Renesting by the Redhead Duck

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Introduction

Duck species that nest in temperate regions are single-brooded; however, individual females of many species may lay replacement clutches (renests) following an unsuccessful attempt at reproduction (Lack 1947; Sowls 1949). Much of the present knowledge of renesting has been derived from experimental studies of surface-feeding ducks: Sowls' (1955) pioneering studies of five species of the genus *Anas*, Gates' (1962) studies of the Gadwall *A. strepera*, Strohmeyer's (1967) studies of the Blue-winged Teal *A. discors*, and Coulter and Miller's (1968) studies of Black Ducks *A. rubripes* and Mallard *A. platyrhynchos*.

Comparatively little is known of the renesting habits of diving ducks. Renesting has been confirmed for the Common Pochard *Aythya ferina* (Cramp & Simmons 1977), the Ring-necked Duck *A. collaris* (Mendall 1958; Hunt & Anderson 1966; Coulter & Miller 1968), the Canvasback *A. valisineria* (Weller & Ward 1959; Bellrose 1976), the Greater Scaup *A. marila* (Bengston 1972), the Lesser Scaup *A. affinis* (Hunt & Anderson 1966), and the Tufted Duck *A. fuligula* (Cramp & Simmons 1977). For practically all of these species the confirmation of renesting is based on few observations.

Renesting has not previously been confirmed for the Redhead *A. americana*. Low (1945) in Iowa and Lokemoen (1966) in Montana both assumed that renesting occurred in their study populations, but Weller (1959) found no indication of renesting in Manitoba and Utah populations.

Study area

The study area was located in the southwestern extremity of the Province of Québec, Canada, on the marshes of Lake St. Francis, a widening of the St Lawrence River. The area consisted of several sedge meadow islands (total area = 105 ha) that were heavily utilized for nesting by an isolated population of Redheads. Physical and vegetative characteristics of the area are described in Auclair *et al.* (1973), Thompson (1974), and Alliston (1979).

Methods

Ecological studies of the Lake St Francis Redhead population were conducted between 1969 and 1972 and have been reported in Alliston (1979). The work presented in this paper is based primarily on experimental studies in 1972.

Nests were found by flushing females from nest cover either by the investigators zigzagging slowing along a transect while beating the vegetation with 5-m bamboo poles, or by dragging a rope (with cans attached) over the vegetation. The stage of incubation could be estimated to within two to three days using a field candler described by Weller (1956). Clutch size (one egg is laid per day—Alliston 1979) was also a useful indication. The 'nest initiation date', defined as the date on which the first egg of the clutch was laid, was estimated by backdating. Attempts were made to identify cases of intraspecific egg parasitism using size, shape, colour, and stage of incubation of eggs as criteria (Weller 1959). Nest locations were sketched and plotted on aerial photographs.

In 1972, females were captured on their nests using automatically activated traps (Weller 1957) and banded. Numbered nasal saddles (Sugden & Poston 1968; R. D. Titman, pers. com.) were applied when possible. My previous use of nasal saddles had resulted in a substantial number of females who had lost their markers and whose nares had been greatly enlarged. When such birds were encountered their wings were spray-painted using different combinations of red and green. After banding and marking, experimental females were released and their clutches removed. Renests were found during regular nest searches (Alliston 1979) or by intensive searches in areas where experimental females had been observed repeatedly. Experimental females with broods were identified during regular brood surveys (Alliston 1979).

Supplementary information was obtained from observations obtained during 1969–1971 of marked females known to have deserted or lost their clutches or broods. In addition, knowledge of the nesting chronology of individual females made it possible to identify their renests when their

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first nest was not found. Any nest initiated four or more weeks later than the 'normal' date for that female was considered to be a renest.

Results

The study population

The population ecology of the Lake St Francis Redheads is fully described in Alliston (1979). This isolated population was located 500 km east of the nearest established breeding population and 1,800 km east of the normal breeding range of the species. The study population consisted of about 134, 166 and 118 successfully nesting pairs in 1970, 1971 and 1972. In the last year nesting began about 1·5 weeks later than 'normal', with a smaller average clutch size (10·91 ± s.d. 1·22 in 1972; 11·91 ± 1·22 in the 'normal' year of 1970) for females with previous nesting experience. Inexperienced females nested, on the average, 2·5 weeks later and had significantly smaller clutches than experienced birds. Parasitic egg laying, which has been extensively documented for the Redhead (for summary see Weller 1959), was infrequent. During 1972 only 43 of 739 Redhead eggs (5·8%) were identified as having been laid parasitically. Nest success was spectacularly high. Using the method of Mayfield (1961, 1975), estimated nest success was greater than 90% in all years from 1969 through 1972 (excluding clutches removed by the investigators).

Experimental nest destruction

From 20 May to 7 June 1972, 22 Redhead clutches were experimentally removed. Eight clutches, all containing eight or more eggs, had not been incubated and the others had all been incubated less than two weeks. Circumstantial evidence suggested that most, if not all, of the females were still paired at the time of clutch removal.

Sixteen of the 22 experimental females (73%) had been captured while nesting in previous years. Two others nested earlier than any known inexperienced females and were therefore considered to be experienced. Thus at least 18 (82%) of the experimental females had previous nesting experience.

Nineteen of the 22 experimental females (86%) were known to have renested. Fourteen renests were found and five other experimental females were identified with broods. One observed on 15 July with a flock of pre-moult Redhead drakes, was not believed to have renested. The remaining two females were not seen after their clutches were removed. Six of the eight females (75%) whose clutches were removed before incubation began were known to renest. Thirteen of the 14 females (93%) whose nests were destroyed during the first two weeks of incubation renested.

Other renesting observations

Casual observations indicated that some Redhead females renested after losing their clutches during late incubation or even after losing their broods. In 1970 a marked female renested following the loss of her clutch on 14 June after 20 days of incubation. A marked female that lost her clutch during hatching on 11 June also renested. In 1971 a marked female left her nest with a brood of six on 11 June. She was seen on 13 July, and on several occasions during the next ten days, attended by a drake. The female may have lost her brood and then renested, but the renest was not found.

First nests and renests compared

The mean distance between the first nest and the renest sites of 15 marked females was 356 m (range 43 to 1,300 m). Fourteen renests were situated an average of 62 m from open water, compared with 92 m for first nests of the same birds (Wilcoxon matched-pairs test; $T = 23{\cdot}5$, $0{\cdot}10 > P > 0{\cdot}05$).

Original as well as renest completed clutch sizes were available for eight of the 14 experimental birds whose renests were found in 1972, and were obtained for one marked female in 1970. Mean clutch size of first nests (10·56 ± 1·42) was non-significantly larger than for renests (10·33 ± 1·58) of the same females (Table 1). If only those females known to have had previous nesting experience are considered, mean clutch size in 1972 was 10·91 ± 1·22 eggs ($N = 11$) for first nests and 10·40 ± 1·35 ($N = 10$) for renests. This small difference is again not significant.

The renesting interval

Sowls (1949) has defined the 'renesting interval' as 'the time between the destruction of

the first nest and the laying of the first egg in the second nest'. During this study the renesting interval for 17 renests averaged 13·2 ± 4·8 and ranged from 7 to 23 days. In none of the five cases where the first nests had been terminated during egg-laying was there continuous laying between first nest and renest.

Table 1. Size of completed clutches in first nests and renests of nine marked Redhead females at Lake St Francis, 1970 and 1972.

First clutch	Second clutch	Difference (1st–2nd)
13	11	−2
12	11	−1
12*	11*	−1
10	11	+1
10	9	−1
10	8	−2
10	8	−2
9	12	+3
9	12	+3
Mean 10·56	10·33	−0·22

Paired t = 0·469, P > 0·5
*1970

The possible dependence of renesting interval (Y) upon stage of incubation when the first nest was destroyed (X_1) and date of nest destruction (X_2) was assessed by multiple linear regression analysis (Steele and Torrie 1960). Relevant data are presented in Table 2. Only the date of nest destruction (X_2) was significantly related to renesting interval ($F = 7·10$; d.f. = 1, 14; $P = 0·019$). The model thus reduced to the simple linear regression equation $Y = 8·939 + 0·387\ X_2$ ($s^2_{x \cdot y_2} = 16·36$; X_2 measured in days after 19 May). Thus females whose nests were destroyed late in the season had a longer renesting interval than those whose nests were destroyed earlier. There was no detectable relationship between stage of incubation at nest destruction and renesting interval in this sample.

Discussion

The very high nest success that prevailed in the study area (90·5% in 1972) virtually assured that

1. nests found were the first nests constructed by these females in that year,

Table 2. Renesting interval, stage of incubation at nest destruction, and date of nest destruction for seventeen marked Redhead females at Lake St Francis, 1970 and 1972.

Days incubation when nest destroyed (X_1)*	Date of nest destruction (X_2)*	Initiation date of second nest	Renesting interval (days) (Y)
0 [9]	24 May	3 June	10
0 [10]	27 May	12 June	16
0 [11]	28 May	6 June	9
0 [10]	31 May	12 June	12
0 [8]	6 June	27 June	21
1	5 June	28 June	23
3	30 May	27 May	7
4	26 May	4 June‡	9‡
5	26 May	7 June	12
6	22 May	1 June	10
6	2 June	11 June	9
8	25 May	6 June	12
9	4 June	19 June‡	15‡
9	4 June	16 June	12
13	20 May	2 June	13
20§	14 June§	27 June§	13§
24§	11 June§	3 July‡·§	22‡·§

Mean renesting interval = 13·2

* The number of eggs laid when clutches were removed are shown in parentheses.
† Coded for analysis as number of days after 19 May.
‡ Estimated from observation of marked hen with newly-hatched brood.
§ 1970.

2. experimental females that did attempt to renest were successful (nest success of the 14 renests by experimental females in 1972 was 100%) and
3. renests and broods that were identified were the product of the first renesting attempt by experimental females.

At least 86% of experimentally-removed clutches (all removed before 7 June) were replaced. Although this is the highest renesting proportion yet recorded for ducks, it is not significantly different from that observed by Gates (1962) for Gadwalls in Iowa (73%; $X^2 = 2{\cdot}01$, $P > 0{\cdot}10$) or by Hunt & Anderson (1966) for the Ring-necked Duck in California (80%; X^2 =$ùú, ≪ > 0·05). Coulter & Miller (1968) summarize estimates of renesting proportions from other North American studies.

The fact that most (ca. 82%) of the experimental Redhead females had previous nesting experience undoubtedly influenced their renesting. That the greater reproductive commitment of older birds (Williams 1966; Cody 1971) is expressed in higher renesting proportions was suggested by Gates (1962) for Gadwall and Grice and Rogers (1965) for Wood Ducks *Aix sponsa*, and demonstrated by Strohmeyer (1967) for Blue-winged Teal and by Coulter & Miller (1968) for Black Ducks and Mallard.

There was an apparently marked difference in the tendency to renest (and in other aspects of reproduction) between the isolated Lake St Francis population and Redheads studied in parts of their normal breeding grounds (Alliston 1979). A possible prevalence of 'semiparasitic' females in western populations (Weller 1959) and the known prevalence of non-parasitic females in the Lake St Francis population may account for much of the apparent difference in tendency to renest. Semiparasitic Redheads parasitize the nests of other ducks early in the season and later construct their own nests (Weller 1959). They may nest several weeks later than non-parasitic females and this later-nesting may in part be associated with their observed 'lack of broodiness' (Weller 1959; Lokemoen 1966; Hines 1977) epitomized by high rates of nest desertion, little or no tendency to renest, and desertion of broods early in the brood-rearing interval.

Redhead females lacking previous nesting experience nested, on the average, 2·5 weeks later than experienced (non-parasitic) birds. A prevalence of inexperienced females in western populations could further contribute to these apparent differences in reproductive behaviour.

Redheads, like other duck species so far studied (Strohmeyer 1967; Coulter & Miller 1968), renested close (an average of 0·36 km) to their original nest sites. The tendency for renests to be closer to open water was part of an apparent trend witnessed in later nests and may be associated with vegetation growth.

The normally marked trend toward smaller clutch size in renests (see summary in Coulter & Miller 1968) was not evident in the present study (Table 1). Coulter & Miller's (1968) observations of the Black Duck, and Hunt & Anderson's (1966) observations of the Ring-necked Duck, also showed little reduction in clutch size. My rather meagre data tend to support Coulter & Miller's hypothesis that females that have nested in previous years may show, on the average, only a small reduction in clutch size between first nests and renests. However, my renesting experiments were carried out during a year when nesting began late and clutch size in first nests was smaller than in 'normal' years (Alliston 1979).

An increase in renesting interval with later dates of nest destruction has not been reported previously, nor can such a relationship be found in the Black Duck and Mallard, the only other species of ducks for which suitable published data are available (Coulter & Miller 1968). For surface-feeding ducks such a trend would likely be masked during late laying and early incubation by the relationship between renesting interval and the stage at which nest destruction occurred (Sowls 1955; Grice & Rogers 1965)—a relationship that is not apparent for the Redhead (this study) or for Ring-necked Ducks and Lesser Scaup (Hunt & Anderson 1966). The tendency for Redhead renesting intervals to increase with later dates of nest destruction may have been a result of a waning tendency to renest as the season progressed.

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Summary

This study presents the first documented cases of renesting by the Redhead Duck *Aythya americana*. Of 22 females whose nests were experimentally terminated 19 (86·4%) were known to renest. At least 18 (81·8%) of these experimental birds were known to have nested in previous years.

The mean distance between first nests and renests of 15 females averaged 356 m (range 43–1,300 m) and renests tended to be closer to open water (mean = 62 m) than first nests (mean = 92 m). There was no significant difference in completed clutch size between first nests and renests.

The renesting interval for 17 females averaged 13·2 days (range 7 to 23 days). The renesting interval was related to the date of nest destruction, females whose nests were destroyed later in the season having longer renesting intervals. No detectable relationship was found between the stage of the nesting cycle at nest destruction and the renesting interval.

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