

## The functional significance of parasitic egg laying and typical nesting in redhead ducks: an analysis of individual behaviour

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**Abstract.** At the population level, redhead ducks, *Aythya americana*, lay as many as 75% of their eggs parasitically but at least some females lay and incubate eggs in their own nests ('typical nesting'). Parasitic egg laying by redheads was documented with remote, time-lapse photography of potential host nests, allowing histories of parasitic egg laying and typical nesting to be compiled for individual females. In 1986 and 1987, years of favourable environmental conditions, many adult ( $\geq 2$  years old) females laid parasitic eggs prior to initiating their own nests in the same season. This dual strategy of individuals was reflected at the population level: the seasonal peak of parasitic egg laying preceded that of typical nesting and per caput rates of both parasitic egg laying and nesting were high. In contrast, redhead females either laid parasitic eggs or nested but did not do both during a drought in 1988. It is suggested that all redhead females employ a flexible, conditional reproductive strategy with four options of increasing reproductive effort: (1) non-breeding, (2) parasitic egg laying, (3) typical nesting, and (4) a dual strategy of parasitic egg laying prior to nesting. When environmental conditions are favourable, a dual strategy enables redheads to increase their fecundity above the normal limits to clutch size. When prospects for successful nesting are poor, females reduce reproductive effort and employ parasitic egg laying as a low-cost alternative to nesting. Age-related differences in reproductive tactics were consistent with this model.

Avian brood parasites are well known for the remarkable adaptations that enable them to obtain parental care from individuals of other species (e.g. Friedmann 1955; Wylie 1981). Although freedom from parental care should allow a dramatic increase in fecundity (e.g. Scott & Ankney 1980), relatively few species employ this seemingly ideal reproductive strategy. Recently, however, there has been growing evidence that parasitic egg laying by species that typically care for their own eggs and young is a widespread phenomenon among birds (MacWhirter 1989; Rohwer & Freeman 1989). Although it is more difficult to detect than obligate parasitism because host and parasite are often conspecific, facultative parasitism is continually being documented in additional species (e.g. Gratson 1989; Petter et al. 1990). Several recent reviews have proposed hypotheses for the functional significance of facultative parasitic egg laying (Yom-Tov

1980; Andersson 1984; Eadie et al. 1988; Sayler, in press), but only a few researchers have collected enough information about the context in which individuals lay parasitic eggs to test these hypotheses (Brown 1984; Emlen & Wrege 1986; Gibbons 1986; Møller 1987; Eadie, in press, see also Lank et al. 1989).

Parasitic egg laying has been documented more often and is probably more common in waterfowl (Anatidae) than any other group of birds (Weller 1959; Rohwer & Freeman 1989). Among all birds, the redhead duck, *Aythya americana*, may exhibit the highest rates of facultative parasitic egg laying: at the population level, up to 50% of redhead ducklings may hatch from parasitically laid eggs (e.g. Olson 1964; Sugden & Butler 1980). Redheads also parasitize other species more frequently than other facultative parasites. In one 12-year study, redheads parasitized 57% of canvasback, *Aythya valisineria*, nests, laying an average of 3.1 eggs in each (Stoudt 1982). Most importantly, however, in all populations studied, at least some redhead females lay and incubate eggs in nests of their own

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and raise their own broods in typical waterfowl fashion ('typical nesting').

As a North American game bird, the nesting biology of the redhead has been studied extensively (Low 1945; Wingfield 1951; Weller 1959; Olson 1964; Lokemoen 1966; Michot 1976; Johnson 1978; Alliston 1979a; Jobes 1980; Sugden 1980; Giroux 1981; Talent et al. 1981; Bouffard 1983; Joyner 1983; Saylor 1985). Research on parasitic egg laying in redheads has focused primarily on the population level rate of parasitism and its effects on hosts. No previous study has systematically documented the reproductive tactics of individual females, in part, because of the difficulty of collecting these data but also because objectives in previous studies have not required it. In this paper, I describe parasitic and typical nesting behaviour of individual redhead females and use these data to address several hypotheses for the functional significance of parasitic egg laying.

## HYPOTHESES AND PREDICTIONS

Previously suggested hypotheses for parasitic egg laying in waterfowl can be organized into two broad categories: (1) those that suggest parasitic egg laying allows fecundity to be increased above the possible through typical nesting alone; and (2) those that suggest parasitic egg laying is a 'best-of-a-bad-job' strategy either forced by or employed in response to unfavourable conditions. Additional hypotheses that explain parasitic egg laying in waterfowl in terms of reproductive error, host advantage, kin selection and the variance reduction effect of egg dispersion are evaluated and rejected in Sorenson (1990).

### The Fecundity Hypotheses

#### *The annual fecundity hypothesis*

Parasitic egg laying enables redheads to increase their annual fecundity. Females obtain care for more than one clutch per season either by (1) laying a large number of parasitic eggs instead of nesting or (2) laying additional eggs parasitically prior to nesting.

#### *The survival (lifetime fecundity) hypothesis*

Avoidance of the predation risks and energetic demands of incubation and brood care results in

higher survival for females laying only parasitic eggs and, as a consequence, higher lifetime fecundity. (It is also possible that both survival and annual fecundity could be higher for females that only lay parasitic eggs.)

### The Best-of-a-bad-job Hypotheses

#### *The constraint hypothesis*

Parasitic egg laying is a relatively unproductive strategy employed by females when environmental or phenotypic factors limit their ability to nest in the typical manner. (1) When a nesting attempt is terminated by predation or flooding, especially during the laying stage, females salvage some reproductive success by continuing to lay in the nests of other birds. (2) Females in poor physiological condition and/or that face reduced food resources are unable to meet the energetic and nutrient demands of nesting but achieve limited success by laying parasitic eggs instead of not breeding at all.

#### *The restraint hypothesis*

Parasitic egg laying is a low cost alternative to typical nesting that enables females to reduce their reproductive effort in response to poor prospects for successful reproduction. When environmental conditions are unfavourable, females 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. Although, the primary advantage of parasitic egg laying (i.e. increased adult survival) is the same as that posited for the survival hypothesis, the restraint hypothesis suggests that the trade-off between reproductive effort and survival favours parasitic egg laying only when unfavourable conditions reduce the probability of successful nesting or increase its costs. In contrast, the survival hypothesis suggests that parasitic egg laying is the better strategy even when conditions for nesting are favourable.

Predictions based on each of the above hypotheses are summarized in Table I. Although part (2) of the constraint hypothesis and the restraint hypothesis will be very difficult to distinguish in practice (see Discussion), the other hypotheses yield distinct predictions about the patterns of

**Table 1.** Predictions following from hypotheses for the functional significance of parasitic egg laying in redheads

Hypothesis	Reproductive tactics of individual females	Reproductive success (RS) of parasitic females	Relationship of environmental factors to individual behaviour
<b>Annual fecundity</b>			
(1) Parasitism instead of nesting	Individual females lay a large number of parasitic eggs (i.e. greater than or equal to clutch size of nesting females)	Annual RS greater than or equal to that of nesting females	Per caput rate of parasitism high when environmental conditions are favourable and host availability is high
(2) Parasitism in addition to nesting	Females lay parasitic eggs prior to nesting. Seasonal peak of parasitism precedes peak of typical nesting	Annual RS greater than or equal to that of females which only nest	Rates of both parasitism and typical nesting high when environmental conditions are favourable and host availability is high
<b>Survival</b>			
Parasitism instead of nesting (lifetime)	Individual females lay only parasitic eggs. Parasitic females have higher annual survival	Lifetime RS greater than or equal to that of nesting females. Annual RS may be lower	Rate of parasitism high when host availability is high and environmental conditions are favourable
<b>Constraint*</b>			
(1) Parasitism after nest loss	Females lay parasitic eggs after their own nest is destroyed. Peak of parasitic egg laying follows peak of nesting	RS lower than that of nesting females	Rate of parasitism high when rate of nest destruction is high
(2) Parasitism instead of non-breeding	Females either lay parasitic eggs or nest but do not do both. Parasitic females younger and/or in poor condition	RS lower than that of nesting females	Rates of parasitism and nesting are negatively correlated between years. Rate of parasitism low when environmental conditions are favourable
<b>Restraint</b>			
Parasitism instead of nesting	Females either lay parasitic eggs or nest but do not do both	Annual RS lower than that of nesting females. Lifetime RS higher	Rates of parasitism and nesting are negatively correlated between years. Rate of parasitism low when environmental conditions are favourable

These predictions assume that the maintenance of alternative reproductive tactics in redhead populations is condition-dependent. The possibility that parasitic egg laying and typical nesting are maintained as alternative strategies by frequency-dependent selection is considered elsewhere (Sorenson 1990).

\*Nest-site limitation is an additional constraint probably leading to parasitic egg laying in cavity-nesting waterfowl (e.g. Eadie, in press) but is unlikely to be an important factor in the biology of redheads.

parasitic and typical nesting behaviour in individuals. A description of the reproductive tactics of individual females thus provides a strong test of

these hypotheses. Therefore, my primary aim in this study was to document 'the entire egg-laying sequence of individually marked females of known

age ... preferably for a number of years' (Andersson 1984).

### STUDY AREA AND NATURAL HISTORY

I conducted field work in southwestern Manitoba, Canada, from April to August each year from 1986 to 1988. The study area, about 3 km southwest of Minnedosa, Manitoba, lies within the prairie pothole region, which extends across the Canadian prairie provinces and includes the majority of both the redhead and canvasback breeding populations (Bellrose 1980; Batt et al. 1989). The particularly high density and diversity of small wetlands just south of Minnedosa makes the area ideal for breeding ducks. Depending on annual water conditions, the number of wetlands in this area may be as high as 33 per km<sup>2</sup> although 72% are less than 0.4 ha in size (Stoudt 1982). The Minnedosa area is described in more detail by Kiel et al. (1972) and Stoudt (1982).

Redheads and canvasbacks arrive in the Minnedosa area in mid-April already in pairs that will have formed during the late winter and spring migration (Weller 1965, 1967). Canvasbacks begin nesting in late April or early May and redheads begin breeding shortly thereafter. Females of both species build nests over water in the residual emergent vegetation (primarily cattail, *Typha* spp., bullrush, *Scirpus* spp., and whitetop grass, *Scholochloa festuacea*), which encircles most wetlands but may completely cover smaller, shallow wetlands. On average, half of all nests are destroyed by predators, primarily raccoons, *Procyon lotor* (Stoudt 1982). Nesting redhead and canvasback females typically lay 7–10 eggs in as many days. Eggs hatch after about 25 days of incubation and, within 48 h, the female and brood leave the nest permanently. Although ducklings feed themselves, females lead and protect their broods for up to 60 days after hatch.

Canvasbacks are about three times as numerous as redheads at Minnedosa and are the most frequent host of redhead parasitism in this area. Parasitic redhead eggs are accepted by both canvasback and redhead hosts and the resulting ducklings are cared for along with the host female's own brood. There is no evidence of discrimination against or recognition of parasitic eggs or ducklings by canvasback or redhead hosts (see Mattson 1973).

### METHODS

#### Trapping and Marking

I trapped redheads and canvasbacks from late April to early June in decoy traps using captive females of both species as bait (Anderson et al. 1980). Birds were weighed and the abdomen of females was palpated to determine whether an egg was present in the oviduct (Weller 1959; Fleischer et al. 1987). Based on plumage characteristics (Dane & Johnson 1975; Serie et al. 1982), I separated females into two age categories: yearlings (ca 1 year old, returning north for the first time) and adults (2 or more years old). All females were fitted with coloured nasal markers for individual identification (Doty & Greenwood 1974; Lokemoen & Sharp 1985). Redhead females were given the same symbol/colour combination on each side of the bill, facilitating identification of birds recorded on film (see below). Females were also nest-trapped late in the incubation stage using a modified drop-door trap (Blums et al. 1983). These females were processed as above and immediately released on to their nesting pond.

I colour-marked 44 adult and 25 yearling redhead females during the study. Five additional females trapped in 1984 and 1985 on an adjacent study area frequented my study area in following years. Several decoy-trapped females were never sighted after being marked and were probably present only transiently. I considered females to be 'resident' on the study area only if they were sighted at least three times after being marked or were known to nest or lay parasitic eggs on or near the study area: 43 adult and 17 yearling females met these criteria.

Eight additional redheads were fitted with neck collar radios in 1986 in an attempt to follow females and observe parasitic behaviour directly. Because most radio-equipped females showed no evidence of breeding (Sorenson 1989), they are excluded from analyses in this paper unless otherwise noted.

#### Nest Searching

All wetlands on a 10.4-km<sup>2</sup> main study area were searched every 8–10 days during May and June to find nests early in the laying stage and before most parasitic eggs had been laid. Additional records of nesting for individual females were obtained during a single search in mid-June in 1987 and 1988 of a 6.3-km<sup>2</sup> area surrounding the main study area

(several nests were found in this peripheral area in 1986 also but the entire 6.3 km<sup>2</sup> was not searched).

### Time-lapse Photography

Parasitic egg laying by marked redhead females was documented by simultaneously monitoring as many as 25 potential host nests with time-lapse photography. I used Super-8 movie cameras equipped with interval timers set to expose one frame per minute. Cameras were attached to the top of a 5 × 5 cm stake, 2 m in length, driven into the wetland substrate about 3 m from the nest and were protected from dust and rain with a case built of flexible, 1.6-mm thick polyethylene and duct tape. Vegetation on one side of the nest was removed to improve the view for the camera while minimizing damage to the nest site. Time-lapse photography was conducted only on the main study area.

Most nests were filmed during the second half of the laying stage and the first week of incubation. Filming was extended at several redhead nests to record nest attentiveness during incubation and at nests where parasitic eggs continued to be laid. I set up cameras and changed film (every other day) in the afternoon and evening to minimize disturbance of laying females. None the less, host females often were present late in the laying stage and were almost always present during incubation. Host females returned to their nests by dawn of the day after the camera was first set up but almost always returned in less than 30 min after subsequent film changes. Only four females (three canvasbacks and one redhead) appeared to have abandoned their nests in direct response to the camera being set up.

Films were viewed one frame at a time to find cases of redhead females intruding at host nests. Each 'film event', any sequence of frames with a female redhead other than the host female on the nest, was assigned to one of two categories. (1) 'Nest visits' accounted for 48% of film events (204/422) and were intrusions of short duration (79% were less than 5 min or about five frames) in which the intruding female probably did not lay an egg. During nest visits, the intruding female made little or no attempt to displace the host female from the nest and often just stood on the edge of the nest or sat on top of the host female. Intrusions of longer duration were also classified as nest visits if the intruding female changed body orientation between every frame and/or was standing in most frames. (2) 'Egg-laying events' were intrusions of longer duration (98% were greater than 5 min) in

which the intruding female appeared to have laid an egg. In egg-laying events, the intruding female usually pushed against and/or tunnelled under the host female often completely displacing her from the nest. Egg-laying events were also characterized by the intruding female remaining in one position for at least two frames but more commonly four to eight frames, apparently while she was actually laying the egg (see McKinney 1954). The time and duration of all film events were calculated from the number of frames exposed and the start and finish time of each film.

Parasitic eggs were rarely visible on film because of the depth of the nest bowl, but the number of egg-laying events on film usually matched the number of new parasitic eggs found in the nest when film was changed. There were two situations in which this was not true. (1) Egg added to nest: no film event. Five per cent (9/188) of parasitic eggs appearing in nests with functioning cameras were not matched by an egg-laying event on film. These eggs may have been laid during the night: the distribution of egg-laying times suggests that about 5% of parasitic eggs were laid shortly before dawn (unpublished data). (2) Egg-laying event on film: no egg added. Eighteen per cent (39/218) of what appeared to be egg-laying events on film were not matched by a new parasitic egg in the nest. At least 25% of all parasitic eggs were displaced from nests into the water (unpublished data) and in 19 of the above cases, an egg that could have been laid during the egg-laying event on film was subsequently found beneath the nest. In three cases, eggs were probably taken by predators between the time they were laid and when the nest was next checked. In the remaining 17 cases, the parasitic eggs may have been displaced from the nest and never found: 27% (52/194) of already-numbered eggs that were displaced from nests were not found subsequently. Alternatively, a missing 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. In nine of 25 cases in which I noted that an egg was cracked at an active nest, the egg in question and only that egg was subsequently missing: none of these was ever found in the water under the nest. Given these possible sources of disappearance, I assume that a parasitic egg was laid in all film events in which the behaviour of the intruding female indicated egg laying.

During the 3 years of the study, I filmed 1499 nest-days at 171 canvasback and 33 redhead nests.

These films included 218 egg-laying events representing 39% of all parasitic redhead eggs laid on the main study area. Unfortunately, the intruding female in 59% of egg-laying events was either unmarked or could not be identified on film. Only 7% of all parasitic redhead eggs laid on the main study area could be attributed to individual females in 1986 but this was improved to 23% in 1987 and 28% in 1988. Intruding redhead females were also recorded in 204 nest visits: 53% of the females involved were identified.

### Indirect Evidence of Reproductive Tactics

Females that were recorded in nest-visits and/or that had an oviductal egg when decoy-trapped were considered likely to have laid parasitic eggs even if they were not recorded in an egg-laying event on film. The justification for these inferences is as follows. (1) There was a strong temporal association between nest visits and parasitic egg-laying events for individual females that were recorded in both, suggesting that nest visits function in parasitic behaviour (unpublished data). (2) Redheads probably locate potential host nests by observing and following canvasback and other redhead females (Weller 1959). Females that had oviductal eggs when trapped may have been attracted to the decoy because they were trying to locate host nests. Consistent with this, female redheads were more likely to be in laying condition when decoy-trapped than were canvasbacks ( $G_{adj} = 4.81$ ,  $P < 0.05$ ), in which parasitic egg laying is much less frequent (Sorenson 1990). In addition, no canvasback or redhead female was ever decoy-trapped during the laying stage of her own nest and one canvasback female that was trapped with an oviductal egg was known to lay that egg parasitically. In general, the females to which these indirect kinds of evidence apply were sighted only infrequently on the main study area and may have laid parasitic eggs in peripheral areas where nests were not filmed.

A few marked females that (1) were sighted regularly with a mate in April and May, (2) 'disappeared' for 2–4 weeks in late May and June and then (3) were sighted several more times without a mate were considered likely to have attempted a nest of their own. These females probably had their nests destroyed before they were found and/or nested just off the main study area. The same pattern of sightings was consistently observed in females known to be incubating a nest.

### Nest and Egg Data

During each nest visit, 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 1 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 redhead and canvasback eggs by M. G. Anderson & B. D. Sullivan, unpublished data).

I used several criteria to identify parasitic eggs in redhead nests. Egg addition rates higher than 1 per day during the host's laying stage, eggs laid during the host's incubation stage, and egg-laying events on film were considered unequivocal evidence of parasitism. Obvious differences in the colour and size of eggs and large clutch size were taken as indications of possible parasitic eggs. Redhead eggs laid in canvasback nests could be classified unambiguously as parasitic (redhead eggs are readily distinguished from those of canvasbacks by their glossy, ivory coloured shell, Bellrose 1980).

After removal of the camera, I visited nests at about 1-week intervals to document nest and egg fate. During a final nest check, conducted 2–3 days after the projected hatch date for each nest, the bottom of the wetland within 1 m of the nest was searched thoroughly for eggs. Numbers on eggs were usually legible even after as many as 25 days in the water. If not, eggs also 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. I derived minimum and maximum estimates of the number of parasitic and host eggs that hatched in each nest 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 the nest, and the number of ducklings in the initial sightings of the brood. Minimum and maximum estimates differed because remains of hatched eggs may be eaten or carried away by females (Weller 1959), while unhatched eggs may be removed by predators before the final nest check (unpublished data). Uncertainty about the number and identity of parasitic eggs in redhead nests also contributed to differences in minimum and maximum estimates.

Because all potential nesting habitat was searched repeatedly and because canvasback and redhead nests are fairly conspicuous, I am confident that almost every nest on the main study area was eventually found. I therefore calculated nest success directly rather than using a method based on days of exposure (e.g. Mayfield 1961; Miller & Johnson 1978). A few females deserted their nests after nest-trapping during the last week of incubation (5/24 nest-trapped redheads and 4/85 canvasbacks). All of these nests remained intact past the projected hatch date and almost certainly would have hatched without my interference. In calculating nest and egg success, these nests were classified as successful and eggs remaining in these nests at the time of trapping were scored as hatched (except for parasitic eggs laid during the host's incubation stage).

### Censuses

Annual variation in rates of parasitic egg laying per host nest or per area may result from changes in host or parasitic population size independent of changes in behaviour. To estimate per caput rates of parasitic egg laying and typical nesting and provide a better indication of annual variation in reproductive tactics, two methods were used to obtain an estimate and an index, respectively, of the density of redhead females on the main study area. (1) Pair counts. Two complete counts of all redheads on the main study area were conducted each year in mid- and late-May. Methods for these counts are described by Sugden & 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 1–4 days by two or three observers rather than during a single morning by eight observers. (2) Roadside counts. A count of all redheads within sight of the road along a 19.3-km route that covered the main study area as well as peripheral areas was conducted once per week in 1986 and three times per week in 1987 and 1988 during April, May and June.

### Statistical Analyses

Parametric statistical analyses were conducted on a Macintosh microcomputer using SYSTAT software (Wilkinson 1987). Nest attentiveness data were arcsine transformed. Categorical analyses used the *G*-test for goodness-of-fit and *G*-test for independence, applying William's correction for

small sample size (Sokal & Rohlf 1981). All analyses of population level data on parasitism and nesting include only nests on the 10.4-km<sup>2</sup> main study area unless otherwise noted.

## RESULTS

### Annual Variation in Environmental Conditions

Environmental conditions varied substantially over the 3 years of the study and clearly affected the reproductive tactics of individual females. Water levels were high in 1986 and 1987 and extensive areas of emergent vegetation were available for nesting. In 1988, wetlands contained less water at the beginning of the season and then rapidly dried out during June. Mean ( $\pm$ SE) water depth on 1 July for 20 semi-permanent and permanent wetlands was 70 ( $\pm$ 4) cm in 1986, 70 ( $\pm$ 6) cm in 1987, but only 47 ( $\pm$ 5) cm in 1988 (M. G. Anderson, unpublished data). Less extensively flooded emergent vegetation resulted in a higher rate of nest predation in 1988. Nesting success for canvasbacks and redheads combined was 47% ( $N=99$ ) in 1986, 52% ( $N=97$ ) in 1987 and 23% ( $N=88$ ) in 1988. The timing of breeding also varied among years. Unusually warm weather in April and early May of 1987 led to the earliest breeding season in the Minnedosa area in 25 years (Arnold & Sorenson 1988). In short, the 3 years of the study can be characterized as follows: 1986, good conditions for nesting, average timing of breeding; 1987, good conditions for nesting, very early breeding; 1988, poor conditions for nesting, slightly late breeding.

### Frequency of Parasitism

Parasitic egg laying by redheads was a prominent feature of the nesting biology of redheads and canvasbacks in all 3 years of the study (Table II). Canvasbacks were by far the most frequent hosts of redhead parasitism: approximately 84% of all parasitic redhead eggs ( $N=564$ ) were laid in canvasback nests, while the rest were laid in the nests of other redheads (13%), mallards, *Anas platyrhynchos*, or ring-necked ducks, *Aythya collaris*.

### Reproductive Tactics of Individual Females

#### Adult females

Known reproductive tactics of decoy-trapped and returning adult females (2 or more years old)

**Table II.** Frequency of parasitic egg laying by redheads per host nest

Year	Canvasback hosts		Redhead hosts	
	% Nests parasitized (N)	Parasitic eggs/nest (range)	% Nests parasitized (N)	Parasitic eggs/nest (range)
1986	82 (55)	4.6 (1–16)	55–70 (20)	3.4–3.5 (1–7)
1987	59 (66)	2.9 (1–11)	22–44 (9)	2.8–4.0 (1–5)
1988	55 (58)	3.5 (1–11)	50 (4)	2.5 (2–3)

Data from nests that survived through completion of the host's egg-laying stage. Values for redhead hosts are minimum and maximum estimates based on known parasitic eggs and known plus likely parasitic eggs, respectively.

**Table III.** Documented reproductive tactics of decoy-trapped and returning adult females (2 or more years old)\*

Year	Number of females	Number of females known to			
		Parasitize only	Nest only	Both parasitize and nest	Neither nest nor parasitize
1986	14	3 (2)	3	6 (3)	2
1987	23	6 (1)	9 (2)	8 (3)	0
1988	32	19 (5)	5 (1)	1	7

Values in parentheses indicate the number of females included in each category based on indirect evidence that they employed a given reproductive tactic (see Methods).

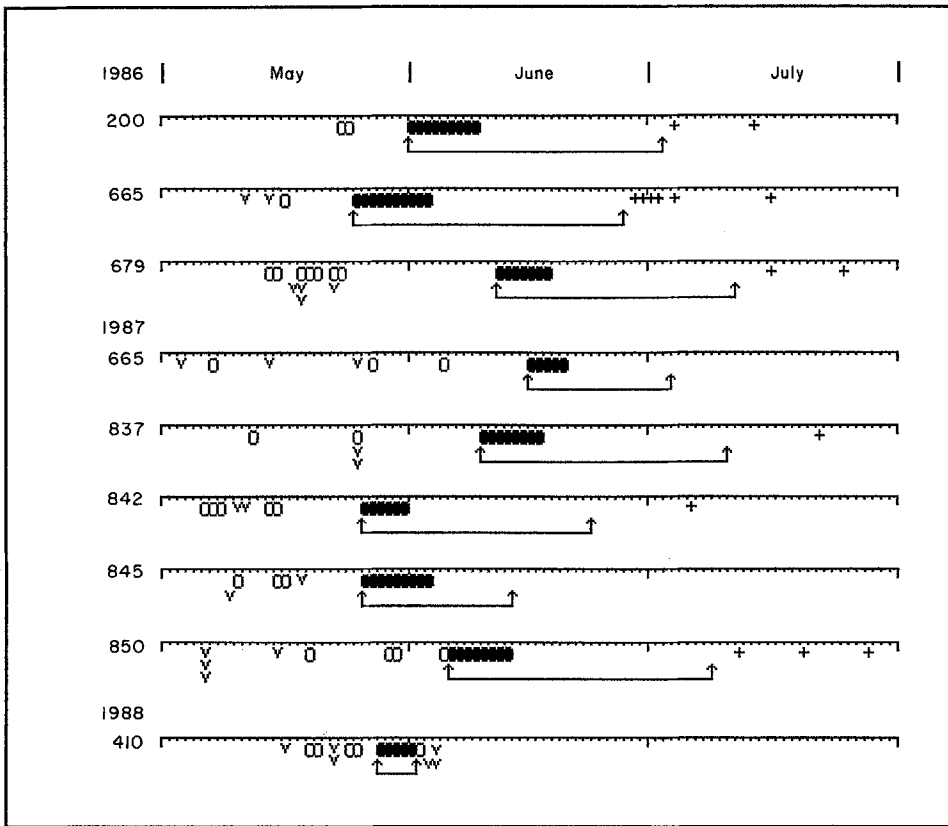
\*There was no opportunity to detect parasitic egg laying by nest-trapped females because they were not marked until late in the incubation stage of their own nest.

are summarized in Table III. Three females in 1986 and five in 1987 were known to lay parasitic eggs prior to initiating a nest of their own (Fig. 1). Although incomplete, egg-laying histories for these females share two common features: (1) in every case, parasitic eggs were laid prior to initiation of the female's own nest; and (2) there was usually an interval of 7–19 days between the last parasitic egg-laying event for a given female and the initiation of that female's own nest ( $\bar{X} \pm \text{SE} = 11.1 \pm 1.6$  days for seven of the eight females in 1986 and 1987; female 850 laid a parasitic egg the day before or perhaps the day after initiating her own nest in 1987 but this followed a 5-day interval during which egg laying was not recorded). These two features also hold for the six females included in the 'both parasitize

and nest' category (Table III) based on indirect evidence.

Twelve decoy-trapped and returning females in 1986 and 1987 were known only to nest in a given year and nine were known only to lay parasitic eggs (Table III). It should be emphasized, however, that lack of evidence of a given reproductive tactic for an individual female does not necessarily imply that the female did not employ that tactic, only that I did not document it. Undoubtedly, parasitic egg laying by many females was not documented because only a portion of parasitic egg laying on the main study area could be attributed to individual females and because 'resident' females laid parasitic eggs in nests both on and off the main study area. Although four females initiated nests before 15 May and may





**Figure 1.** Histories of parasitic egg laying and typical nesting for eight females (9 female-years) known to lay parasitic eggs prior to nesting. Dates of known parasitic eggs (○), nest visits (V), eggs laid by the female in her own nest (●), initiation and termination of each female's own nest (arrows) and sightings of the female with her brood (+) are indicated below each dateline.

not have had time to lay parasitic eggs prior to nesting, 24 of 28 adult females (including nest-trapped females) nesting in 1986 and 1987 did not initiate nests until late May or June and could have laid parasitic eggs earlier in the season. Similarly, any of the nine females known only to lay parasitic eggs in 1986 and 1987 could have also initiated a nest that either was destroyed before I found it or was situated off the study area and never found. Five redhead nests in 1986 and four in 1987 were already destroyed or abandoned when found and therefore could not be attributed to individual females.

In contrast to 1986 and 1987, only one of 32 decoy-trapped and returning adult females in 1988 was known to lay parasitic eggs prior to nesting (Table III). This female initiated her own nest 2 days after she was last recorded to lay a parasitic

egg (Fig. 1). The proportion of resident females known to nest in 1988 (6/32) was lower than in 1986 and 1987 ( $G_{adj} = 19.1$ ,  $df = 2$ ,  $P < 0.001$ , this test and the two following use totals from Table III in which indirect evidence was used to categorize some females, see Methods) and more resident females were known only to lay parasitic eggs in 1988 ( $G_{adj} = 8.71$ ,  $df = 2$ ,  $P < 0.025$ ). In addition, no evidence of breeding was obtained for a larger proportion of females in 1988 ( $G_{adj} = 7.67$ ,  $df = 2$ ,  $P < 0.025$ ) even though detection of parasitism and nesting was improved during the study.

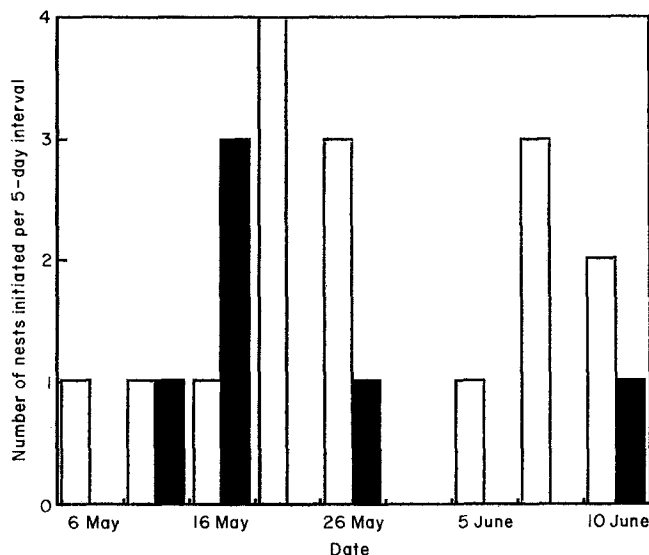
#### *Young females*

In 1987 and 1988 there were marked differences in the reproductive tactics of yearling and adult females (only one yearling was marked in 1986). In 1987, only two decoy-trapped yearlings were

**Table IV.** Age-related reproductive tactics of decoy-trapped and returning females in 1987 and 1988

Age	Number of females	Number of females known to			
		Parasitize only	Nest only	Both parasitize and nest	Neither nest nor parasitize
1987					
1 year	8	2	2 (1)	1 (1)	3
2+ years	7	2 (1)	4 (1)	1 (1)	0
3+ years	16	4	5 (1)	7 (2)	0
1988					
1 year	3	3 (1)	0	0	0
2 years	9	7 (3)	0	0	2
2+ years	3	3	0	0	0
3+ years	20	9 (2)	5 (1)	1	5

Values in parentheses indicate the number of females included in each category based on indirect evidence that they employed a given reproductive tactic (see Methods). 2+ includes unknown age adult females. 3+ includes returning adult females known to be at least 3 years old.

**Figure 2.** Nest initiation dates for yearling (■) and adult (□) redheads nesting on and off the main study area in 1987.

known to lay parasitic eggs, while two showed evidence only of nesting and one initiated a nest after making several nest visits (Table IV). Four additional yearlings were nest-trapped in 1987.

Interestingly, five of the six yearlings with known nest initiation dates in 1987 nested relatively early in the season (Fig. 2). The mean date of nest initiations for yearlings (24 May) was 6 days earlier than that of adults (30 May). Although these data are consistent with a null hypothesis of no difference

( $t = 1.012$ ,  $df = 20$ ,  $P > 0.2$ ), this result is contrary to the almost universal finding that young birds nest later than experienced adults (Rohwer, in press). For example, yearling canvasbacks nested 10.6 days later, on average, than older females ( $F_{1,137} = 21.7$ ,  $P < 0.001$ ). The relationship between age and nest initiation date in redheads differed from that in canvasbacks as indicated by a significant age by species interaction in a combined analysis for 1987 ( $F_{1,76} = 6.78$ ,  $P < 0.02$ ). Relatively early

Female	1986		1987		1988	
	P	N	P	N	P	N
133	X		X			
169		X	?			
174						
186	X	X	?		X	
200	X	X	X			
663			X			
665		X	X	X	X	
668			X			
674		?	X		X	
679		X	X			
686		X				
691					X	
696		?		X	X	
837		?		X	X	
839			X		X	
840			X			
841			X	X	?	
842			X	X	X	
843			X			
844			X	X		
845			X	X	X	?
846			X		?	X

Female	1986		1987		1988	
	P	N	P	N	P	N
847	X					
848	X		X			
849	X		?	?		X
850	X		X	X		X
851	X					
579			X			
586				?		X
592			?		?	
595			X		X	
597				X		
860				X		
886			?	X		
406			X			X
409				X	X	
410				X	X	X
428					X	
429					X	
434					X	
441						X
442						X
443						X

Females marked as yearlings	1987		1988	
	P	N	P	N
587	?	X		
681			?	
861		X		
868		?		
881	X		X	
883				
890	X		X	
892			X	
407		X	?	
408		X		
411		X	X	
412		X	?	
424			X	
435			?	
438			X	

**Figure 3.** Documented reproductive tactics of all 'resident' and returning redhead females. Females recorded in at least one parasitic egg-laying event in a given year are indicated by an 'X' under P. Females known to nest in a given year are indicated by an 'X' under N. Females with a '?' are those for which there is only indirect evidence that they employed a given reproductive tactic. Empty boxes indicate that the female was sighted on the study area but was not known to employ a given reproductive tactic. Missing boxes indicate that a female was not yet marked or that she did not return to the study area in a subsequent year. Boxes framed with dotted lines indicate four females in 1988 that were sighted for less than 7 days after they returned in the spring.

nest initiation dates suggest that yearling redheads did not lay parasitic eggs prior to nesting in 1987.

In contrast to 1987, very few young females nested in 1988. None of three decoy-trapped yearlings and none of nine returning 2-year-old females were known to initiate a typical nest (the one yearling known to nest in 1988 was nest-trapped very late in the season). Also in contrast to 1987, however, almost all yearling and 2-year-old females were recorded on film laying parasitic eggs (Table IV).

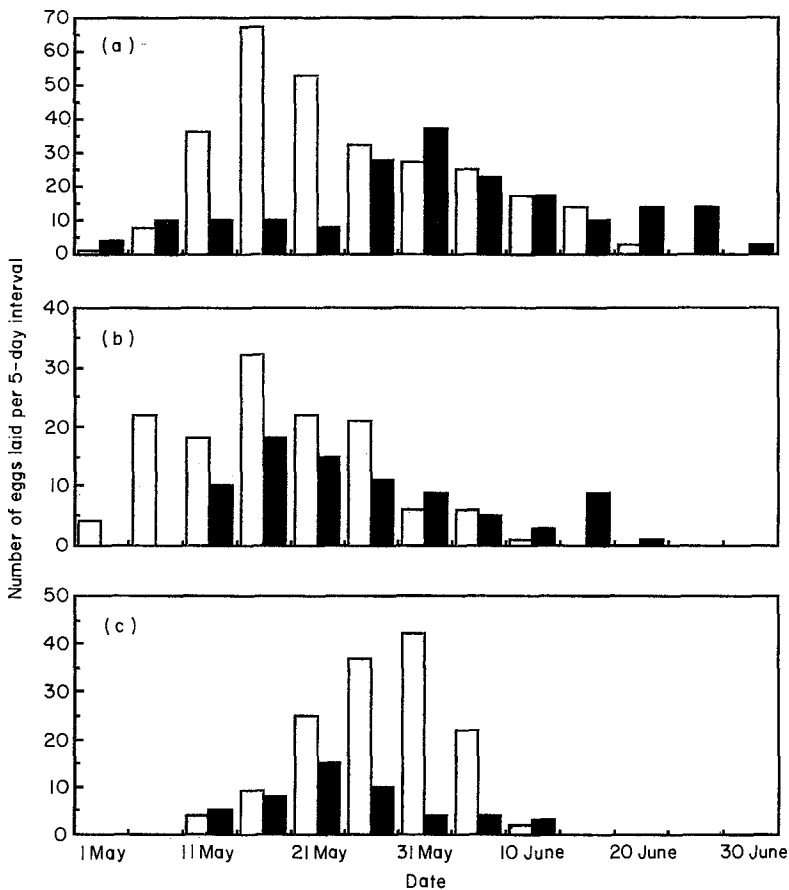
### *Parasitic egg laying after nest loss*

I documented parasitic egg laying after natural nest loss only once. In 1988, female 410 initiated her own nest on 28 May and had laid five eggs when the nest was destroyed on 2 June at 1729 hours. At 1939 hours the same day, she laid a parasitic egg in a canvasback nest 950 m away. This female was recorded in nest visits at three more nests on 3 and 4 June, but was not known to lay additional parasitic eggs. A similar response by another female was

apparently elicited by my disturbance. While I was setting up a camera at her own nest, female 850 laid a parasitic egg (the last egg she laid in 1988) at a canvasback nest about 1.0 km away. Female 850 returned to her nest the next day (28 May) and incubated her own clutch of eight eggs until it was destroyed on 6 June.

### Annual changes in reproductive tactics

Individual females changed reproductive tactics from one year to the next and most returning females were known both to lay parasitic eggs and to build a nest, though not necessarily in the same year (Fig. 3). Eight of 12 females that were present in all 3 years of the study showed evidence of both parasitic egg laying and nesting. Similarly, nine of 15 returning females that were nest-trapped in 1986 or 1987 laid parasitic eggs in a following year. Three of the 12 females present in all 3 years (174, 691 and 696), however, were known only to lay parasitic eggs and were recorded on film in 2, 2 and 3 years, respectively.



**Figure 4.** Seasonal chronology of parasitic (□) and non-parasitic (■) egg laying by redheads. The total number of redhead eggs of each category laid on the main study area is shown for each 5-day interval during the breeding season. (a) 1986; (b) 1987; (c) 1988.

### Seasonal Chronology of Parasitism and Nesting

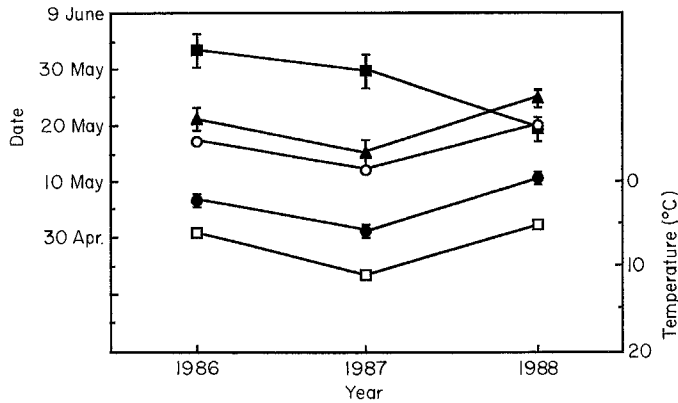
Differences between years in the reproductive tactics of female redheads were reflected in the seasonal chronology of parasitic egg laying and typical nesting (Fig. 4). As would be expected if most females laid parasitic eggs prior to nesting, the mean date of 'parasitic clutch initiations' (see Appendix) preceded the mean date of typical nest initiations (for adult females both on and off the main study area) by 12.2 days and 14.7 days in 1986 and 1987, respectively. In 1988, when only one female was known to lay parasitic eggs prior to nesting, the pattern was reversed: the peak of parasitic clutch initiations followed the peak of typical nest initiations by 5.4 days.

Differences between years in the timing of parasitic egg laying by redheads reflected variation in

spring weather and paralleled differences between years in the timing of canvasback and American coot, *Fulica americana*, nesting (Fig. 5). Dates of typical nesting by redheads, however, did not fit this pattern. Adult redheads initiated nests earliest in 1988, the latest year for other species and the year with the lowest spring temperatures. While canvasbacks nested 9.4 days later in 1988 than in 1987, adult redheads nested 10.3 days earlier. Thus, relative to canvasback nesting and spring weather, redheads initiated nests about 19.7 days earlier in 1988 than in 1987. This finding strongly suggests that the few redhead females that did nest in 1988 did not lay parasitic eggs prior to nesting.

### Population Level Reproductive Output

Per caput production of parasitic eggs and typical nests was high enough in 1986 to account for



**Figure 5.** Seasonal timing of redhead parasitism (▲) and nesting (■), canvasback nesting (●) and coot nesting (○) by year. For redhead nesting, the mean nest initiation date ( $\pm$  SE) is shown for all nests of known adults on and off the main study area. For redhead parasitism, the mean data of 'parasitic clutch initiations' ( $\pm$  SE) is plotted (see Appendix). For canvasbacks, the mean nest initiation date ( $\pm$  SE) for 30 adult females that nested in at least 2 of the 3 years is shown (renests excluded). For coots, the median date of nest initiation on a nearby study area is shown (T. W. Arnold, unpublished data). The mean daily temperature for 16 April–15 May (□) is also plotted for each year as a summary of spring weather. Redhead nest initiation dates differed significantly among years ( $F_{2,41} = 3.94$ ,  $P < 0.03$ ).

**Table V.** Population level production of parasitic eggs and typical nests

Year	Redhead* females	Parasitic† eggs	Parasitic eggs/ female	Redhead‡ nests	Nests/ female
1986	23–29	279–287	9.6–12.5	24	0.8–1.0
1987	18–24	132–136	5.5–7.6	12	0.5–0.7
1988	21–29	139–141	4.8–6.7	8	0.3–0.4

\*Minimum and maximum estimate of the density of redheads on the main study area obtained from pair counts. Roadside counts were variable but were consistent with pair counts indicating fewer birds in 1987.

†Minimum and maximum estimate of the number of parasitic redhead eggs laid on the main study area. The range of uncertainty is small because most parasitic eggs were laid interspecifically.

‡Number of redhead nests initiated on the main study area.

about 10 parasitic eggs as well as a typical nest for every redhead female (Table V), suggesting that most redhead females laid parasitic eggs prior to nesting. Although population level reproductive output was lower in 1987, the reproductive tactics of adult females were probably not much different from those seen in 1986. First, the true level of red-head nesting in 1987 is probably underestimated in Table V because an inordinate number of females nested in areas immediately surrounding the main study area. Adding nests found in the 6.3-km<sup>2</sup> peripheral area and the number of marked females that appeared with broods in peripheral areas (helping to correct for the lack of a systematic nest search in

peripheral areas in 1986), the total numbers of red-heads nesting in 1986, 1987 and 1988 were 31, 28 and 15, respectively, indicating that nesting effort in 1986 and 1987 was similar and much higher than in 1988.

Second, a higher proportion of yearlings, many of which nested but did not lay parasitic eggs (see above), and fewer adults in the redhead population in 1987 may explain the lower per caput production of parasitic eggs. Very low nest success in 1985 yielded few returning yearlings in 1986 (two of 19 decoy-trapped females, including females that were subsequently fitted with radio transmitters) while favourable conditions in 1986 resulted in a large

**Table VI.** Fate of parasitic and non-parasitic redhead eggs in successful nests

Year		Hatched	Left unhatched	Displaced into water	Sample size	
					Eggs	Nests
1986	Parasitic	32–44%	30–31%	26–30%	155 (2)	30 C, 7 R
	Non-parasitic	71–82%	4%	14–21%	114 (4)	14 R
1987	Parasitic	46–56%	19–21%	24–28%	100 (3)	29 C, 3 R
	Non-parasitic	84–98%	0–3%	2–7%	101 (9)	12 R
1988	Parasitic	14–25%	53–56%	22%	36	11 C, 1 R
	Non-parasitic	92–100%	0%	0%	24	3 R
Total	Parasitic	35–46%	29–31%	25–28%	291 (5)	70 C, 11 R
	Non-parasitic	79–91%	2–3%	8–13%	241 (13)	31 R

Sample for parasitic eggs includes all successful, parasitized canvasback (C) and redhead (R) nests on the main study area. To increase sample size, calculations of non-parasitic egg fate include all successful redhead nests on and off the main study area. All values for egg fates are minimum and maximum estimates. In general, the true value for eggs hatched is probably close to the maximum estimate. Estimates for eggs hatched reflect uncertainty about the number of eggs hatched in all nests and also about the number and identity of parasitic eggs in redhead nests (parenthetical value under eggs is the number of eggs of uncertain status in redhead nests). Ranges for eggs left unhatched and eggs displaced into water reflect uncertainty only about the number or identity of parasitic eggs in redhead nests. No significant differences in nest success were found between parasitized and unparasitized nests or between redhead and canvasback nests (Sorenson 1990).

cohort of yearlings in 1987 (16 of 31 decoy-trapped females). At the same time, the number of adults was reduced because eight females that were radio-marked in 1986 did not return to the study area in 1987 (Sorenson 1989).

### Fitness Effects of Reproductive Tactics

#### *Success of parasitic and non-parasitic eggs*

The success of parasitic redhead eggs was consistently lower than that of non-parasitic eggs (i.e. those laid by redhead females in their own nests). At least 29% of all parasitic eggs in successful nests were left unhatched (Table VI), most having been laid during the host's incubation stage and abandoned by the host female after her own eggs hatched. A larger proportion of parasitic eggs also were displaced from nests. Over the 3 years of the study, a maximum of 90.4% of non-parasitic redhead eggs in successful nests hatched compared with 45.7% of parasitic eggs.

#### *Parasitic clutch size*

The number of parasitic eggs laid by redhead females is difficult to evaluate with the data available from this study because most egg-laying histories are far from complete. None the less, several

lines of evidence suggest that individual females generally do not lay a very large number of parasitic eggs. (1) The maximum number of parasitic egg-laying events recorded for an individual female in one season was seven. (2) In most cases, all of the egg-laying events and nest visits recorded for a given female fell within a short time period. The 'duration' of parasitic egg laying (i.e. the number of days inclusive from the first to the last recorded egg-laying event) was 10 or fewer days for 17 of 24 females recorded in at least two egg-laying events in one season, and 44 of 48 nest visits made by these 17 females fell within a 10-day period that also included all of a given female's egg-laying events. (3) Long durations of parasitic egg laying for individual females probably included intervals during which no parasitic eggs were laid. For example, female 665 (30-day duration in 1987, see Fig. 1) apparently initiated a nest of her own (which was already destroyed when found and could not unambiguously be attributed to 665) between 22 and 31 May and then laid additional parasitic eggs before initiating a second nest on 16 June. Similarly, the last parasitic egg laid by female 850 in 1987 (18-day duration) followed 5 days during which no egg laying was recorded and probably was, physiologically, part of the clutch she laid in

**Table VII.** Percentage nest success in relation to initiation date in canvasbacks

Initiation date*	1986	N	1987	N	1988	N
Early	75%	20	74%	23	42%	19
Middle	60%	20	64%	22	36%	22
Late	38%	21	67%	21	8%	24
$G_{adj}$	5.71		0.57		7.90	
	$P < 0.06$		$P > 0.1$		$P < 0.025$	

\*For each year, all canvasback nests on the main study area were divided as nearly as possible into three equal groups based on nest initiation date. In 1986, 1987 and 1988, respectively, early nests were initiated on or before 8 May, 1 May and 9 May and late nests were initiated after 15 May, 10 May and 17 May. Abandoned nests were excluded from the analysis.

her own nest. (4) Females known only to lay parasitic eggs in a given season were recorded in fewer egg-laying events ( $\bar{X} \pm SE = 2.3 \pm 0.3$ ,  $N = 24$ ) than females laying parasitic eggs prior to nesting ( $\bar{X} \pm SE = 3.6 \pm 0.5$ ,  $N = 11$ , Mann-Whitney  $U = 73$ ,  $P = 0.032$ , test includes all females recorded in at least one egg-laying event in a given season).

Based on these results, I tentatively conclude that most redhead females laid only one 'parasitic clutch' of 10 or fewer eggs each season. A few females with longer durations of parasitic egg laying may have laid more. For example, the duration of parasitic egg laying for female 174 was 16 days in 1987 and 14 days in 1988 and this female was not known to nest during the study.

#### *Costs of delayed nesting*

Females laying parasitic eggs prior to nesting may delay the initiation of their own nest until relatively late in the season and may be subject to seasonal declines in nest success and clutch size. Although the sample size was too small to evaluate the relationship for redhead nests, the success of canvasback nests declined during the season in 1986 and 1988 (Table VII). This seasonal decline probably affected redhead nests as well because it was caused by an increasing rate of nest predation rather than abandonment.

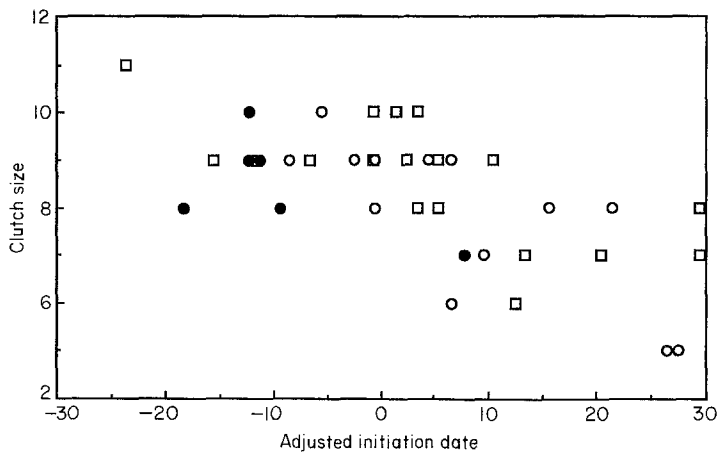
Clutch size of nesting redheads was also negatively correlated with initiation date (Fig. 6). Clutch size was relatively constant, however, until it declined sharply later in the season and many

clutches of 8–10 eggs initiated before this sharp decline were probably those of females employing a dual strategy (see Fig. 1).

#### *Relative success of hypothetical reproductive strategies*

Estimates of the potential annual reproductive success of redhead females employing five hypothetical reproductive strategies are presented in Table VIII. In general, I calculated reproductive success for each strategy as the product of number of eggs laid, nest success and egg success. The number of eggs laid is part of the definition of each hypothetical strategy: (1) nesting: 10 eggs laid in own nest; (2) nesting/renesting: 10 eggs laid in first nest; 75% of females whose first nest is destroyed lay 8 eggs in a second nest (see Alliston 1979b; Doty et al. 1984); (3, 4) parasitism prior to nesting: 10 parasitic eggs laid prior to 10 or 8 eggs in own nest; (5) parasitism only: 20 parasitic eggs laid. First nests in strategies 1 and 2 and the first 10 parasitic eggs in strategies 3, 4 and 5 were subject to 'early season nest success' (58.1, 63.0 and 36.0% for 1986, 1987 and 1988, respectively), the combined success of the first half of redhead nests each season and midseason canvasback nests (see Table VII). Renests in strategy 2, nests in strategies 3 and 4, and the second 10 parasitic eggs in strategy 5 were subject to 'late season nest success' (43.8, 59.3 and 11.5% for 1986, 1987 and 1988, respectively), the combined success of the second half of redhead nests and last third of canvasback nests. Maximum estimates of parasitic and non-parasitic egg success (up to 96%) were taken from Table VI. Egg success for renests in strategy 2 and for nests in strategies 3 and 4 was also assumed to be 96% because the rate of intraspecific parasitism is low late in the season (Sorenson 1990).

According to these calculations, females laying parasitic eggs prior to nesting would have had the highest reproductive success in 1986 and 1987. In 1988, nesting females would have had higher success because of a strong seasonal decline in nest success and lower success of parasitic eggs. In all 3 years, a purely parasitic strategy would have been relatively unsuccessful because all 20 eggs would be subject to the low success of parasitism. Because the number of parasitic eggs laid by redhead females employing different reproductive tactics is not precisely known and because possible seasonal effects on post-hatch survival are not incorporated (see Discussion), these estimates should be considered



**Figure 6.** Relationship between initiation date and clutch size for typical redhead nests (both on and off the main study area) in which clutch size (total number of redhead eggs minus parasitic redhead eggs) could be estimated (clutch size =  $8.55 - 0.069 \times \text{adjusted date}$ ,  $r^2 = 0.45$ ,  $P < 0.001$ ).  $N = 19$ , 13 and 6 in 1986 ( $\square$ ), 1987 ( $\circ$ ) and 1988 ( $\bullet$ ), respectively. Adjusted initiation date is the actual date minus the mean date of parasitic egg laying for each year.

**Table VIII.** Reproductive success, measured as number of hatched ducklings, for five hypothetical reproductive strategies (number of eggs laid in parentheses)

Year	Nesting (10)	Nesting/ re-nesting (10, 8)	Parasitism prior to nesting (10, 10)	Parasitism prior to nesting (10, 8)	Parasitism only (20)
1986	4.77	5.83	6.76	5.91	4.47
1987	6.05	7.31	9.22	8.08	6.85
1988	3.45	3.88	2.00	1.78	1.19

indicative of the relative potential of different reproductive tactics rather than accurate measures of reproductive success.

### Evidence of Constraints

Although this study was not specifically designed to evaluate possible physiological constraints on reproductive tactics, I analysed several reproductive parameters for evidence consistent with constraints that may have been imposed by drought conditions in 1988.

#### Body mass

If physiological condition influences reproductive tactics, females employing the relatively high cost tactic of typical nesting should have greater body mass at the beginning of the season

than females that do not nest. Combining data from all 3 years, decoy-trapped adult females that subsequently nested were heavier than females that were not known to nest (Table IX). This result was due primarily to a year effect: fewer females nested in 1988 and females tended to be lighter in 1988, although this result was not significant ( $F_{2,38} = 2.35$ ,  $P > 0.1$ , this analysis and the one following include females subsequently equipped with radios). The above analysis does not include decoy-trapped yearlings, which were significantly lighter than adults (yearlings:  $\bar{X} \pm \text{SE} = 957 \pm 18$  g,  $N = 21$ ; adults:  $1060 \pm 12$  g,  $N = 41$ ;  $F_{1,58} = 16.8$ ,  $P < 0.001$ ) and which employed lower cost reproductive tactics than adults in both 1987 and 1988 (see Discussion).

#### Egg size

Captive mallards fed an enriched diet lay larger eggs than females fed a poor diet (Eldridge &



**Table IX.** Mean  $\pm$  SE body mass (g) of decoy-trapped, adult female redheads in relation to reproductive tactics subsequently employed in the same season

Year	Females known to nest	Females not known to nest
1986	1093 $\pm$ 39 N=6	1094 $\pm$ 34 N=4
1987	1110 $\pm$ 19 N=8	972 $\pm$ 26 N=3
1988	965 N=1	1023 $\pm$ 24 N=6
Combined*	1093 $\pm$ 20 N=15	1033 $\pm$ 20 N=13

Analysis uses all decoy-trapped, adult females that showed some evidence of being resident on or near the main study area.

\*( $t=2.13$ ,  $df=26$ ,  $P=0.043$ ).

Krapu 1988). If females in poor physiological condition lay parasitic eggs, then parasitic eggs should be smaller than non-parasitic eggs and eggs laid during a drought should be smaller than those laid in years of more favourable conditions. Parasitic and non-parasitic eggs did not differ in size (parasitic:  $\bar{X} \pm \text{SE} = 59.4 \pm 0.2 \text{ cm}^3$ ; non-parasitic:  $60.1 \pm 0.4 \text{ cm}^3$ ;  $F_{1,209} = 2.38$ ,  $P > 0.1$ ; analyses use mean egg size for 159 host and 54 redhead nests). Egg size did differ slightly between years (1986:  $60.2 \pm 0.3 \text{ cm}^3$ ,  $N=90$ ; 1987:  $59.0 \pm 0.3 \text{ cm}^3$ ,  $N=67$ ; 1988:  $59.3 \pm 0.3 \text{ cm}^3$ ,  $N=56$ ;  $F_{2,209} = 3.39$ ,  $P=0.036$ ) but, contrary to expectation, eggs were smallest in 1987 rather than 1988, the drought year.

#### *Incubation constancy*

During incubation, female diving ducks, *Aythya* spp., spend an average of 84% of the day on the nest and greatly reduce time spent feeding (Afton & Paulus, in press), thereby providing the necessary thermal environment for the development of eggs and perhaps reducing the risk of nest predation. Females in poor physiological condition might be expected to show lower nest attentiveness during incubation. Although sample size was small for 1988, nest attentiveness of incubating redheads did not differ significantly between years (1986:  $\bar{X} \pm \text{SE} = 85.4 \pm 1.6\%$ ,  $N=132$  days at 17 nests; 1987:  $78.5 \pm 2.3\%$ ,  $N=34$  days at seven nests; 1988:  $88.3 \pm 4.0\%$ ,  $N=21$  days at three nests;  $F_{2,24} = 1.82$ ,  $P > 0.1$ , covariance analysis control-

ling for ambient temperature, precipitation and stage of incubation) and was actually highest in 1988, the drought year.

## DISCUSSION

### **A High Fecundity Dual Strategy**

In general, results from 1986 and 1987 are consistent with predictions of the fecundity hypothesis, part (2) (see Table I). Individual females laid parasitic eggs prior to initiating their own nests and population level data suggested that most adult females may have employed this dual strategy: the seasonal peak of parasitic egg laying by redheads preceded that of typical nesting and per caput rates of both parasitic egg laying and typical nesting were high in 2 years of favourable environmental conditions. Most importantly, the reproductive success of a dual strategy estimated from empirical data was higher than that of a typical nesting strategy.

A female strategy that includes both parasitic egg laying and nesting has been referred to as a 'mixed strategy' (Emlen & Wrege 1986; Lank et al. 1989), analogous to mixed copulation strategies employed by males (Trivers 1972). This analogy is appropriate to the behaviour of swallows (*Hirundo* spp.) that lay one or two parasitic eggs (analogous to extra-pair copulations by males) at about the same time they are laying eggs in their own nests (Brown 1984; Møller 1987). In redheads, however, parasitic egg laying is not a secondary tactic employed concurrently with a typical nesting attempt. I use the term 'dual strategy' for the separate and sequential use of parasitic and typical nesting tactics.

Most prairie-nesting ducks have the ability to lay many more eggs over the course of a breeding season than those laid in a single clutch: females readily re-nest after a first nest is destroyed (e.g. Sowls 1955; Doty et al. 1984). Only one successful nest is possible each season, however, because of the time necessary for incubation and brood rearing. Annual reproductive success in most species is therefore limited to the number of eggs laid in a single clutch at best. In contrast, a redhead female may lay two productive 'clutches' in one season by laying a 'clutch' of parasitic eggs in several host nests prior to laying a second clutch in a nest of her own. Although parasitic egg laying is inefficient on a per egg basis, it enables female redheads to obtain care for a greater total number

of eggs and to increase their annual reproductive success above that possible through typical nesting alone: efficiency is not necessarily an important component of fitness.

The observed interval between parasitic egg laying and typical nesting for individual females in this study ( $\bar{X} \pm SE = 11.1 \pm 1.6$  days) was similar to the reneest interval observed in one population of redheads (Alliston 1979b, 13.2 days) and in other diving ducks (e.g. Doty et al. 1984, 9.8 days). This suggests that the dual reproductive strategy of the redhead employs (and is perhaps constrained by) physiological mechanisms evolved in the context of reneesting and that the evolution of a dual strategy may have required relatively few changes in physiology.

Previous studies provide only anecdotal information about the reproductive tactics of individual females, but parasitic egg laying prior to nesting has been documented in redheads before. Females that were trapped at host nests later initiated nests of their own in two studies (Weller 1959,  $N=2$ ; Johnson 1978,  $N=2$ ) and Saylor (1985), using time-lapse photography, recorded 'several' marked females laying parasitically prior to nesting.

Population level data from previous studies are also consistent with the occurrence of a dual strategy in redheads. As in this study, Weller (1959) found parasitic egg laying by redheads to be most frequent prior to the peak of nesting and concluded that many redhead females must have laid parasitic eggs before nesting. High per caput rates of both parasitic egg laying and nesting in the same season have also been reported. Weller (1959) found 936 parasitic eggs and 46 redhead nests produced by a population of 90 to 95 females and Sugden (1980) found 217 parasitic eggs and 35 redhead nests produced by a population of 43 females.

### **Constraint Versus Restraint and the Drought of 1988**

In 1988, in contrast to the first 2 years of the study, the behaviour of individual females was consistent with either the restraint hypothesis or the constraint hypothesis, part (2) (see Table I). Only one marked female was known to lay parasitic eggs prior to nesting and only six females were known to nest. Even though the success of typical nesting would have been higher than that of a purely parasitic strategy (Table VIII), most females only laid parasitic eggs. Population level data were also consistent with these changes in individual behaviour:

parasitic egg laying and nesting by redheads occurred at essentially the same time during the season and the per caput rate of nesting was much lower than in the previous 2 years. Clearly, the fecundity hypothesis cannot explain parasitic egg laying by redheads in 1988.

### *Constraint*

Water levels appear to have a substantial effect on the reproductive performance of prairie-nesting ducks (e.g. Olson 1964; Rogers 1964; Stoudt 1971). Drought conditions probably reduce the availability of food resources through a reduction in the number and size of wetlands (Krapu et al. 1983; Batt et al. 1989) and may force changes in diet composition and foraging habitat (Swanson & Meyer 1977). Experimental reductions of food supply and diet quality reduce the rate of reneesting and other measures of reproductive performance in captive ducks (Swanson & Meyer 1977; Eldridge & Krapu 1988), suggesting that reduced food availability may be responsible for the lack of reneesting and increased rates of non-breeding observed during drought (e.g. Stoudt 1982; Afton 1984).

Although not measured in this study, availability of food resources for redheads was probably reduced in 1988, perhaps limiting the ability of females to acquire endogenous reserves for egg laying and incubation. Faced with such constraints, females may have laid parasitic eggs instead of not breeding at all. Comparisons of female body mass, incubation constancy, and egg size between years, however, provided little evidence for physiological constraints imposed by drought conditions in 1988. A within-year comparison of body mass between females employing different reproductive tactics is suggestive but inconclusive (Table VIII). Detailed time and energy budgets for both parasitic and nesting females under different sets of environmental conditions would provide a better understanding of the relationship between possible constraints imposed by a variable food supply and the reproductive tactics of redheads.

### *Restraint*

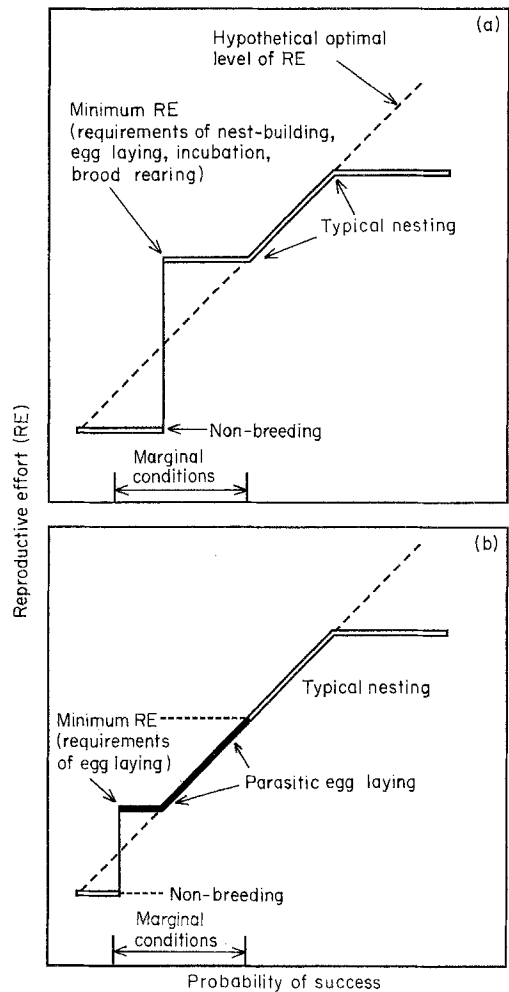
Williams (1966a) showed that reproductive investment should be proportional to the prospects for success and that, when conditions for reproduction are unfavourable, an animal may improve its lifetime reproductive success by investing in its

own survival and delaying reproduction until conditions improve. Drought conditions clearly reduce the probability of successful nesting for prairie-nesting diving ducks. Rates of nest loss increase because nests in emergent vegetation are exposed to mammalian predators at low water levels (e.g. Olson 1964; Stoudt 1982) and perhaps because alternative prey such as small mammals and amphibians become less available (Rogers 1964; Byers 1974). In this study, nest success was much lower in 1988, especially as water levels dropped later in the season, than in 1986 and 1987 when emergent vegetation was well flooded.

At the beginning of the breeding season, only two reproductive options are available to most prairie-nesting waterfowl, non-breeding and typical nesting. Nesting requires a high minimum reproductive effort, which includes the time and energy invested and risks taken in nest building, egg laying, incubation and brood rearing. In drought years, the lower expected pay-off of typical nesting may not justify even this minimum level of reproductive effort and females might respond by not breeding at all. Afton (1984), for example, concluded that non-breeding during drought in lesser scaup, *Aythya affinis*, represented a reduction in reproductive effort made in response to an increased rate of nest predation.

There should be a range of marginal conditions, however, in which the 'all or none' decision between non-breeding and typical nesting forces a female to expend either much more or much less reproductive effort than conditions would merit (Fig. 7a). A purely parasitic strategy does not require nest building, incubation or brood rearing, and therefore represents much less reproductive effort than nesting. By laying only parasitic eggs when conditions are marginal, a female redhead may be able to adjust more precisely her reproductive effort in relation to the probability of success (Fig. 7b). A higher probability of survival until the next breeding season would compensate for the lower success of laying only parasitic eggs.

The essential requirement of the restraint hypothesis is that there be a cost of reproduction. Direct mortality risks associated with breeding are almost certainly important as costs for female diving ducks. Incubating females are killed by red fox, *Vulpes vulpes*, mink, *Mustela vison*, and raptors such as *Bubo virginianus*, *Buteo swainsoni* and *Circus cyaneus* (Mendall 1958, Eberhardt & Sargeant 1977; Alliston 1979a; Afton 1984; M. G.



**Figure 7.** (a) Reproductive options available to most prairie-nesting waterfowl upon arrival to the breeding grounds. A high level of reproductive effort is necessary to meet the minimum requirements of typical nesting. (b) Facultative parasitic egg laying may be employed to lower reproductive effort in marginal conditions.

Anderson, personal communication). At least one incubating canvasback female was killed during my study and the remains of a marked female that had been tending a brood were also found. I knew of no redhead females that were killed but four of 11 marked females were never sighted again after their nests were destroyed during incubation.

Time and energy spent in incubation and brood rearing may also represent significant costs of reproduction. Female diving ducks lose a large proportion of lipid reserves and up to 20% of body mass during incubation (e.g. Noyes & Jarvis 1985;

Barzen & Serie 1990). In addition, while some females are still incubating, male redheads leave breeding areas and eventually move up to 300 km north to large, food-rich lakes where they undergo the wing moult in relative safety from predators (Weller 1964; Bergman 1973). The presumably important survival advantages of this moult migration are not available to brood-rearing females (McKinney 1986). Female redheads that lay only parasitic eggs might moult earlier and in a safer place and might begin autumn migration earlier and in better physiological condition than nesting females.

In practice, it is difficult to distinguish between constraint (environmental or physiological limitations) and restraint (reduced reproductive effort) as the explanation for reduced reproductive performance (Nichols et al. 1976; Curio 1983). Changes in reproductive parameters consistent with constraint are also consistent with a reduction of reproductive effort. For example, body mass of female diving ducks reaches an annual peak during the pre-breeding or egg-laying stage (Noyes & Jarvis 1985; Barzen & Serie 1990), suggesting that the optimal body mass for survival is somewhat less than that for breeding. Lower body mass during drought might occur because females are constrained by reduced food resources or because females that 'choose' not to nest adaptively avoid the costs of accumulating and maintaining endogenous reserves necessary for nesting. An additional problem is that the relationship between reproductive effort (i.e. cost to future reproduction) and energetic measures of reproductive input is usually not known (Clutton-Brock 1984) and the shape of this relationship may vary with conditions (Pianka & Parker 1975; Evans 1990).

A striking, qualitative change in reproductive tactics during the 1988 drought, however, does suggest an adaptive reduction of reproductive effort consistent with the restraint hypothesis. The few redheads that initiated nests in 1988 did so 19 days earlier (relative to spring temperatures and the nesting of other species) than in 1987. Instead of laying parasitically early in the season and employing a dual strategy, these females laid their first clutches in their own nests.

In reality, the costs of reproduction, the probability of success and the severity of constraints probably all vary with environmental conditions and operate in concert to modify observed levels of reproductive performance (see Curio 1983). In the

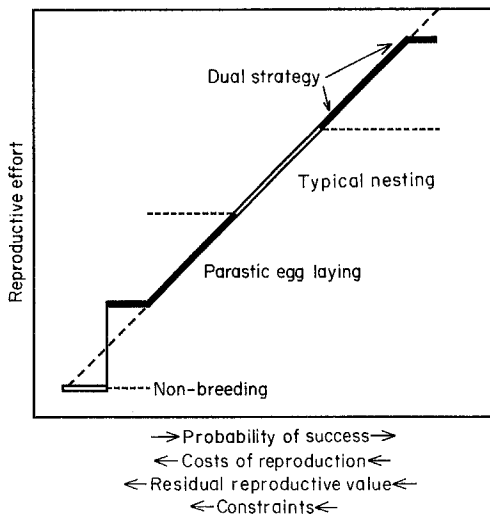
case of redheads, drought conditions might simultaneously reduce rates of nest success, increase energetic costs and predation risks for breeding females, and create physiological constraints on reproduction by reducing resource availability (Sayler 1985). An increased rate of nest predation was the most obvious effect of drought in this study and certainly altered the trade-off between current and future reproduction for redheads. Although much more difficult to measure, greater energetic costs and/or physiological constraints imposed by a possible reduction in food availability also may have influenced the reproductive performance of redheads in 1988.

Regardless of the relative importance of constraint and restraint in determining the reproductive tactics of redheads, however, parasitic egg laying during the 1988 drought can be characterized, in game theory parlance, as a 'best-of-a-bad-job' strategy (Dawkins 1980; Davies 1982) employed in response to environmental conditions which made a generally better strategy (i.e. typical nesting or a dual strategy) impossible or unprofitable.

### **A Decision Model of Redhead Reproductive Strategies**

Williams' (1966a) original formulation of the trade-off between current and future reproduction was put in terms of a reproductive decision. For example, should a female bird lay an additional egg or not? Natural selection will favour the course of action (or inaction) which, depending on its costs (reduction in residual reproductive value) and benefits (increase in current reproduction), maximizes lifetime reproductive success. When the conditions an animal faces are variable, selection should favour 'yes-if' genes (Williams 1966b), which allow animals to 'decide' on the appropriate level of reproductive investment for any given set of conditions. In redheads, this kind of 'decision' results not only in adjustments of quantitative parameters such as clutch size but also in qualitative changes in reproductive tactics.

A reproductive decision model that combines the fecundity and restraint hypotheses may provide an explanation for redhead reproductive tactics in all 3 years of my study. I propose that at the beginning of each breeding season redhead females choose from four reproductive options of increasing reproductive effort: (1) non-breeding, (2) parasitic egg laying, (3) typical nesting and (4) a dual strategy of



**Figure 8.** Reproductive options available to redhead females at the beginning of the breeding season. In addition to the probability of success, females may alter reproductive effort in response to changes in the costs of reproduction and their own residual reproductive value, while constraints may directly affect reproductive performance.

parasitic egg laying prior to typical nesting (Fig. 8). When conditions are poor, females respond to reduced prospects for success and/or increased costs of reproduction by employing strategies of low reproductive effort (i.e. non-breeding or parasitic egg laying). When environmental conditions are ideal and the probability of successful nesting is high, females increase their reproductive effort (above the maximum that could be invested in a single nest) and reproductive success by laying parasitic eggs prior to initiating their own nests.

Weller (1959) was the first to recognize three distinct types of nesting behaviour in redhead populations: 'normal nesting', 'semiparasitism' and 'obligate parasitism'. It is not clear whether Weller intended to imply that the 'simultaneous existence of these stages' (1959, page 357) was attributable to genetic polymorphism, but several subsequent authors clearly have made this interpretation (e.g. Hamilton & Orians 1965; Yom-Tov 1980). Evidence from this study allows this possibility to be rejected: the reproductive tactics of individual females change from year to year and most or all redhead females probably employ both parasitic egg laying and typical nesting tactics during their lifetime. Applying a strict definition of strategy (Davies 1982), the four reproductive options of redheads are not really 'alternative

strategies' but rather parts of a single conditional strategy for reproduction in a variable environment.

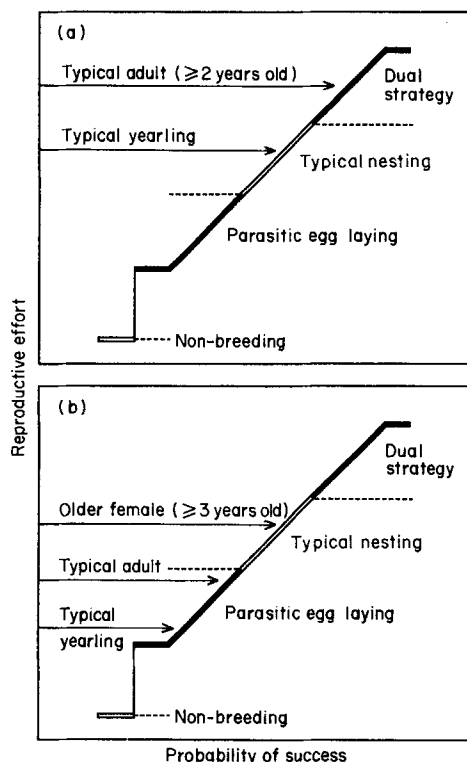
The above model considers reproductive options only at the beginning of the breeding season: the conditional reproductive strategy of redheads also may provide flexibility in other contexts as well. For example, parasitic egg laying may be the usual response of a redhead female whose own nest is destroyed in the laying stage. Nest loss (the constraint hypothesis, part 1), however, accounted for only a very small proportion of parasitism in this study.

#### *Age-related reproductive tactics*

Young birds are almost always found to have lower reproductive performance than experienced adults (Søther 1990). Perhaps because they are less proficient at acquiring resources, young birds may be more susceptible to constraints or may experience higher costs of reproduction and a lower probability of success (Curio 1983). Whatever the relative importance of these factors, young female waterfowl lay fewer eggs and nest later in the season (reviewed in Rohwer, in press) and have higher rates of non-breeding (e.g. Finney & Cooke 1978; Baillie & Milne 1982) and lower rates of renesting (e.g. Afton 1984; Mitchell et al. 1988).

In redheads, lower reproductive performance of young females was also manifest in qualitative differences in reproductive tactics, which provides additional support for the above model (Fig. 9). In 1987, many adults employed a dual strategy, while many yearlings apparently only nested. In 1988, a few females that nested were at least 3 years old while yearlings and 2-year-olds were known only to lay parasitic eggs. As a result of drought conditions in 1988, most females switched to tactics of lower reproductive effort, but this change depended on age: the oldest females switched from a dual strategy to only nesting while yearlings switched from only nesting to laying only parasitic eggs. Saylor's (1985) finding that adult females were probably responsible for most parasitic egg laying while yearling females apparently did not breed at all in a year of extreme drought suggests an age effect consistent with the present model and an even greater reduction in reproductive effort than was observed during a less severe drought in this study.

Changes in reproductive tactics with age and environmental conditions suggest that the reproductive strategy of female redheads is a relatively sophisticated conditional strategy. In general,



**Figure 9.** (a) Reproductive strategies of a typical adult and yearling in 1987. (b) Reproductive strategies in 1988. Lower reproductive performance of yearlings might result from age-related differences in constraints, costs of reproduction and residual reproductive value in addition to differences in the probability of success.

reproductive tactics are probably adaptive conditional responses to proximate factors that reliably indicate the probability of successful nesting and the costs of reproduction. Likely proximate cues to which redheads might easily respond include water depth, the extent and density of flooded emergent vegetation, food availability, physiological condition and, perhaps, host availability. Long-term records of parasitic and typical nesting behaviour for individual females in addition to experimental manipulations of the proximate factors to which redheads presumably respond are needed to further assess the relevance of the reproductive decision model presented here.

#### Effect of Reproductive Strategy on Survival

Although more information on the number of parasitic eggs laid by individual females is needed, estimates of annual reproductive success suggest that a purely parasitic strategy would not be viable in my study population. A purely parasitic strategy

could compete, however, if avoidance of the costs of incubation and brood rearing resulted in higher survival for the adult female and greater lifetime reproductive success. Too few data were collected in this study to estimate female survival rates and it is therefore impossible to evaluate the survival hypothesis fully, but it is at least possible that the three females that were present in all 3 years of the study and that were never known to nest were 'pure parasites'. Ultimately, a purely parasitic strategy may be rare because the dual strategy is more successful. The success of a female's last clutch will always be highest if laid in a nest of her own while a seasonal decline in host availability may limit the number of eggs a purely parasitic female could effectively lay, especially if a 're-nesting' interval is required between 'parasitic clutches'.

Early nest initiation dates for redhead females that only nested (i.e. yearling females in 1987 and the few females that nested in 1988) strongly suggest that redheads employing a dual strategy delay their own nesting to lay parasitic eggs. Several factors potentially reduce the success and increase the costs of late nesting, perhaps threatening the conclusion made here that a dual strategy is more successful than a typical nesting strategy. By delaying nesting, females may be affected by seasonal declines in nest success and perhaps clutch size and may also forgo the option of re-nesting if their own nest is destroyed. Interestingly, re-nesting in redheads has only been documented in one isolated population in which parasitic egg laying is infrequent (Alliston 1979b). Incorporating all of these factors, however, the annual reproductive success of a female laying 10 parasitic eggs prior to nesting may still be higher than that of a nesting/re-nesting female when environmental conditions are favourable (Table VIII).

Possible effects of a dual strategy on survival, however, could not be measured in this study. If delayed nesting results in delayed moult and migration and greater mortality for the adult female (see above) or if late hatching results in lower offspring survival and recruitment (e.g. Cooke et al. 1984; Dow & Fredga 1984; Gauthier 1989; but see Hepp et al. 1989), the relative success of a dual strategy would be lower than indicated in Table VIII. The same would be true if parasitic ducklings are less likely to survive than non-parasitic ducklings. Although sample size was small for redhead broods, there was no difference in survival to 30 days after hatch between redhead

ducklings in canvasback broods and redhead ducklings in redhead broods, and there was also no effect of hatch date on the survival of canvasback ducklings (unpublished data). No data were obtained on the relative over-winter survival of early and late-hatched or of parasitic and non-parasitic redheads in this study but it is known that redheads hatched from both parasitic and non-parasitic eggs do return to natal areas and breed (Johnson 1978; personal observation).

Possible negative effects of delayed nesting on survival in combination with a seasonal decline in nest success may reduce the relative success of a dual strategy but both of these effects are probably more severe in drought years when habitat conditions deteriorate rapidly (see Table VII). In contrast, when environmental conditions are favourable, effects of late nesting on the survival of the adult female and/or ducklings may be minimal and annual estimates of reproductive success may accurately reflect the relative fitness of a dual strategy. The relationship between survival and reproductive tactics in redheads will be a challenging and fascinating topic for future research.

## APPENDIX

Ideally, a comparison of the seasonal timing of parasitic egg laying and typical nesting would be based on dates of 'clutch initiations' for females laying parasitic eggs and dates of nest initiations. Unfortunately, the laying date of first eggs in 'parasitic clutches' was unknown because histories of parasitic egg laying were incomplete. The mean date of parasitic egg laying is analogous, however, to the mean laying date for middle eggs in typical nests. Thus, if parasitizing females lay 10 parasitic eggs on 10 consecutive days, the mean date of 'parasitic clutch initiations' would be 4.5 days earlier than the mean laying date of all parasitic eggs. This 'corrected' mean is plotted in Fig. 5.

In addition, the standard error of the mean date of parasitic egg laying is artificially small because the laying dates for parasitic eggs laid by a given female are not independent. By making the same assumption that all parasitizing females lay 10 parasitic eggs on 10 consecutive days, I calculated an approximate standard error of the mean date of 'parasitic clutch initiations'. If  $y_{ij}$  is the date of laying for the  $j$ th egg in the  $i$ th parasitic clutch, then the variance in parasitic egg-laying dates,  $s^2$ , is

$$\sum_{ij} (y_{ij} - y_{..})^2 / (n - 1),$$

where  $y_{..}$  is the mean date of laying for all parasitic eggs and  $n$  is the total number of parasitic eggs laid. The sum of the squared deviations,  $\sum (y_{ij} - y_{..})^2$ , can be partitioned into that attributable to variation in egg date within clutches and that attributable to variation between clutches as follows:

$$\sum_{ij} (y_{ij} - y_{..})^2 = \sum_{ij} (y_{ij} - y_{i.})^2 + b \sum_i (y_{i.} - y_{..})^2,$$

where  $y_{i.}$  is the mean egg date for clutch  $i$  and  $b$  is the number of eggs in a clutch. If all parasitizing females lay 10 eggs, then  $\sum (y_{ij} - y_{i.})^2 = 82.5 \times$  (number of clutches or females,  $f$ ) and the variance of 'parasitic clutch initiation' date,  $s_i^2$ , is

$$[(\sum (y_{ij} - y_{..})^2 - 82.5 \times f) / 10] / (N - 1),$$

where  $N$  is the number of parasitic clutches, approximately  $(n/10)$ . Thus, an approximate standard error of the mean date of parasitic clutch initiation is  $\sqrt{(s_i^2/N)}$ . This is the standard error used in Fig. 5.

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