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PARASITIC EGG LAYING IN CANVASBACKS: FREQUENCY, SUCCESS, AND INDIVIDUAL BEHAVIOR

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ABSTRACT.—Time-lapse photography and frequent nest checks conducted at Canvasback (*Aythya valisineria*) nests revealed a high frequency of intraspecific parasitic egg laying. At least 36% of completed Canvasback clutches were parasitized by other Canvasbacks, and at least 9.7% of all Canvasback eggs were laid parasitically during the three-year study. The maximum hatching success of nonparasitic Canvasback eggs in successful nests was 79%, while the maximum success of known parasitic eggs was only 29%. Individual patterns of parasitic and typical nesting behavior were variable. In 15 cases, however, a marked female laid one or a few parasitic eggs before initiating her own nest. These parasitic eggs and subsequent nest initiations followed the seasonal peak of Canvasback nest initiations, suggesting that these females may have abandoned or had destroyed an initial nest prior to laying parasitically. I suggest that some females lay parasitic eggs after an initial nesting attempt is terminated early in the laying stage and before a second nest is initiated because the time-consuming task of nest building prevents them from having a second nest immediately ready to receive eggs. Parasitic egg laying in Canvasbacks also may function as a low-cost alternative to typical nesting when environmental conditions are unfavorable. Several younger females were known only to lay parasitic eggs in 1988, when drought conditions reduced the probability of successful nesting. Parasitic egg laying is a regular feature of the biology of Canvasbacks, but is a relatively unsuccessful reproductive tactic employed only in "best-of-a-bad-job" situations. *Received 17 April 1991, accepted 20 January 1992.*

FACULTATIVE BROOD parasitism (i.e. parasitic egg laying by species that typically care for their own eggs and young) is probably more frequent in the waterfowl (Anatidae) than in any other group of birds (Weller 1959, Rohwer and Freeman 1989). Although parasitic egg laying has been documented extensively in many species, including the Black-bellied Whistling-Duck (*Dendrocygna autumnalis*), Common Shelduck (*Tadorna tadorna*), Redhead (*Aythya americana*), Wood Duck (*Aix sponsa*), Common Goldeneye (*Bucephala clangula*), and Ruddy Duck (*Oxyura jamaicensis*), hypotheses for the functional significance of parasitic egg laying (see Yom-Tov 1980, Andersson 1984, Eadie et al. 1988, Sayler in press) have received little evaluation. Patterns of parasitic and typical nesting behavior in individual females and the relationship between ecological factors and the frequency of parasitism have been addressed in only a few recent studies (Eadie 1989, Lank et al. 1989, Sorenson 1991).

Parasitic egg laying by Redheads is a prominent feature of the nesting biology of Canvasbacks (*Aythya valisineria*) and has been noted since biologists began studying waterfowl nests in the prairie-pothole region of North America (e.g. Job 1899, Bent 1902). Redheads parasitize over 50% of Canvasback nests in many areas, usually laying an average of three or more parasitic eggs per nest (e.g. Weller 1959, Bouffard 1983, Sorenson 1991). Little information is available, however, about parasitic egg laying by Canvasbacks. Canvasback eggs are rarely found in the nests of Redheads (e.g. Hochbaum 1944, Erickson 1948), and intraspecific parasitism among Canvasbacks has been noted only infrequently when clutches larger than could have been laid by a single female were observed (e.g. Furniss 1938, Olson 1964, Stoudt 1982). More recently, M. G. Anderson (cited in Andersson 1984) directly observed four cases of parasitic egg laying among Canvasbacks, and Sayler (1985) documented seven cases of intraspecific parasitism with time-lapse photography. To date, however, no study has provided

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estimates of the proportion of Canvasback nests parasitized by conspecifics or of the proportion of eggs that are laid parasitically.

I (Sorenson 1991) used time-lapse photography to document parasitic egg laying by Redheads at Canvasback host nests. This method in combination with frequent nest checks also revealed a high rate of intraspecific parasitism among Canvasbacks and, in addition, allowed the identification of individual Canvasback females that laid parasitic eggs. In this paper, I report on the frequency and success of parasitic egg laying for one Manitoba population of Canvasbacks. In addition, I address for Canvasbacks alternative hypotheses for the functional significance of parasitic egg laying. A preliminary test of these hypotheses is provided by an examination of the contexts in which individual Canvasback females employ parasitic tactics and of population level patterns of parasitic egg laying and typical nesting. These hypotheses are briefly stated below.

The fecundity hypotheses.—(1) Parasitic egg laying enables females to increase their annual fecundity by obtaining care for more than one clutch per season. Females might lay a large number of parasitic eggs instead of nesting or they might lay additional eggs parasitically prior to nesting. (2) Alternatively or in addition, avoidance of the predation risks and energetic demands of incubation and brood care result in higher survival for females that only lay parasitic eggs and, as a consequence, higher lifetime fecundity.

The best-of-a-bad-job hypotheses.—(1) Parasitic egg laying is a relatively unproductive strategy employed by females when environmental or phenotypic constraints limit their ability to nest in the typical manner. Females might lay parasitic eggs after constraints such as nest predation or flooding result in the termination of a typical nesting attempt, or when constraints such as limited availability of food resources or nest sites prevent them from initiating a typical nest in the first place. (2) As a low-cost alternative to typical nesting, parasitic egg laying may represent an adaptive reduction in reproductive effort (i.e. restraint) in response to poor prospects for successful reproduction (see Curio 1983, Sorenson 1991). When environmental conditions are unfavorable, females could avoid the costs of incubation and brood rearing by laying only parasitic eggs and thereby improve their own probability of surviving to the next breeding season.

METHODS

Study area and natural history.—I conducted field work from April through August in 1986 through 1988 on a 10.4-km² study area about 3 km southwest of Minnedosa, Manitoba. The area just south of Minnedosa hosts a relatively high-density population of Canvasbacks, which has been studied almost continuously since the 1950s. More detailed information on the Minnedosa area is provided in Kiel et al. (1972) and Stoudt (1982). Canvasbacks arrive in the area in mid-April, pairs already having formed during spring migration (Weller 1965, Anderson 1985). Females begin nesting by late April or early May, building nests over water in residual emergent vegetation. Typically, seven to nine eggs are laid on consecutive days and hatch after about 25 days of incubation by the female only. Ducklings feed themselves, but females lead and protect their brood for up to 60 days after hatching. Many nests are destroyed by predators (Stoudt 1982), and females often renest after a first nest is destroyed (Doty et al. 1984).

Trapping, marking, and nest searching.—I trapped Canvasbacks from late April to early June with decoy traps that used captive Canvasback and Redhead females as bait (Anderson et al. 1980). Based on plumage characteristics (Serie et al. 1982), females were separated into two age categories: second-year (SY) and after-second-year (ASY) females. All females were fitted with colored nasal markers for individual identification (Doty and Greenwood 1974, Lokemoen and Sharp 1985). I also trapped females on their nests late in the incubation stage using a modified drop-door trap (Blums et al. 1983). I color marked 77 ASY and 73 SY Canvasback females during the study. Several decoy-trapped females were never sighted after being marked and probably were transients. I considered females to be "resident" only if they were sighted at least three times on or near the study area, or were known to nest on or near the study area; 71 ASY and 61 SY females met this minimum criterion.

The emergent vegetation in all wetlands on the 10.4-km² main study area (as many as 350 separate wetlands, or potholes, depending on annual water conditions) were searched every 8 to 10 days during May and June to find nests early in the laying stage. All time-lapse photography (see below) was conducted on this main study area and all analyses of population-level data on parasitism and nesting include only nests on the main study area.

Time-lapse photography.—Parasitic egg laying by individual females was documented by continuously and simultaneously monitoring as many as 25 potential host nests with time-lapse photography. I filmed a total of 1,159 nest-days at 171 Canvasback nests and 340 nest-days at 33 Redhead nests during the study. I filmed during the second half of the laying stage and first week of incubation at as many nests as possible with Super-8 movie cameras equipped with an interval timer set to expose one frame per minute. I set up cameras and changed film (every other day) in the afternoon and evening to minimize disturbance, but host females often were flushed from the nest. Females returned to their nests by dawn of the day after the camera was first set up and almost always returned in less than 30 min after subsequent film changes. To minimize the possible effect of my frequent visits on rates of nest predation, I always walked into a wetland at some distance from a known nest site and then waded through open water to approach the nest from the inside edge of the emergent vegetation.

I viewed films one frame at a time to find cases of intruding females laying parasitic eggs. Each film event, any sequence of frames with a female Canvasback (other than the nest owner) on the nest, was assigned to one of two categories: (1) "Nest visits" were events in which the intruding female did not appear to lay an egg and were usually of short duration (79% were less than 5 min). (2) "Egg-laying events" were those in which the intruding female appeared to have laid an egg and were usually of longer duration (99% were more than 5 min). Behavioral criteria used to classify film events are described in Sorenson (1991); qualitatively, the behavior of intruding Canvasback and Redhead females in egg-laying events was very similar. The time and duration of film events were calculated by interpolation between the start and finish times of films based on the number of frames exposed.

The number of egg-laying events involving intruding Canvasback females on a given roll of film was consistent with the number of new Canvasback eggs found in the nest when film was changed for 85% of egg-laying events (n = 96). In 3 of the remaining 14 cases, an egg that could have been laid during the presumed egg-laying event was subsequently found beneath the nest. No parasitic egg was ever found in 11 cases. In three cases, however, nests were destroyed by predators after the egg-laying event and before the next film change. In the remaining eight cases, the parasitic egg may have been cracked or broken during egg laying and then removed by the host female before my next visit to the nest, or may have been displaced from the nest and never found (see Sorenson 1991). In five of the eight cases, the intruding female failed to displace the host female from the nest and the parasitic egg may have immediately rolled into the water after it was laid on the edge of the nest. In this paper, I consider these 11 cases as likely but not definite instances of parasitic egg laying.

I recorded 96 parasitic egg-laying events on film, representing 40% of all parasitic egg laying by Canvasbacks on the main study area (n = 174 parasitic eggs plus 65 likely parasitic eggs). Intruding Canvasback females were also recorded in 97 nest visits. The intruding female was marked and could be at least tentatively identified in 47 egg-laying events (20% of all parasitic eggs laid) and 42 nest visits. Film records of parasitic egg laying were combined with information on typical nesting to produce egg-laying histories for individual females. These histories may be incomplete, however, because only 40% of parasitic egg laying on the study area was recorded on film.

Nest and egg data.—During each nest check, all new eggs were measured for length and width and numbered on both ends with permanent ink. The numbers of previously laid eggs remaining in the nest were noted. I calculated nest initiation dates by back-dating one day for each host egg in the nest and, for nests found after the laying stage, the number of days of incubation. Incubation stage was estimated from the angle and buoyancy of eggs placed in water (Westerskov 1950; technique calibrated for Canvasback eggs by M. G. Anderson and B. D. Sullivan unpubl. data).

I used several criteria to detect parasitic egg laying. Eggs added to a nest at a rate of greater than one per day, eggs laid during the incubation stage, and egg-laying events on film were considered unequivocal evidence of parasitism. Nests with 13 or more Canvasback eggs also were classified as parasitized. Obvious differences in the color and size of eggs, a total clutch size greater than 10 eggs (see Results for justification), and differences in incubation stage within a clutch were taken as indications of likely parasitic eggs. The opportunity to detect parasitism varied among nests. While 142 of 179 Canvasback nests in which the host's clutch was completed were filmed, only 78 nests were filmed during the laying stage. On average, these 78 nests were found 4.6 days before the end of the laying stage and were filmed during the last 2.7 days of laying and the first 5.9 days of incubation.

After removing the camera, I visited nests at about one-week intervals to document nest and egg fate. During the final nest check, the bottom of the wetland within 1 m of the nest was searched thoroughly for eggs. Numbers on eggs usually were legible even after as many as 25 days in the water. If not, eggs often could be identified from length and width measurements as these were highly repeatable and sufficiently variable. Nests in which one or more eggs hatched were classified as successful (including one Canvasback nest in which only Redhead eggs hatched).

For each successful nest, I derived a maximum estimate of the number of host and known parasitic Canvasback eggs that hatched. This estimate was 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 found outside of the nest, and the number of ducklings in the initial sighting of the brood. Because remains of hatched eggs may be eaten or carried away by the female (Weller 1959), or crushed beyond recognition in the bottom of the nest bowl, this maximum estimate assumes that a given egg hatched unless there was some evidence that it did not. Because of uncertainty about the identity of parasitic eggs, the sum of the maximum estimates of the number of host and parasitic eggs hatched could exceed the total number of Canvasback

TABLE 1. Rate of intraspecific parasitism in Canvasback nests with completed clutches.

Year	Percent of nests parasitized[a] (no. parasitized/total)	Parasitic eggs/nest[b] (range)
1986	25–33% (14–18/55)	1.8–2.4 (1–4)
1987	41–44% (27–29/66)	2.4–2.9 (1–7)
1988	41–45% (24–26/58)	2.8–3.7 (1–10)
1986–1988	36–41% (65–73/179)	2.4–3.1 (1–10)

[a] Higher value includes nests for which evidence of parasitism was inconclusive.

[b] Only nests with unequivocal evidence of parasitism used to calculate mean number of parasitic eggs per parasitized nest. Minimum and maximum estimates of number of parasitic eggs in those nests include known parasitic eggs, and known plus likely parasitic eggs, respectively.

eggs that hatched in a given nest. For example, if four Canvasback eggs were added to a nest over a two-day interval and two egg-laying events were recorded on film, I knew without doubt that two parasitic eggs had been laid. I did not necessarily know, however, which of the four eggs were parasitic. If two of the four eggs eventually hatched and two were displaced into the water, then I assumed that two parasitic eggs hatched when determining the maximum success of parasitic eggs, and I assumed that two host eggs hatched when determining the maximum success of host eggs. I used similar assumptions to derive minimum estimates of the number of parasitic and nonparasitic eggs that were left unhatched and displaced into the water.

Censuses.—To estimate per capita rates of parasitic egg laying and typical nesting by Canvasbacks, two complete counts of all Canvasbacks on all wetlands on the main study area were conducted each year in mid- and late May. The methodology for these counts is described by Sugden and Butler (1980). Two additional counts in 1987 and three additional counts in 1988 were conducted in a similar manner, but each count was completed over three to four days instead of one morning. These counts are subject to various sources of error, including movement of birds during the count and a male-biased sex ratio, and should be considered only rough estimates of the population density on the study area.

TABLE 2. Population-level frequency of parasitic egg laying by Canvasbacks and species distribution of parasitic eggs.

Year	Canvasback eggs[a]	Percent of eggs parasitic[b]	No. parasitic eggs laid in nests of: Canvasbacks[b]	Redheads	Mallards
1986	545	5.5–8.6	27–44	2	1
1987	667	10.5–13.8	68–90	2	0
1988	580	12.8–17.2	73–99	1	0
1986–1988	1,792	9.7–13.3	168–233	5	1

[a] Total number of Canvasback eggs laid on 10.4-km^2 main study area.

[b] Minimum and maximum estimates include known parasitic eggs, and known plus likely parasitic eggs, respectively.

Statistical analyses.—Statistical analyses were carried out using SYSTAT software (Wilkinson 1987) on a Macintosh computer. Categorical analyses used the G-test for goodness-of-fit or G-test for independence, applying William's correction for small sample size (Sokal and Rohlf 1981).

RESULTS AND DISCUSSION

FREQUENCY OF PARASITIC EGG LAYING

Over the three years of the study, at least 64 of 179 (36%) Canvasback nests in which the host's clutch was completed were parasitized by other Canvasbacks (Table 1). Inconclusive evidence indicated parasitism in eight additional nests. In two cases, a single egg-laying event was recorded on film but no new egg was found in the nest. Two egg-laying events were recorded in the middle of the host's laying stage at a third nest, but the rate of egg addition was consistent with the host female laying one egg per day. Eggs that differed in color and size from the rest of the clutch and were also behind in development indicated parasitism in two nests. Three nests not found until the incubation stage had clutches of 11 eggs and were probably intraspecifically parasitized (see below). The number of parasitic Canvasback eggs laid per nest ranged from 1 to 10 and was, on average, at least 2.4 (Table 1). One Redhead nest in each year of the study and one Mallard (*Anas platyrhynchos*) nest in 1986 were also parasitized by Canvasbacks.

At the population level, at least 9.7% of all Canvasback eggs were laid parasitically (Table 2). The higher estimates for all of the parameters in Tables 1 and 2 may still be underestimates of the actual frequency of parasitism in the study population because some parasitic egg laying almost certainly went undetected. Slightly higher estimates are obtained when only completed clutches that were followed for at least part of the laying stage are considered. At least 38% (n = 101) of these nests were parasitized and at least 11.6% (n = 909) of the Canvasback eggs in these nests were parasitic.

The proportion of nests parasitized, the number of parasitic eggs per nest, and the proportion of Canvasback eggs that were parasitic were all lowest in 1986 and highest in 1988 (Tables 1 and 2). Although detection of parasitic egg laying was improved in 1987 and 1988 by increasing filming effort, these results also reflect real differences in the frequency of parasitism among years. I recorded 0.035, 0.097 and 0.091 parasitic egg-laying events per day of filming at Canvasback nests in 1986, 1987, and 1988, respectively ($G_{adj} = 10.8$, $P < 0.005$, df = 2).

Although previous studies of Canvasback nesting biology provide no quantitative estimates of the frequency of intraspecific parasitism, most have suggested that parasitic egg laying by Canvasbacks was infrequent (e.g. Hochbaum 1944, Erickson 1948, Sayler 1985). The relatively high rates of intraspecific parasitism observed in my study probably can be explained primarily by the more intensive documentation of the egg-laying stage at individual nests. Nest checks were made only once or twice during each nest's history in most previous studies of Canvasbacks in the interest of minimizing the effects of disturbance by the investigator (e.g. Olson 1964, Sugden 1978, Stoudt 1982). Infrequent nest visits, however, provide little opportunity to detect patterns of egg addition that indicate parasitic egg laying.

Stoudt (1982) suggested that "clutches larger than 12 or 13 eggs may indicate that two or more Canvasbacks laid eggs in one nest." Total "clutch size" alone, however, provides a poor measure of the frequency of parasitism. In this study, only 7% of nests with completed clutches had 13 or more Canvasback eggs, while at least 36% of nests were actually parasitized (Fig. 1). The indicated rate of parasitism would have been even less if I had not numbered eggs and thoroughly searched underneath nests for eggs displaced into the water—only 5 of 179 nests (3%) were observed with 13 or more Canvasback eggs in the nest at one time.

Clutch size of greater than 12 eggs, therefore, is a very conservative criterion for intraspecific parasitism in Canvasbacks. Even clutches of 10 or 11 eggs were more likely to be the result of intraspecific parasitism than the laying of a single female (Fig. 1). In fact, most clutches of 10 or 11 eggs for which I had no evidence of parasitism were not found until they had their full complement of eggs and, therefore, after parasitism could have been detected. Only two nests that were followed through the laying stage accumulated 10 or 11 Canvasback eggs without evidence of intraspecific parasitism. One of these clutches included an unusual skip in the laying sequence and may actually have been the result of a second female laying six eggs in an abandoned nest that already contained five eggs.

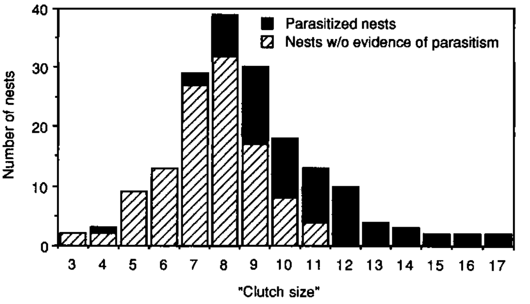

Fig. 1. Relationship between total number of Canvasback eggs in a nest (i.e. "clutch size") and incidence of intraspecific parasitism. "Parasitized nests" include only those with unequivocal evidence of parasitism.

Nest checks made every other day during the laying stage and periodically during incubation would have detected parasitism in 55 of the 65 nests known to be parasitized in this study (Table 3). Inability to detect parasitic eggs laid on days immediately following the host's laying stage is the primary weakness of frequent nest checks as a method for documenting intraspecific parasitism. Frederick and Shields (1986) suggested a technique to correct for this problem, but the required assumptions of only one parasitic egg per host nest and a constant rate of parasitism through the laying stage are not met in Canvasbacks (Table 1, unpubl. data). Time-lapse photography was an effective means of documenting parasitic egg laying at the end of the host's laying stage and was the only evidence of parasitism for 10 nests in which only one or two parasitic eggs were laid (Table 3).

Erickson (1948) made the most intensive observations of nesting in any previous study of Canvasbacks and, although he apparently made several nest checks during each nest's history and carefully accounted for eggs displaced from the nest into the water, he concluded that "there was no evidence to indicate that much, if any, intraspecific nest parasitism occurred among Canvasbacks." This raises the question of whether rates of parasitic egg laying observed in my study are representative of all Canvasback breeding populations or are for some rea-

TABLE 3. Evidence of parasitic egg laying in Canvasback nests. Parenthetical values are numbers of nests in which parasitism was indicated by only that particular criterion.

Year	No. nests parasitized[a]	No. nests in which parasitism indicated by: Rate of egg addition >1 per day	Eggs laid during incubation	Clutch size (≥13)	Time-lapse photography
1986	14[b]	3 (0)	7 (3)	3 (2)	6 (1)
1987	27	8 (2)	18 (7)	2 (0)	17 (5)
1988	24	8 (2)	15 (5)	8 (1)	15 (4)
1986–1988	65	19 (4)	40 (15)	13 (3)	38 (10)

[a] Analysis includes only completed clutches with known parasitic eggs.

[b] Two nests in 1986, each with a total of 11 Canvasback eggs, were classified as parasitized on basis of clear differences in size, shape and color of eggs within clutch.

son exaggerated. Three factors may have contributed to high rates of parasitic egg laying in my study.

First, the population density of Canvasbacks on my study area was high compared to that encountered in previous studies in the prairie pothole region. Pair counts indicated 4.8, 6.7, and 7.7 pairs/km^2 in 1986, 1987, and 1988, respectively. Stoudt (1982) recorded densities of 2.1 to 4.1 pairs/km^2 during a 12-year study in the Minnedosa area; Dzubin (1955) recorded an average of 3.1 pairs/km^2 over 7 years on another Manitoba study area; and Sugden (1978) recorded 1.2 to 3.1 pairs/km^2 during a 5-year study in Saskatchewan. Density-dependent social interactions and competition for food resources could lead to increased rates of parasitic egg laying. Alternatively, by making host nests easier to find, a high density of breeding birds may create opportunities for parasitic egg laying that otherwise would not be available.

Second, relatively high rates of nest success and restrictive hunting regulations in 1986 and 1987 resulted in a large proportion of SY females in the Canvasback population (as well as higher population densities) in 1987 and 1988. I captured 0.04, 0.23, and 0.23 SY females per trap-day in 1986, 1987, and 1988, respectively ($G_{adj} = 20.9$, $P < 0.001$, df = 2). If younger females are more likely to lay parasitically (see below), this change in the age structure of the population may explain higher rates of parasitism in 1987 and 1988.

Third, disturbance associated with time-lapse photography and frequent nest searching may have led to higher than normal rates of parasitic egg laying, particularly if females abandoning nests during the laying stage go on to lay parasitic eggs (see below). In this study, 61 of 240 Canvasback nests were terminated during the laying stage. However, 33 already were abandoned or destroyed when they were found, suggesting that nest destruction and abandonment during the laying stage are regular and natural features of Canvasback nesting biology.

Six laying-stage nests probably were abandoned as a direct result of my finding the nest or setting up a camera. One of the six females was known to lay a parasitic egg, and very tenuous evidence suggested that three others laid parasitic eggs after abandoning their nests. It is possible that disturbance was a factor in the abandonment of 10 other laying-stage nests, but eight of these nests already were in poor condition or were not attended by a female when found. Twelve laying-stage nests were destroyed by predators after I found them, but there was no indication that rates of nest predation were substantially increased by my activities. Overall, I can identify only seven parasitic eggs that appear to have been laid as a direct result of my interference. My activities probably contributed slightly but not substantially to the frequency of parasitic egg laying on the study area.

SUCCESS OF PARASITIC EGG LAYING

Considering only known parasitic eggs in successful nests, the maximum hatching success of parasitic eggs was only 29% compared to 79% of nonparasitic eggs (Table 4). The primary source of this difference was the large proportion of parasitic eggs laid during the host's incubation stage. These eggs contained developing embryos but were abandoned by host females when their own eggs hatched. The success of both parasitic and nonparasitic Canvasback eggs also was reduced by egg displacement, which was the direct result of parasitic intrusions by both Canvasback and Redhead females (unpubl. manuscript).

This analysis probably underestimates the actual success of parasitism because I was less likely to detect parasitic eggs laid during the host's laying stage and before a nest was found, parasitic eggs that also would be relatively likely to hatch. To compensate for this bias, I determined the maximum hatching success of parasitic eggs in successful Canvasback nests that were followed (i.e. monitored either with nest checks at least every other day or with both nest checks and filming) for at least three days during the laying stage. Sample size was small, but 42% of known parasitic eggs in these nests hatched ($n = 26$ eggs in 11 nests). Because the frequency of intraspecific parasitism was low early in the host's laying stage (see below), nearly all parasitic eggs in this sample of nests would have been detected.

An alternative measure of parasitic egg success that allows a larger sample of nests to be considered is the proportion of parasitic eggs laid during the host's laying stage. In all nests that were followed for at least three days during the laying stage, 51% of known parasitic eggs ($n = 69$ eggs in 22 nests) were laid before or on the first day of incubation (parasitic eggs laid on the first day of incubation sometimes hatched). The proportion of parasitic eggs laid in synchrony with the host's laying stage can also be estimated from daily rates of parasitic egg laying at all monitored host nests. No parasitism was detected more than four days before host clutch completion in 43 days of monitoring at 26 nests, while 0.119 and 0.099 parasitic eggs were detected per day of monitoring during the last five days of egg laying ($n = 318$ days at 97 nests) and the first nine days of incubation ($n = 647$ days at 112 nests), respectively. Ignoring the low rate of parasitism after the ninth day of incubation, 47% of parasitic eggs would have been laid before or on the first day of incubation. Comparing these estimates to the 100% of nonparasitic eggs that, by definition, are laid during the host's laying stage suggests that the success of parasitic Canvasback eggs was only about one-half that of nonparasitic eggs.

Canvasback parasitism of Redhead nests may be particularly ineffective because Canvasback eggs have a slightly longer incubation time, on average, than Redhead eggs (Erickson 1948). Although all four Canvasback eggs laid in successful Redhead nests hatched, these ducklings may not have been ready to leave the nest at the same time as the Redhead ducklings. In one case, two parasitic Canvasback ducklings were left behind on the nesting pond when the Redhead female moved her brood to another wetland shortly after hatch.

Parasitic egg success is lower in Canvasbacks than in other waterfowl species in which parasitic egg laying is relatively frequent. Parasitic eggs laid by Redheads (46% of parasitic eggs hatched, Sorenson 1991), Snow Geese (*Chen caerulescens*, 63% hatched, Lank et al. 1990), Barrow's and Common goldeneyes (*Bucephala islandica* and *B. clangula*, 74% hatched, Eadie 1989), and Wood Ducks (78% of parasitic eggs laid during host's laying stage, Clawson et al. 1979) have higher hatching success because a larger proportion are laid during the host's laying stage.

TABLE 4. Fate of Canvasback eggs in successful nests.

Year	Percent[a] Hatched	Percent[a] Left unhatched	Percent[a] Displaced into water	Sample size[b] Eggs	Sample size[b] Nests
Parasitic Canvasback eggs					
1986	42	42	16	19	8 C, 1 R
1987	33	59	9	46	19 C, 1 R
1988	6	71	23	17	8 C
1986–1988	29	57	13	82	35 C, 2 R
Nonparasitic Canvasback eggs					
1986	75	3	23	279	34 C
1987	85	2	13	334	42 C
1988	75	3	22	139	18 C
1986–1988	79.4	2.5	18.1	752	94 C

[a] Values for egg fates are maximum estimates for proportion of eggs hatched and minimum estimates for proportions of eggs left unhatched and displaced into water (see Methods).

[b] Analysis includes known parasitic eggs in successful Canvasback (C) and Redhead (R) nests that were parasitized by Canvasbacks, and nonparasitic eggs in all successful Canvasback nests.

Parasitic and Typical Nesting Behavior of Individual Females

Histories of parasitic egg laying and typical nesting for individual females recorded in egg-laying events on film were somewhat variable, but could be divided into two general categories: parasitic egg laying by nesting females; and parasitic egg laying by females not known to nest.

Parasitic egg laying by nesting females.—Fifteen cases in which a Canvasback female laid one or more parasitic eggs prior to initiating her own nest accounted for 25 of 47 parasitic egg-laying events in which the intruding female was identified. Most of these females initiated their own nests almost immediately after laying only one or two parasitic eggs. For example, in 1987, female #286 laid parasitic eggs in the nest of fe-

TABLE 5. Comparison ($\bar{x}$ ± SE, with range in parentheses) of egg-laying histories for individual Canvasback and Redhead females known to lay parasitic eggs prior to nesting.

	Canvasbacks (n = 15)	Redheads[a] (n = 9)	P[b]
No. egg-laying events on film	1.7 ± 0.2 (1–4)	3.4 ± 0.6 (1–7)	0.007
No. nest visits on film	0.2 ± 0.1 (0–1)	2.4 ± 0.4 (0–4)	<0.001
Days between last detected parasitic egg and nest initiation[c]	2.7 ± 0.7 (1–9)	9.9 ± 1.9 (1–20)	0.002

[a] Data for Redheads are taken from Sorenson (1991:fig. 1).
[b] Mann-Whitney U-test.
[c] If nest initiation date not precisely known, all available evidence other than date(s) of parasitic egg laying was used to make a "best" estimate.

male #406 on 4 and 5 May and then initiated laying a clutch of eight eggs in a nest of her own on 6 or 7 May. She incubated this clutch until hatch on about 8 June and then accompanied her brood of four Canvasbacks and four Redheads until 22 July. In 13 of 15 cases, the parasitic female was recorded in only one or two parasitic egg-laying events, although circumstantial evidence based on egg characteristics suggested that two of these females may have laid four and five parasitic eggs, respectively. Dates of nest initiation for many females were not known precisely, but in 12 of 15 cases the female may have initiated her nest only one or two days after she was last recorded laying a parasitic egg. In five cases, the parasitic female was known to initiate her own nest the day after laying a parasitic egg.

This pattern of behavior in Canvasbacks differed in several respects from the "dual strategy" of Redheads (Sorenson 1991). Canvasback females did not lay an entire "clutch" of parasitic eggs prior to nesting and there was no "renest interval" between parasitic egg laying and typical nesting. Although intruding Canvasbacks were easier to identify on film, Canvasback females were recorded in fewer egg-laying events and fewer nest visits than Redhead females laying parasitic eggs prior to nesting (Table 5). In addition, the time interval between the last parasitic egg detected for a given female and the initiation of her own nest was much shorter for Canvasbacks than for Redheads (Table 5).

Any analysis of clutch size in Canvasbacks is complicated by undetected intraspecific parasitism and egg displacement resulting from Redhead parasitism. However, Canvasback females laying parasitic eggs prior to nesting may have laid fewer eggs, on average, in their own nests than females not known to lay parasitic eggs. Mean clutch size of ASY Canvasback females (excluding known parasitic eggs and renests) was 8.3 ± SE of 0.2 (n = 32), 8.3 ± 0.2 (n = 37), and 8.0 ± 0.2 (n = 31) eggs in 1986, 1987, and 1988, respectively. For ASY females recorded laying parasitic eggs prior to nesting, mean completed clutch size was 7.1 ± 0.6 (n = 10, assuming that two females with an undetermined number of parasitic eggs in their own nests laid nine eggs each). Three parasitic females had unusually small clutches of three or five eggs. In total, however, parasitic Canvasbacks may lay a slightly larger number of eggs ($\bar{x}$ = 8.7 ± 0.7 known eggs; parasitic egg-laying histories may be incomplete). Female #264 laid at least 11 and perhaps 12 eggs on consecutive days in 1987, something never documented for a female laying only in her own nest.

Given that the success of parasitic Canvasback eggs is so low and that only one or a few parasitic eggs are laid immediately prior to nest initiation, it is not clear why females would not lay these additional eggs in their own nests where they would be much more likely to hatch. If a female laid as many as 12 eggs in her own nest, the viability of the first few eggs laid might be reduced slightly by the delayed onset of incubation (Arnold et al. 1987), but these eggs would still have higher hatching success than parasitic eggs. In addition, the advantage of laying one or a few eggs in another nest as a means of spreading the risk of predation (e.g., Rubenstein 1982) would be insignificant compared to the disadvantage of lower hatching success (Sorenson 1990). That the total number of eggs laid by these females is sometimes greater than would be laid in a typical nest may simply be a consequence of a lack of proximate stimuli usually associated with the onset of incubation—a parasitizing female does not experience the accumulation of eggs in her own nest—rather than an evolved mechanism for increasing fecundity.

Although the sequence of events is consistent with the fecundity hypothesis, laying parasitic eggs prior to nesting probably is not an effective means of increasing annual reproductive success in Canvasbacks. As an alternative explanation for this pattern of behavior, I suggest that female Canvasbacks lay one or two parasitic eggs after they abandon nests (or have their nests destroyed) during the nest-building or early laying stages and before initiating a second nest, because the second nest is not immediately ready to receive eggs. In some cases, the laying of all these eggs is essentially continuous, one egg being laid on each consecutive day. Five observations support this hypothesis.

First, Canvasbacks sometimes abandon nests in the early stages. Hochbaum (1944:47) stated that "The hen sometimes begins, and abandons, one or two nests before the final choice is made, dropped eggs [apparently meaning eggs laid outside of any nest] are found occasionally during this prenesting period." I found 10 Canvasback nests that contained only one or two eggs and that were already abandoned. Possible nests under construction that were abandoned before any eggs were laid also were found.

Second, Erickson (1948:146) noted that "A number of females apparently proceeded from an earlier attempt without a break in egg laying when the earlier attempt consisted of one to three or four unincubated eggs. Such renests seemed to entail compensatory egg laying, for these renesting females laid clutches that approached in number of eggs the size of interpreted, initial, final clutches." I also recorded two cases in which a female initiated laying in a second nest the day after abandoning a nest with two eggs. I suggest here that this kind of continuous laying may often include one or more parasitic eggs between the first and second nest. Erickson's observation of "compensatory egg laying" is consistent with my observation that females laying parasitic eggs prior to nesting sometimes laid a larger number of eggs in total than would be laid in a single nest.

Third, unlike ground-nesting ducks, which typically lay the first egg of a clutch in a simple scrape, Canvasbacks must build a structure that will contain eggs above the water. Although females often lay the first one or two eggs on a very minimal platform of floating vegetation and continue to build the nest during the laying stage, the process of nest-site selection and nest building typically takes several days (Hochbaum 1944, Erickson 1948, M. G. Anderson pers. comm.). In most cases, a female probably would not have a second nest of her own ready to receive eggs the day after abandoning a first nest.

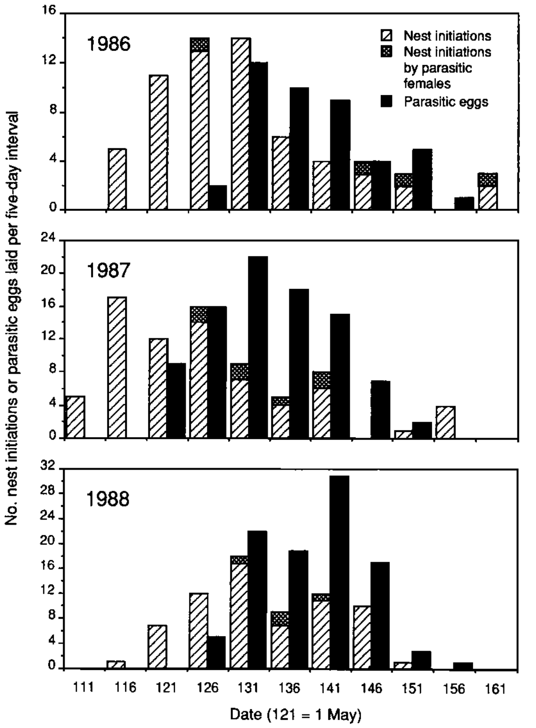

Fig. 2. Seasonal chronology of typical nest initiations and parasitic egg laying by Canvasbacks. Number of typical nests initiated and number of parasitic eggs laid are shown for each five-day interval during breeding season. Both known and likely parasitic eggs are included.

Fourth, the seasonal peak of parasitic egg laying by Canvasbacks followed the peak of typical nest initiations and parasitic females initiated their own nests relatively late in the season (Fig. 2). It seems likely that many of these females would have attempted a first nest before laying parasitic eggs.

Fifth, several cases (some of which were the result of my disturbance) suggest that females typically lay parasitic eggs after nests are destroyed or after abandoning nests during the laying stage. For example, female #784 laid a parasitic egg at 1201 CST on 29 May 1987 after abandoning her own nest with four eggs, which was found at 1015 the same day. In a similar case, female #160 laid a parasitic egg at 0931 on 23 May 1988 after her nest with one egg was found at 0800 the same day (this female resumed laying in her own nest the next day). In

TABLE 6. Comparison ($\bar{x} \pm$ SE, with range in parentheses) of egg-laying histories for females that laid parasitic eggs prior to nesting and females that were known only to lay parasitic eggs.

No. on film	Parasitism prior to nesting ($n = 15$)	Parasitism only ($n = 7$)	P[a]
Egg-laying events	1.7 ± 0.2 (1-4)	2.9 ± 0.6 (1-5)	0.078
Nest visits	0.2 ± 0.1 (0-1)	1.6 ± 0.4 (0-3)	0.005

[a] Mann-Whitney *U*-test.

each of three more possible cases, two parasitic eggs were laid in a nearby nest on the two days following the abandonment or destruction of a laying-stage nest. In two cases, the parasitic females were unmarked and, in the third, the nearby nest was not being filmed.

In general, a large proportion of parasitic egg laying by Canvasbacks probably is associated with disruptions in the typical nesting cycle. If a first nest is terminated at an early stage, females may proceed with parasitic egg laying and a second nesting attempt essentially continuously. Several cases that did not fit this scenario may be explained by variation in the timing of events. For example, if a first nest is terminated later in the laying stage, a female might lay parasitic eggs but then might not initiate a second nest until after a renest interval. In two cases, females initiated nests eight or more days after they were last recorded to lay a parasitic egg.

Parasitic egg laying by females not known to nest.—A significant portion of parasitic egg laying by Canvasbacks appears to be attributable to females that do not initiate a nest of their own during the season. Seven females in 1987 and 1988 that were not known to nest laid 20 of the 47 parasitic eggs laid by identified females. Female Canvasbacks known only to lay parasitic eggs were recorded in more egg-laying events and more nest visits than females known to initiate nests after laying parasitic eggs (Table 6). Although it is possible that any of these females initiated her own nest either before or after laying parasitic eggs, the larger number of parasitic eggs and nest visits in comparison to females that were known to nest suggests that at least some of these females only laid parasitically. Although sample sizes were small, the proportion of eggs laid during the host's laying stage or first day of incubation, a measure of parasitic egg success, did not differ between females known only to lay parasitic eggs (45%, $n = 20$) and females laying parasitic eggs before nesting (64%, $n = 25$; $G_{adj} = 1.58$, $P > 0.1$, df = 1).

Given its low success, parasitic egg laying could not compete as a pure alternative to typical nesting in Canvasbacks; no female was known to lay enough parasitic eggs (e.g. 18 or more) to even approach the success of laying one clutch in a typical nest. Females that lay only parasitic eggs also would be unlikely to have higher lifetime reproductive success. Although avoidance of the costs and risks of incubation and brood-rearing might result in higher survival for a parasitic female, an improbable increase in annual survival from 74.5% (Anderson et al. in press) to 88.7% would be needed to compensate for the low success of parasitic eggs, assuming no increase in number of eggs laid and 50% lower hatching success.

Relationship of age to reproductive tactics.—Reproductive tactics of individual Canvasback females were strongly related to female age, and annual variation in population-level rates of parasitic egg laying and typical nesting was correlated with variation in the age structure of the population. Almost all older Canvasback females initiated a nest of their own, even when conditions for nesting were poor (Table 7). Younger females, however, were much less likely to initiate a typical nest, especially in 1988 when drought conditions resulted in very low rates of nest success (see Sorenson 1991). In 1988, 33 of 39 females that were at least three years old were known to nest, while only 5 of 20 females known to be two years old and 2 of 21 SY females were known to nest ($G_{adj} = 40.6$, $P < 0.001$, df = 2). When conditions were better in 1987, the frequency of typical nesting by SY males (8 of 28) may have been slightly higher (for 1987 SY females vs. 1988 SY females; $G_{adj} = 2.73$, $P < 0.1$, df = 1), but was still much lower than that of ASY females (for SY females vs. ASY females in 1987; $G_{adj} = 32.5$, $P < 0.001$, df = 1).

In contrast, parasitic egg laying was more likely to be employed by younger females. Of the seven females known only to lay parasitic eggs in a given year, two were SY females and two were two years old. The remaining three

TABLE 7. Age-related reproductive tactics of decoy-trapped and returning Canvasback females resident on or near the study area.[a]

Age[b]	No. females	No. females known to[c]: Parasitize only	Nest only	Both parasitize and nest	Neither nest nor parasitize
		1986			
SY	2	0	1	1	0
2+ years	9	0	5	3	1
		1987			
SY	28	2	5	3	18 (3)
2 years	4	0	3	1	0
2+ years	4	0	2	0	2
3+ years	28	0	25	3	0
		1988			
SY	21	0	2	0	19 (2)
2 years	20	2	4	1	13 (4)
2+ years	7	3	2	0	2 (1)
3+ years	39	0	30 (1)	3	6

[a] Because they were not marked until their own nests were near hatch, nest-trapped females could not have been recorded laying parasitic eggs and, therefore, are not included.

[b] 2 years = returning females trapped as SY birds in the previous year. 2+ years = newly decoy-trapped, unknown age ASY females. 3+ years = returning females trapped as ASY birds in a previous year.

[c] Parenthetical values are number of birds in each category recorded in at least one nest visit at another female's nest, but which were not known to lay parasitic eggs.

TABLE 8. Per capita production of parasitic eggs and typical nests by Canvasbacks.

Year	Females[a]	Parasitic eggs[b]	Parasitic eggs/ female	Nests[c]	Nests/ female
1986	~50	30–47	0.6–1.0	75	~1.5
1987	~70	70–92	1.0–1.3	85	~1.2
1988	~80	74–100	0.9–1.3	80	~1.0

[a] Rough estimates of density of Canvasbacks on 10.4-km² study area obtained from pair counts (see Methods).

[b] Minimum and maximum estimates include known parasitic eggs, and known plus likely parasitic eggs, respectively.

[c] Total number of typical nests initiated by Canvasbacks on study area.

were unknown-age ASY females decoy-trapped in 1988. After two years of extensive trapping efforts, most older females resident on the study area were marked; these three new females were probably younger ASY females (e.g. two years old). Females that were recorded in nest visits but were not known to lay parasitic eggs also were younger females that were not known to nest (Table 7). Although not enough data were available to assess the relationship in Canvasbacks, nest visits and egg-laying events by individual Redhead females were temporally associated, suggesting that nest visiting functions in parasitic behavior (Sorenson 1990).

Parasitic egg laying by younger females that did not nest may explain higher per capita rates of parasitic egg laying and lower rates of typical nest initiations in 1987 and 1988 than in 1986 (Table 8), when there were few SY females in the population (see above). The larger number of individual females that were known only to lay parasitic eggs and a much higher frequency of nest visiting in 1988, in particular (Table 7), also suggest that drought conditions in 1988 may have increased the frequency of parasitism.

Parasitic egg laying prior to typical nesting was also more frequent in younger females. Considering only nesting females, 4 of 12 SY females (33%), 2 of 9 known two-year-olds (22%) and 6 of 61 females that were at least three years old (10%) were known to lay parasitic eggs prior to nesting (for SY females and two-year-olds combined vs. three-year-olds and older females; $G_{adj} = 3.70$, $P < 0.06$, df = 1).

GENERAL DISCUSSION

The hypothesis I have offered to explain parasitic egg laying prior to nesting in Canvasbacks is a slight variation on the constraint hypothesis. Females apparently lay parasitic eggs not only after nests are destroyed by predators but also after abandoning nests in the early stages. In many cases, these females initiate a second nest of their own shortly or immediately after laying parasitic eggs. Unfortunately, females whose nests were terminated by natural causes at an early stage could rarely be identified in this study, leaving the first step in this hypothesized sequence of events largely undocumented. An experiment in which the nests of marked, identified females are disturbed or destroyed at an early stage and in which subsequent egg laying by these females is monitored (see Haramis et al. 1983, Eadie et al. 1987) is needed to verify that parasitic egg laying and initiation of a renest can proceed continuously after nest loss. In a recent study, female European Starlings (*Sturnus vulgaris*) laid one to three parasitic eggs in nearby nests immediately after their own clutches were removed during the laying stage (Feare 1991). These females also went on to initiate a renesting in the same season, but not until 8 to 14 days after they were last detected laying a parasitic egg.

Also unknown are the specific proximate stimuli that might cause a Canvasback female to abandon a nest at an early stage and the costs and benefits of this action. Females might respond to perceived threats to their own survival or indications that the current nesting attempt is likely to fail (e.g. appearance of a predator near nest site). Prior experience at a given location might be another factor determining the response of females to disturbance early in the nesting cycle. Canvasbacks are noted for their high degree of philopatry (Anderson et al. in press), and successful females in my study often nested in the same part of the same wetland in successive years (unpubl. data). Younger females are less likely to have nested successfully in the past and may be more sensitive to disturbance in the nest-building or early egg-laying stages.

Parasitic egg laying in Canvasbacks also appears to function in a second context consistent with either the restraint hypothesis or constraint hypothesis. Several younger females were known only to lay parasitic eggs, particularly in 1988 when drought conditions resulted in a reduction in the number and size of wetlands and much lower rates of nest success (see Sorenson 1991). Olson (1964) and Sayler (1985) also reported a higher frequency of parasitic egg laying among Canvasbacks during drought years. Although it is almost impossible to verify that a given female never initiated a nest of her own in a given year, parasitic egg laying may function as an alternative to typical nesting when conditions for nesting are poor. Females laying only parasitic eggs may have experienced energetic constraints imposed by a reduced food supply during drought and/or may have reduced their reproductive effort in response to poor prospects for success (see Sorenson 1991). Regardless of the relative importance of constraint and restraint, however, a higher frequency of parasitic behavior among young females strongly supports a best-of-a-bad-job hypothesis.

The data presented here indicate that parasitic egg laying is a regular feature of the nesting biology of Canvasbacks and not just an infrequent anomaly. This fact should be considered in any study of breeding Canvasbacks, particularly those in which clutch size, egg success or parentage is of interest. Parasitic egg laying does not, however, play the central role in Canvasback reproductive biology that it does in the biology of Redheads (Sorenson 1991). Even when conditions for typical nesting are poor, older Canvasback females initiate a typical nesting attempt while most younger females respond to poor conditions by not breeding at all (Table 7). The parasitic behavior of Canvasbacks may be representative of the wide variety of waterfowl species in which parasitism is a regular but relatively infrequent event.

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