DO NORTHERN HARRIERS LAY REPLACEMENT CLUTCHES?

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ABSTRACT - An ecological difference between North American and European populations of *Circus cyaneus* is the apparent lack of replacement clutches laid by the North American form (the Northern Harrier) on the failure of the first clutch. I present several lines of evidence that Northern Harriers do lay replacements, but only if their clutches are disturbed during laying or shortly thereafter. Two of the five females that renested were successful in their attempts and the quality of the new nest sites was higher, despite most renests being within 200 m of the old sites.

In 2 detailed and long term (>20 y) studies of *Circus cyaneus*, one in Orkney, Scotland (where it is called the Hen Harrier), and one in Wisconsin, U.S.A., a major ecological difference is evident. Harriers in Scotland may lay 1 and occasionally 2 replacement clutches following the failure of their original clutch (Balfour 1957), while harriers in Wisconsin have never been recorded as laying a replacement (Hamerstrom 1969, pers. comm. 1981; Schmutz and Schmutz 1975). Since Simmons and P.E. Barnard (MS) found few behavioural differences in a comparison of the 2 continents' populations, other than migratory habits, then this apparent difference warrants attention and explanation.

Here, I present evidence that harriers in a large Canadian population laid replacement clutches in all 3 y in which they were studied, and that renesting females picked higher quality sites for their second attempts.

STUDY SITE AND METHODS

One of North America's largest assemblages of breeding harriers was studied on the 60 km² Tantramar Marsh (45°53'N, 64°20'W), New Brunswick. The objectives were to document breeding and feeding ecology of the population in relation to polygyny. In so doing, the location of each nest was mapped and its history detailed; the date of settling, habitat type, courtship displays, clutch size, and male and female activity (see Simmons 1983 for details). About 2500 h of observation were made, of which 562 h were specific nest watches to record feeding rates.

As no birds were marked, the evidence presented here consists of the followng categories: (a) recognition of plumage characteristics and voice; (b) identical reaction to human disturbance at both nests, which varied significantly among females; (c) short relaying period; (d) lack of "sky dancing" (Hamerstrom 1969) from any male involved following nest predation; (e) close proximity of nest and renest; and (f) alarm-calling at the nest up to 2 d after nest failure.

To determine nest site quality, I recorded dominant vegetation, moisture level, and visibility at each of 64 nests found. Moisture was ranked as Dry if no water existed within 1 m of the nest, Wet if water appeared due to my weight, and Very Wet if water was already present at the site. Vegetation was ranked as cattail (*Typha* spp.), marsh grasses (*Spartina pectinata* or *Calamagrostis canadensis*), Spirea (*Spirea latifolia* and other low shrubs), and alder (*Alnus* spp. and willow *Salix* spp.). Visibility, which was later found to have no effect on the success or failure of each nest (Simmons and Smith 1985), is disregarded here since it does not affect quality. Quality reflects the probability of success, and the quality score for each nest site is a combination of the percentage success of moisture and vegetation categories arcsine transformed, and summed (see Simmons and Smith 1985).

RESULTS AND DISCUSSION

Suspected renesting occurred twice among 30 nests in 1980, and in 3 of 22 nests in 1981. The original nest of a suspected renest in 1982 was not found, and details of 2 renests in 1983 (R.B. MacWhirter and G.L. Hansen *in litt.*) were not taken, and are not discussed further here.

In the first case in 1980, a yellow-eyed female distinguished by a very dark terminal tail band had just completed a clutch of 5 eggs (determined by egg colour: Sealy 1967; Hamerstrom 1969, pers. obs.) in Cattails. She reacted to me by flying 300-400 m east and circled at low altitude while alarm calling. On my next visit, a bird already 300-400 m east of me started cackling. Later, the same bird flew to the new nest and was recognized by her eye and rectrix colour. The fact that she alarm-called near her new nest on my first visit would have been unusual for any other harrier with no prior experience of my activities. In my experience at 59 other first nests, a female never called until I was closer than approximately 80 m on my first visit.

The second nest-renest evidence in 1980 ("Alders": Table 1) consisted of (a) close circling and calling but no stooping by the female, (b) a 7-d relaying interval, (c) a lack of sky dancing by her polygynous mate who otherwise performed a greater number of displays than any other male (Simmons 1983), and (d) a renest only 160 m from the original site. She was 1 of 2 polygynous females (Table 1) who relaid with the same male (polygynous males were identified by watching them feed one, then another female in succession).

In 1981, in an effort to gain accurate data on egg laying and incubation periods, I disturbed several females with 0- or 1-egg clutches. Five of 6 females

Nest	Renesting Factors*						
	I	II	III	IV	Va	VIp	VII
Midgic 1	8	320	9 May 1980	Just completed clutch	5	144	
Renest			27 May 1980		5	140	S
Alders y	7	160	18 May 1980	Egg-laying	4	117	
Renest			31 May 1980		4	114	$\mathbf{F}^{\mathbf{C}}$
Midgic 2	11	100	14 May 1981	First egg	1	92	
Renest			25 May 1981	00	2	133	S
Alders β	4	120	14 May 1981	First Egg	1	92	
Renest			18 May 1981	00	5	118	$\mathbf{F}^{\mathbf{d}}$
Phoebe	7	200	1 June 1981	First egg	1	140	
Renest			8 June 1981	00	4	140	$\mathbf{F}^{\mathbf{e}}$

Table 1. Factors associated with 5 renests located on the Tantramar Marsh of New Brunswick, 1980-1981.

*— I = days between failure and relaying; II = proximity of nests (m); III = clutch initiation dates; IV = stage at failure; V = clutch size; VI = quality score of nest site; VII = outcome of renest attempt: S = successful, F = failed.

^aAll renest clutches were full clutches and hatched.

^bBased on moisture and vegetation at the nest site (see text); range of scores 92-144.

^CDiseased chicks

^dObserver induced

e_{Predation}

deserted, and 2 of 5 relaid. A third female, whose 1-egg clutch was taken by a lone Common Raven (Corvus corax), also relaid. In each case, a renest was established using 2 or more of the categories outlined in METHODS. One β female continued to defend her destroyed renest for 2 d following its destruction. This is in contrast to evidence presented by Hamerstrom (1969) for Wisconsin harriers which left the area within 24 h of nest loss, and indicates the potential for a female to remain and renest on the Tantramar Marsh.

Three characteristics common to all 5 renesters emerge from their histories: (1) all failed while in the process of egg-laying or shortly thereafter; (2) the distance between the nests was, in 4 of 5 cases, closer than the minimum distance recorded between concurrently occupied nests (260 m); and (3) the period between failure and relaying was short, averaging 7.4 (\pm 3) d. Morrison and Walton (1980), in their review of replacement clutches in raptors, reported that the frequency of relaying was greater among birds whose clutches were disturbed early in the breeding attempt, and that renesting generally took place within "several hundred metres". These facts concur with (1) and (2) in this study. The significance of the short relaying period (3) can be seen in light of the fact that on the Tantramar Marsh, females settling into new territories (i.e. courting and preparing to lay eggs) required at least 1 wk and usually longer (Simmons 1983) to put on sufficient fat/protein reserves (cf. Newton et al. 1983, Hirons et al. 1984) before laying their first egg. Since the *average* relaying interval was only 1 wk for renesters, this implies that a female part way through laying finds it easier to begin a new clutch, having not fully depleted her protein reserves, than a female starting afresh. This may explain the short relaying interval (Table 1). It is also significant in this regard that the female with the longest relaying interval (Midgic 2) also produced the smallest repeat clutch (Table 1), and was fed very little by her monogamous mate (Simmons 1983).

A related but paradoxical fact arises from a comparison of relaying intervals reported for other

small falconiforms (12-18 d : Morrison and Walton 1980) and those found in this study (7.4 d). This difference may be related to the fact that many of the falcons and accipiters cited (*ibid.*) were deliberately double-clutched and therefore "failed" after producing a full clutch, while the harriers failed earlier in their attempts. The relaying intervals (Table 1) concur with those found by Balfour (1957) who stated that replacements were often completed within a fortnight by Hen Harriers in Orkney. The frequency of renesting (8 nests in 96: 8% [Simmons 1983, 1983a; G.L. Hansen and R.B. MacWhirter *in litt.*]) over 4 y on the Tantramar Marsh is also similar to that found in Orkney (N. Picozzi, pers. comm.).

Newton (1979:136) argued that the proportion of relaying raptors in a population is determined by food supply; evidence from this study does not support this hypothesis. Microtines and shrews (Sorex spp.), principal prey of the harriers on the Tantramar Marsh (Barnard 1983), were sampled each year (*ibid*. and G.L. Hansen *in litt*.) and related to the proportion of renesters. Spring vole abundance could be ranked from highs in 1980 and 1983 to lows in 1981 and 1982, yet renests accounted for 6.3%, 6.6%, 13.6% and 8.3% of all nests in these years respectively. Several factors (other than my research activities) therefore must have been operating over and above food abundance to produce these results.

Further evidence which does not support the food-related hypothesis comes from a survey of other records of renesting among Northern Harriers. Riendahl (1941) reported 1 nest among 5; Craighead and Craighead (1956) reported 1 renest among 9 in a year of low vole abundance, but none in a "high" year; Smith (1971) recorded 1 among 5 nests, and Duebbert and Lokemoen (1977) reported 1 among 3 nests. If low numbers of nests were indicative of a low vole population (cf. Hamerstrom 1979; Simmons et al. in prep.) in these studies, then none of them support the food-related renesting hypothesis (Newton 1979).

If nests are destroyed by predators, it is surprising that the harriers studied generally renested within 200 m of their original sites; their mates often held territories up to 1 km in diameter (Simmons 1983), and suitable nesting substrate appeared to be relatively unlimited. This unusual situation was investigated through an estimation of the quality of the nest and renest in terms of anti-predator adaptations. This was based on the knowledge that Very Wet cattail sites were significantly more successful than most other combinations (Simmons and Smith 1985). The results indicate that harriers could afford to locate their renests close to their original nests, since on average they chose better quality sites. Four of the 5 renests stayed in high quality sites or increased in quality, while overall the quality scores increased by an average of 12 points; this was not significant, however (Wilcoxson test, U = 10, P = 0.3). Even so, all 5 renesters hatched eggs; 2 raised flying young and only 1 renest failed again due to predation.

I conclude that North American harriers do lay replacement clutches if their original clutch fails early in the attempt, at about the same frequency as their European conspecifics. As the Northern Harrier is behaviourally very similar to the Hen Harrier, the fact that they both lay replacement clutches adds to the contention that they are also ecologically very similar.

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