PARASITIC EGG LAYING IN REDHEADS AND RUDDY DUCKS IN UTAH: INCIDENCE AND SUCCESS

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ABSTRACT.—North American Ruddy Ducks (*Oxyura jamaicensis*) and Redheads (*Aythya americana*) lay eggs parasitically in other waterfowl nests. Interspecific egg parasitism at Farmington Bay Waterfowl Management Area (WMA), Utah during 1972–1974 affected 290 (36%) of 809 duck nests. Redheads deposited 812 eggs into 264 nests of other species, whereas Ruddy Ducks deposited 146 eggs into 62 nests. Of 620 Redhead eggs deposited interspecifically and for which success rates were known, 21% hatched, compared with 24% of 146 Ruddy Duck eggs. Forty-three percent of the Redheads and 7% of the Ruddy Ducks produced on the study site hatched from eggs deposited interspecifically. An unknown number of Redhead and Ruddy ducklings hatched from eggs deposited intraspecifically. Rates of egg parasitism in Redheads and Ruddy Ducks did not increase in response to severe fluctuations in water levels affecting habitat used by nesting waterfowl, nor was a lack of suitable nesting cover associated with Redhead or Ruddy Duck parasitism. These results counter the contention that parasitic tendencies in the Redhead, and perhaps the Ruddy Duck, are environmentally induced. *Received 20 August 1982, accepted 7 February 1983.*

PARASITIC egg laying in birds is a much studied evolutionary phenomenon. Since the classic papers of Friedmann (1929, 1948, 1955, 1960) and Baker (1922, 1923, 1942), research has emphasized obligate (brood) parasitism, with three areas of interest prevailing: (1) the identification of parasitic taxa and hosts (80+ obligate parasitic species worldwide representing 5 families; for reviews see Lack 1968, Payne 1977); (2) descriptions of proximate and ultimate effects of obligate parasitism on host (Rothstein 1975a, b) and/or parasite (Lack 1968); and (3) the formulation of hypotheses about evolutionary pathways to obligate parasitism (Davis 1940, Hamilton and Orians 1965, Lack 1968). Considerably less, however, is known about the incidence or success of facultative parasitism, a breeding strategy in which individuals may behave parasitically but the species as a whole is not restricted to the parasitic mode of reproduction. Unlike obligate parasitism, which is interspecific, facultative parasitism can be either interspecific (Rienecker and Anderson 1960, Keith 1961, Lokemoen 1966, Bolen and Cain 1968) or intraspecific (see Yom-Tov 1980).

Of 45 species of North American waterfowl, only the Redhead (Weller 1959, Joyner 1976, Sugden 1980) and the Ruddy Duck (Joyner 1976, Siegfried 1976) regularily parasitize other species as well as their own. These species should be of particular interest evolutionarily, because, as Lack (1968: 97) has stated, "One can conceive of brood parasitism being evolved only through a transitional stage in which it coexisted with normal breeding, and that such a transitional stage has been eliminated presumably means that it resulted in fewer offspring than wholly normal or wholly parasitic breeding. Such an intermediate condition is found today only in a few nidifugous ducks." Only one anatid, the South American Black-headed Duck (*Heteronetta atricapilla*), has become parasitic (Weller 1968).

For obligate parasitism to develop in waterfowl, parasitic egg laying must produce more offspring than ordinary breeding would have done, and the behavior must be heritable (Weller 1959, Hamilton and Orians 1965, Lack 1968, Andersson and Eriksson 1982). Assuming that parasitic behavior is heritable in Redheads and Ruddy Ducks, there are at least four pathways toward greater fitness. (1) Eggs deposited parasitically have a higher mean probability of hatching than eggs deposited nonparasitically, all other factors being equal. (2) If hatching

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rates are comparable, ducklings produced from parasitically deposited eggs are more likely to reach sexual maturity and reproduce than are ducklings from nonparasitically deposited eggs. (3) If hatching and survival rates of eggs and ducklings are similar, parasitic (obligate and facultative) females deposit more eggs per breeding season than do nonparasitic females; this would be accomplished by increasing clutch size or number of clutches. (4) Survival rates are higher for obligate parasites than for nonparasitic females within the same population. Although there is no reason to believe parasitic females are less susceptible to natural or hunter-induced mortality outside of the breeding season, rates of predation might be higher for normally nesting females than for obligate parasites not bound to a nest or brood (Andersson and Eriksson 1982). Such would not be the case for "semiparasites" (Weller 1959), which parasitize first and nest subsequently.

The objectives of this paper are twofold. First, I compare success rates of Redhead and Ruddy Duck eggs deposited interspecifically with success rates of eggs in the nests of Redheads and Ruddy Ducks. No attempt was made to verify and quantify the success of intraspecific parasitism. Second, I relate several environmental factors reported to induce or increase facultative parasitism in waterfowl to parasitic egg laying by Redheads and Ruddy Ducks at Farmington Bay WMA, Utah during 1972–1974. The effects of interspecific parasitism by these two species on other waterfowl have been reported elsewhere (Joyner 1976).

METHODS

Farmington Bay refuge consists of 4,310 ha of emergent marsh (primarily *Typha* and *Scirpus* spp.), barren or sparsely vegetated mudflats, and lakes and ponds. Nest searches were conducted 3–4 times weekly in 1972 on two marshes (hereafter referred to as the West and North Turpin marshes) totalling 210 ha and in 1973–74 on three marshes (North Turpin, Central Turpin, Crystal) initially totalling 266 ha. The Central Turpin and Crystal marshes were added to the study in 1973 due to the destruction of the West Turpin Marsh through saltwater inundation from the Great Salt Lake in March. As a result, the West Turpin Marsh has not been included in the discussion of environmental factors influencing the incidence of egg parasitism.

All duck nests were marked with numbered cloth flags (12.5 × 5.0 cm) placed 5 m from the nest site. Interspecific parasitism was readily identified using egg color and size as criteria. Intraspecific parasitism was difficult to verify unless clutches were abnormally large or eggs were deposited after the initiation of incubation. For this study, I assumed an average clutch size of 7 for Ruddy Ducks (Siegfried 1976, Gray 1980) and a maximum potential clutch size of 10 (Siegfried 1976). For Redheads, I assumed an average clutch size of 11 and a maximum of 13 (Bellrose 1976, Alliston 1979). Nests were revisited once each week until eggs hatched or the nests were abandoned or destroyed. Redhead or Ruddy Duck eggs remaining in host nests were broken open and developing embryos aged according to Weller (1957). Nest initiation dates were noted or calculated by backdating from day of hatch.

RESULTS AND DISCUSSION

Extent and timing of interspecific parasitism.—Interspecific parasitism by Redheads and Ruddy Ducks during 1972–1974 affected 290 (36%) of 809 duck nests. Redheads parasitized 264 nests of four species and deposited 812 eggs, 50% of all Redhead eggs found. The 62 nests parasitized by Ruddy Ducks contained 146 parasitic eggs, or 9% of the 1,595 Ruddy Duck eggs found. Of the 809 nests 49 (6%) were parasitized by both species (dual parasitism). Ruddy Duck and Redhead pair counts were approximately equal, totalling 1,104 and 1,037, respectively, for the 3 yr combined (Joyner 1976). Within the study area, 158 Ruddy Duck nests were found compared with 93 Redhead.

Redhead nest initiation in 1973 and 1974 spanned a 7-week period, peaking in mid-May. Although Redhead nests were not followed to completion in 1972, initiation dates can be approximated. Of 30 Redhead nests, 47% were initiated before 1 June; the remaining 16 nests were completed after 15 May but before 15 June. Interspecific parasitism by the Redhead was first observed in early May of 1973–1974 and continued through June. Redhead eggs were deposited parasitically several weeks after the initiation of the last known Redhead nests on the study site. Interspecific parasitism during 1973 and 1974 peaked 5–7 days after the peak nest initiation date (15–21 May) for Redheads, which contrasts somewhat with Weller's (1959) observations for Redheads on Knudson's Marsh, Utah, where interspecific parasitism peaked *before* the peak date of Redhead nest initiation. Redhead nest initiation on Knudson's Marsh peaked during the first and second weeks of

June rather than in mid-May. Both Weller's observations and my own, however, indicate that Redhead parasitism in Utah is most prevalent in May and extends into June.

Interspecific parasitism by Ruddy Ducks was first apparent in late April or early May of each year, and host nests were parasitized through June; one parasitic egg was deposited in July 1972. Although few (4), parasitic eggs were deposited as late as 2 weeks after the initiation of the last Ruddy Duck nests located on the study site.

The first Ruddy Duck nests found each year were also initiated during the last week of April or the first week in May, and the last nests were initiated during the second week of June. Parasitic egg deposition and Ruddy Duck nest initiation each peaked in mid-May and coincided with peak nest initiation in Cinnamon Teal (*Anas cyanoptera*), Mallards (*A. platyrhynchos*), and Northern Pintails (*A. acuta*), the three species most commonly parasitized by Redheads and Ruddy Ducks at Farmington Bay (Joyner 1976). Gadwalls (*A. strepera*), which nested later, were parasitized infrequently.

Success.—Of 620 Redhead eggs deposited interspecifically during 1973–1974 and for which success rates are known, 21% were successful, compared with 34% of 500 Redhead eggs in 51 Redhead nests (includes successful and unsuccessful nests as well as an undetermined number of eggs deposited intraspecifically). Success rates for parasitic eggs versus eggs in Redhead nests differed significantly ($P < 0.01$, $t_s = 2.68$, Sokal and Rohlf 1969: 607). Success rates for 146 parasitic Ruddy Duck eggs deposited over the three nesting seasons averaged 24%, whereas 31% of 1,449 eggs deposited in Ruddy Duck nests were successful. The two percentages did not differ statistically ($P > 0.05$, $t_s = 1.77$).

Although success rates of Redhead and Ruddy Duck eggs deposited interspecifically were lower than the rates of eggs in Redhead or Ruddy Duck nests, success rates for parasitic eggs were higher than the 10–15% average reported for the Redhead by Weller (1959). As was also suggested by Weller (1959), the deposition of eggs into host nests already under incubation was a major cause of parasite egg loss, accounting for 37% of the 620 Redhead eggs and 15% of 146 Ruddy Duck eggs. This was not surprising, because intrusion by a parasitic female during host incubation apparently elicits minimal defense by the host in most nonterritorial anatids (Weller 1959, Kear 1970; but see Grenquist 1963, Sugden 1978). Some species [e.g., Common Goldeneyes (*Bucephala clangula*), Andersson and Eriksson 1982] may desert if parasitic eggs are deposited during host incubation.

In the Ruddy Duck, only 35 ducklings hatched from eggs deposited interspecifically, whereas 446 eggs hatched in 152 Ruddy Duck nests. Nesting Ruddy Ducks accounted for a maximum of 92% of all progeny produced. Unfortunately, there is no way of knowing how many of those 446 ducklings hatched from eggs deposited intraspecifically. The average nest success rate for Ruddy Ducks at Farmington Bay was low (34%) compared with the 60–70% average summarized by Bellrose (1976). In the Redhead, 130 young were produced from 620 parasitic eggs, whereas 170 ducklings hatched from the 500 eggs in 51 Redhead nests. Thus, 43% of the young Redheads produced during 1973–1974 came from eggs deposited interspecifically. Similarly, Sugden and Butler (1980) found that 40–50% of the total Redhead production on their study area in Saskatchewan came from Canvasback (*Aythya valisineria*) nests.

Two related points of interest can be addressed using data from Joyner (1975). First, did host-nest success decrease as the number of foreign eggs deposited per nest increased? Second, were certain host species more appropriate than others in terms of parasite-egg success rates?

Although parasitism *per se* (i.e. irrespective of numbers of foreign eggs deposited) did not increase rates of nest abandonment or predation (Joyner 1976), host-nest success may have varied inversely with numbers of parasite eggs deposited per nest. This would have adversely influenced only those parasite eggs deposited prior to host incubation because eggs deposited after initiation of incubation would not have had sufficient time to develop. Eleven Mallard nests averaged 5.7 Ruddy Duck and Redhead eggs per nest, whereas 24 Pintail and 237 Cinnamon Teal nests averaged 3.0 and 3.1 parasite eggs per nest, respectively. Ruddy Ducks parasitized 10 Redhead nests at an average of 1.7 eggs per nest, whereas 6 Ruddy Duck nests contained 10 Redhead eggs (Joyner 1976).

Ideally, parasitism should have little or no impact on host-nest success regardless of the

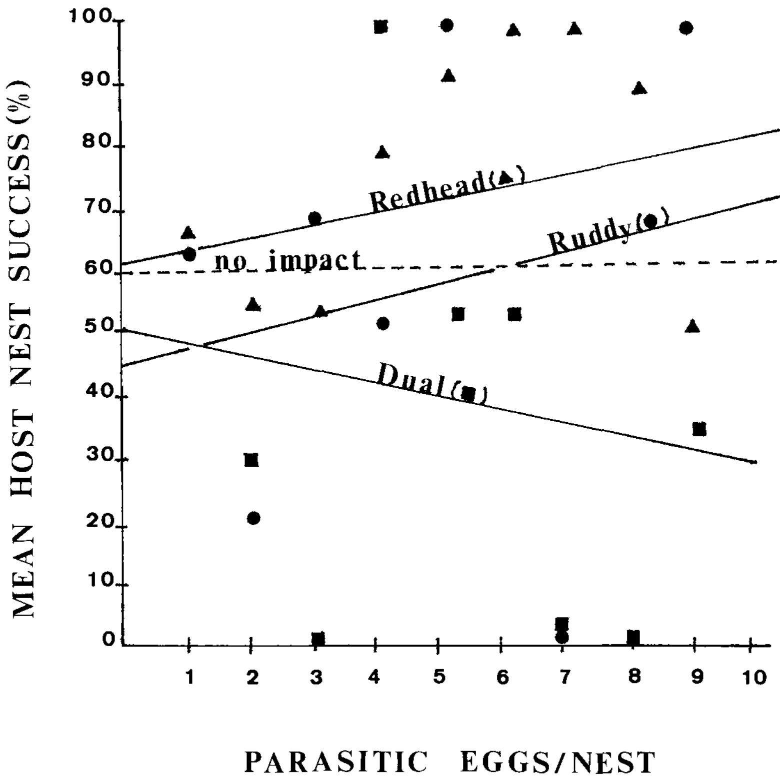

Fig. 1. Mean nest success (%) for 176 Cinnamon Teal, Mallard, and Pintail nests as a function of number of parasite eggs deposited per nest by Ruddy Ducks or Redheads or in nests dually parasitized. Nests were considered successful if one or more eggs hatched. For Redheads, $\hat{Y} = 61.0 + 2.0X$, $P > 0.05$, $r^2 = 0.09$, $n = 129$ clutches. For Ruddy Ducks, $\hat{Y} = 45.0 + 3.0X$, $P > 0.05$, $r^2 = 0.04$, $n = 21$ clutches. Dual parasitism, $\hat{Y} = 51.0 - 3.0X$, $P > 0.05$, $r^2 = 0.05$, $n = 26$ clutches. Mean nest success rate for 279 Cinnamon Teal, Mallard, and Pintail clutches not parasitized by Redheads or Ruddy Ducks was 60%.

number of eggs deposited. Undoubtedly, there is a threshold beyond which nest desertion will certainly result, but the number of foreign eggs required to induce such a response may vary by individual or host species. On the other extreme, deposition of one foreign egg may be sufficient to force abandonment. Most probably, the response typical of most anatids is somewhere in between the two extremes.

To determine the impact of increased rates of egg deposition on host-nest success, and thus parasite egg success, I regressed success rates for 176 Cinnamon Teal, Mallard, and Pintail clutches parasitized by Redheads and Ruddy Ducks during 1973–1974 on numbers of eggs deposited per nest by Ruddy Ducks and by Redheads and in nests that had been dually parasitized (Fig. 1). Regression coefficients did not differ ($P > 0.05$) from zero; hence, increasing the number of foreign eggs from 1 to 9, regardless of the temporal sequence of deposition (early, mid, or late host egg laying or during host incubation), did not progressively decrease host-nest success rates. Two coefficients were positive, and only as a result of dual parasitism did host-nest success decrease.

In a previous paper (Joyner 1976) I reported that Ruddy Ducks and Redheads each had access to five potential host species and that each parasitic species expressed some degree of host bias, whether through actual preference or as a result of sharing habitats. Given a potential of five host species, might one have been more suitable than another? For example, were Ruddy Duck or Redhead eggs more likely to hatch in the nests of Mallards than in nests of Cinnamon Teal? Using data from Joyner (1975), I estimated the hypothetical average number of newly hatched female ducklings that would have been produced per obligate parasite had each parasite deposited all of its eggs during one nesting season (11 eggs for Redheads, 7 for Ruddy Ducks) into the nests of a single host species (Fig. 2). The average number of ducklings produced per year for obligate parasites would be a function of the number of eggs laid, host-specific nest success rates, and average success rates of parasitic eggs within the clutches of each host species. Although the host suitability depicted in Fig. 2 would also apply to eggs deposited by semiparasites, the average number of female ducklings produced per year by semiparasites might differ from that produced by obligate parasites, because ducklings would result both from parasitism and from the subsequent nesting of the semiparasites.

Ruddy Duck and Redhead eggs were most successful when deposited into the nests of Pintails (Fig. 2). Parasitism of Pintail nests was common, affecting 50% of the 48 nests found during 1972–1974. Although parasite eggs were generally less successful in the nests of Cinnamon Teal, the percentage of nests parasitized equalled that observed in the Pintail (50% of 474 nests). Cinnamon Teal were the most abundant species present, and nests were readily available. Presumably, quantity outweighed quality. Ruddy Ducks deposited fewer eggs into the nests of Mallards and Pintails than did Redheads (30 vs. 106), but Ruddy Duck eggs were more successful. It was apparent (Fig. 2) that Ruddy Ducks would not be successful parasitizing Redheads (although 11% of 93 Redhead nests were parasitized by Ruddy Ducks) and that Ruddy Ducks were also not a suitable host species for Redheads.

Factors influencing rates of parasitism.—Hypotheses addressing the incidence of egg parasitism in waterfowl often stress the interrelationships between the chronology of nesting and the chronology, quantity, or quality of nesting cover (Kear 1970, Siegfried 1976, Clawson et al. 1979, Heusmann et al. 1980). Siegfried (1976), for example, noted that female Ruddy Ducks may be physiologically ready to lay soon after their arrival on the Delta, Manitoba nesting grounds but fail to do so until fresh, green plant material is available for constructing nests. Such hypotheses deviate little from that originally proposed by Friedmann (1932).

Contrary to Siegfried's observations for Ruddy Ducks in Manitoba, Ruddy Ducks in Utah

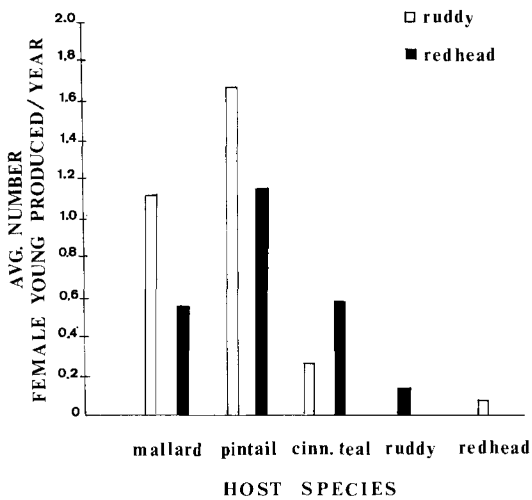

Fig. 2. Host suitability as reflected by the hypothetical average number of newly hatched female ducklings produced per obligate parasite per year. Averages were derived using the formula: mean number of female Redhead or Ruddy Duck ducklings = (mean clutch size of parasite/2)(mean host-specific nest success rate)(parasite egg success rate). Mean clutch sizes for Redheads and Ruddy Ducks were 11 and 7, respectively. Host-specific nest success rates for Mallards, Pintails, Cinnamon Teal, Ruddy Ducks, and Redheads were 0.67, 0.73, 0.55, 0.33, and 0.10, respectively. Success rates for eggs deposited into nests of the above listed species are 0.50, 0.67, 0.16, and 0.18 for Ruddy Ducks, and 0.15, 0.31, 0.20, and 0.10 for Redheads.

commonly used residual vegetation from the previous year's growth for nest-bowl construction; new growth served primarily for nest concealment and occasionally as a platform for dump nests (Joyner 1977). Consequently, egg laying was not restricted temporally to a nesting period defined by the presence of new, green vegetation.

Redheads also frequently used residual vegetation for nest-bowl construction, as was reported previously by Low (1945) and Weller (1959), although, as new growth became available, it too was incorporated into nest bowls. New growth of the type (*Typha, Scirpus, Distichlis*) used by nesting Ruddy Ducks and Redheads on Farmington Bay generally was not evident until mid-May and reached maximum height by mid- to late June.

Thus, whether or not a shortage of suitable nesting cover is a situation normally encountered by Ruddy Ducks and Redheads is questionable, at least on the Utah marshes. Because Ruddy Ducks apparently lay as soon as they are physiologically ready, Siegfried's explanation does not seem appropriate for Utah's Ruddy Duck population, nor would it apply to the Redhead. Weller (1959) also found no evidence that a shortage of nesting cover influenced the degree of egg parasitism by Redheads. Factors promoting parasitic behavior may differ in other areas, however (Titman and Lowther 1975, Siegfried 1976).

It is conceivable, however, that in tree-hole nesting species such as the Wood Duck (*Aix sponsa*), and perhaps Common Goldeneyes and Buffleheads (*B. albeola*), competition among females for suitable nest sites could trigger parasitic egg laying or dump nesting (Robinson 1958, Clawson et al. 1979, Heusmann et al. 1980, Andersson and Eriksson 1982). Similar parasitic responses have been reported in burrow-nesting shelducks [*Tadorna tadorna* (Hori 1969), *T. variegata* (Williams 1979)].

Low (1945) and Cooke and Mirsky (1972) suggested that environmental catastrophes (e.g. severe water fluctuations) might increase the incidence of parasitism in waterfowl. Presumably, females having lost their nest before completion of egg laying deposit one or more eggs into the nests of conspecifics or other species. During 1972–1974, ducks nesting on various tracts of marsh at Farmington Bay were subjected to environmental perturbations of varying severity. This provided an opportunity to determine whether or not rapidly fluctuating water levels and loss of nesting habitat during the egg-laying period of Redheads and Ruddy Ducks increased rates of parasitism.

The North and Central Turpin marshes were adjacent, separated only by a 2-m-high, 4-m-wide, earth-and-gravel dike, whereas the Crystal Marsh was located 4 km to the south. Portions of the 81-ha North Turpin Marsh were inundated repeatedly with saltwater from March through June 1973, resulting in drastic fluctuations in water levels, the loss of 57 ha of nesting habitat, and the destruction of numerous duck nests (Joyner 1977). Flooding reoccurred from March through June 1974, and less than 0.5 ha of marsh remained unaffected by saltwater inundation by July. Both the Central Turpin and the Crystal marshes were unaffected by saltwater inundation; each, however, became partially dry during May or June of 1973 and 1974. The flow of freshwater into each marsh was reduced substantially during mid- to late June 1973 and mid-May 1974 in the Central Turpin Marsh and in late June 1973 and 1974 in the Crystal Marsh. Approximately 50–70% of each marsh dried up in less than 1 week, affecting nesting habitat used by Ruddy Ducks, Redheads, Mallards, Pintails, and Cinnamon Teal. Although the impact appeared to be minimal on most species, Ruddy Duck nest abandonment on the Central Turpin Marsh was substantial during both years (Joyner 1975).

If environmental catastrophes during egg laying (May) increase the incidence of egg parasitism, then rates of parasitism by Redheads and Ruddy Ducks on the North and Central Turpin marshes should have increased noticeably, whereas rates on the more distant Crystal Marsh should have remained unaffected, at least for Ruddy Ducks. It would be difficult to predict the response of Redheads because of their greater mobility during the nesting season.

On the North Turpin Marsh the number of nests parasitized interspecifically by Ruddy Ducks decreased 60% from 1972 to 1973 (Table 1), although the percentage of nests parasitized remained constant (6–7%). No nests were parasitized by Ruddy Ducks in 1974. Redhead interspecific parasitism, which had been moderate in 1972, was evident in neither 1973 nor 1974. Thus, 24% (25 nests, some parasitized by both species) of the available host nests on the North Turpin Marsh were parasitized in 1972, with a total of 50 Redhead and Ruddy Duck eggs; 5% were parasitized in 1973 (3 eggs in 2 nests), and none in 1974. Approximately 30–50 adult female Ruddy Ducks used the North Turpin Marsh during each of 1972 and 1973, and only 8 pairs were sighted in 1974. Because of the greater mobility of Redheads during the nesting season, no estimate could be made of the number of Redheads using this or other tracts of marsh. Dietz (Refuge manager pers. comm.), however, reported that Redhead pair counts for the refuge as a whole averaged 413 pairs in 1972, 392 in 1973, and 232 for 1974.

A 26% reduction in potential host nests occurred from 1973 to 1974 on the Central Turpin Marsh. This decrease was attributed to a general decline in population size for all duck species involved (Dietz pers. comm.). The Central Turpin Marsh supported a relatively large number of Ruddy Ducks each year, with counts of 100–120 pairs in May and June. Interspecific parasitism by both species affected 50 nests

TABLE 1. Interspecific nest parasitism by Ruddy Ducks and Redheads on three tracts of marsh at Farmington Bay Waterfowl Management Area, Utah.[a]

		North Turpin		Central Turpin		Crystal	
Parasite	Year	Total nests	Parasitized nests	Total nests	Parasitized nests	Total nests	Parasitized nests
Ruddy Duck	1972	103	5 (6)[b]				
	1973	43	2 (7)	127	3 (3)	124	1 (1)
	1974	3	0	94	4 (5)	95	5 (6)
	Total	149	7 (6)	221	7 (4)	219	6 (3)
Redhead	1972	103	20 (22)				
	1973	43	0	127	47 (44)	124	55 (47)
	1974	3	0	94	19 (24)	95	39 (47)
	Total	149	20 (15)	221	66 (35)	219	94 (47)

[a] Overall rates of parasitism for Farmington Bay reported in Joyner (1976).
[b] Percentage of nests parasitized interspecifically. Percentage based on total nests available minus number of Ruddy Duck nests when referring to Ruddy Duck parasitism, and total nests minus number of Redhead nests when referring to Redhead parasitism.

(39%) in 1973, and 23 (24%) in 1974, a 38% reduction. Ruddy Ducks deposited 6 eggs into 3 host nests in 1973, and 4 eggs into 4 nests in 1974. Redheads parasitized 47 nests in 1973 and 19 in 1974, which represents a 45% reduction in percentage of nests parasitized. In 1974 65% (54 eggs) fewer Redhead eggs were deposited parasitically than in 1973 (153 eggs), and the average number of Redhead eggs per parasitized nest decreased between years (1973 = 3.3, 1974 = 2.8), as did the number of parasitic eggs per potential host nest (1.4 vs. 0.7).

The Crystal Marsh, which presumably was least affected by water fluctuations during the egg-laying period, also showed a 23% decrease in total nests from 1973 to 1974. Approximately 20 pairs of Ruddy Ducks and an unknown number of Redheads used this marsh each year. The percentage of nests parasitized by both species varied little (1%) between years, with 56 (45%) nests parasitized in 1973 and 44 (46%) in 1974. Again, Ruddy Duck parasitism was minimal each year, involving 1 nest in 1973 and 5 nests in 1974. Although rates of Redhead parasitism remained constant at 47% of available nests, the number of Redhead eggs deposited interspecifically dropped 33%, from 183 to 122. This, too, was attributed to a decline in numbers of Redheads present, because the mean number of Redhead eggs per parasitized nest (3.3 to 3.1) and per available host nest (1.6 to 1.5) varied little between years.

Intraspecific parasitism, which may be of importance in the evolution of parasitic nesting in these two species (Yom-Tov 1980), was difficult to verify. Because interspecific parasitism was most prevalent during late egg laying or incubation of the host and presumably had minimal impact on host clutch size (Weller 1959, Andersson and Eriksson 1982), a comparison between years of mean clutch size for Ruddy Ducks and Redheads might indicate whether or not intraspecific parasitism was more prevalent on marshes subjected to environmental perturbations. If an average clutch of 7 eggs for Ruddy Ducks (Siegfried 1976, Gray 1980) and a maximum potential clutch size of 10 (Siegfried 1976) is assumed, then the 38% of 158 Ruddy Duck clutches that exceeded 10 eggs were probably parasitized. This represented 15% of 1,449 eggs found in Ruddy Duck nests. Similarly, if a mean clutch of 11 (Bellrose 1976, Alliston 1979) and a maximum of 13 is assumed, 17% of 51 Redhead nests found during 1973–1974 may have been parasitized intraspecifically, representing 6% of 500 eggs. These values obviously represented minimal rates of parasitism, as nests with smaller total clutches presumably were equally likely to have been parasitized.

Mean clutch size for Ruddy Ducks on the North Turpin Marsh in 1972 was 9.5, compared to 8.3 in 1973. On the Central Turpin Marsh, Ruddy Duck clutches averaged 11.1 eggs in 1973 and 10.0 in 1974, while on the Crystal Marsh clutches averaged 10.4 eggs in 1973 and 6.8 in 1974. Redhead clutches on the Central Turpin Marsh in 1973 averaged 10.3 eggs, whereas in 1974 clutches averaged 10.9 eggs. Mean clutch size for Redheads on the Crystal Marsh was 11.0 in 1973 and 8.4 in 1974.

The above data suggest that severe water fluctuations and habitat loss during egg laying did not increase the incidence of egg parasitism in Redheads or Ruddy Ducks. This is in agreement with Weller (1959). Nor was egg parasitism particularily evident in the other species present. In the two marshes where water fluctuations and habitat loss were most severe and occurred during the early to mid-egg-laying period of Ruddy Ducks and Redheads, the percentage of nests parasitized decreased rather than increased. In the Crystal Marsh where conditions remained stable until late June, rates of parasitism were similar between years and reflected only relative changes in population densities between years. Apparently, few Redheads or Ruddy Ducks moved onto the Crystal Marsh to nest as neighboring marshes became less suitable; either they frequented other nearby marshes not included in this study or they did not lay.

In conclusion, I found no evidence to support previous contentions (Low 1940, Siegfried 1976) that rates of parasitism in Redheads and Ruddy Ducks were subject to modification by the physical environment. Although Redhead parasitism was common, eggs deposited interspecifically were less successful than Redhead eggs in Redhead nests. Ruddy Duck interspecific parasitism was neglibible, but intraspecific parasitism may have been extensive.

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