parasitic laying and perhaps even the approach of the parasitic female to the nest site. Aggressive interactions between canvasback hosts and intruding redheads have been observed in three cases in which parasitic egg laying by redheads has been directly observed (Hochbaum, 1944; McKinney, 1954; Weller, 1959) but not in a fourth (Nudds, 1980). Although the extent of aggressive behavior was somewhat difficult to evaluate from time-lapse films, egg-laying events were consistent with McKinney's (1954) report, in which a nesting canvasback delivered a "rain of blows" to the back of an intruding female's head. Resistance by hosts was perhaps successful in some instances: parasitic females sometimes failed to gain access to the nest bowl and laid eggs on the edge of the nest after repeated attempts to tunnel under the host female from different angles.

Although canvasbacks clearly respond aggressively to intruding parasites, the extent of their actions may be constrained by associated risks. Leaving the nest site to attack an approaching parasitic female might attract the attention of predators or other parasitic females, and more vigorous defense of the nest would probably result in greater displacement of eggs, egg breakage, and damage to the somewhat fragile over-water nest (see also Nudds, 1980; Sayler, 1985). Indeed, given that resistance by canvasback females almost certainly contributes to egg displacement, the best option may be not to resist at all (Nudds, 1980).

Alternative explanations for the lack of specific antiparasite adaptations can be divided into those implying evolutionary equilibrium (Lotem et al., 1992; Rohwer and Spaw, 1988) and those implying evolutionary lag (Rothstein, 1975a, 1982). I have argued that canvasbacks face a situation in which either high costs (in the case of more aggressive defense of the nest at the time of parasitic laying) or minimal benefits (in the case of egg rejection or nest desertion) preclude the evolution of obvious and effective adaptations against parasitism. To the extent that this is true, the responses of canvasback hosts may represent the best solution to the problem of parasitism given the constraints they face (Rohwer and Spaw, 1988; Petit, 1991). Nonetheless, certain aspects of canvasback behavior may be in a state of evolutionary lag: significant costs of parasitism for canvasbacks should select for any behavior that makes it more difficult for parasitic females to find host nests. Subject to counter selection by nest predation and mortality risks for adult females, choice of nest sites and surreptitious behavior around nests are two likely aspects of canvasback behavior that might be under continuing selection due to parasitism (Sayler, 1985). There was no evidence that canvasbacks allow parasitism because of subsequent advantages that accrue to their own young (see Nudds, 1980). The results of this study suggest that, if anything, parasitism may have negative effects on duckling survival.

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