RENESTING ECOLOGY OF NORTHERN PINTAILS ON THE YUKON-KUSKOKWIM DELTA, ALASKA¹

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Abstract. We used radio telemetry to study renesting by wild, free-ranging Northern Pintails (Anas acuta) on the coastal Yukon-Kuskokwim Delta in 1994 and 1995. Fifty-six percent of females (n = 39) renested at least once. Propensity to renest declined among females that initiated later first nests. Renesting interval was not related to female weight, year, or initiation date of first nests. Mean interval between first and second nests was 11.4 \pm 1.0 days, and mean interval between second and third nests was 11.3 \pm 1.5 days. Median distance observed between first and second nest attempts was 276 m (range 33-6,098 m). Clutch size declined 2.3 \pm 0.4 eggs between first and second nests. Weight of females captured on first nests in early incubation declined with nest initiation date. Our results suggest that food availability does not limit renesting ability of pintails in coastal tundra.

Key words: Northern Pintail; Anas acuta; Alaska; initiation date; renesting; subarctic; clutch size; nutrient reserves.

INTRODUCTION

Renesting, laying a replacement clutch following the loss of a previous clutch, is an important reproductive strategy that allows ducks of many species to increase the probability of reproductive success within years (Sowls 1955, Hunt and Anderson 1966, Cowardin and Johnson 1979). However, not all females renest following the loss of a clutch. Renesting propensity is the likelihood that a female will renest, and renesting interval is the time between the loss of a nest and initiation of a renest. Propensity to renest and renesting interval are related to stage of incubation at time of nest loss, habitat conditions, and food availability (Sowls 1955, Gates 1962, Krapu et al. 1983). Cowardin and Johnson (1979) developed a simple theoretical model to predict hen success, the proportion of females that nest successfully at least once during a breeding season, from nest success, the proportion of nests that hatch. Their model assumes that nest success and renesting propensity are inversely proportional and that renesting propensity declines with successive nest attempts. Our goal in this study was to examine factors influencing renesting ability independent of nest success and nest stage of wild Northern Pintails (hereafter pintails) on the Yukon Delta National Wildlife Refuge in western Alaska. Our objectives were to measure renesting propensity, renesting interval, distance between successive nest sites, and changes in nutritional investment among nest attempts.

STUDY AREA AND METHODS

The study area and nest search methods were described by Flint and Grand (1996a). We defined nest initiation date as the day the first egg was laid. We candled eggs in each nest to determine stage of incubation at time of discovery (Weller 1956). Nest initiation dates were estimated from the stage of incubation and the number of eggs, assuming that one egg was laid per day (Sowls 1955).

We captured pintail hens on nests on the fourth (± 1) day of incubation to ensure that females had completed laying, and to reduce the likelihood of nest abandonment. In order to sample only females incubating first nests, we only marked hens that initiated nests before 1 June in 1994 and 6 June in 1995. Previous investigations indicated that in years with similar phenology nearly all nests initiated in May and early June were first nests (Esler and Grand 1994). We marked hens using numbered aluminum leg bands, yellow plastic leg bands, and radio transmitters weighing approximately 10 g. Transmitters were attached using the method described by Pietz et al. (1995). We weighed each hen and removed all eggs from the nest before releasing the hen at the nest site.

On foot or using aircraft, we located radiomarked hens every 1–10 days beginning 10 days after egg removal or nest destruction. On foot,

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FIGURE 1. Initiation date of first nest and probability of renesting by Northern Pintails on the Yukon-Kuskokwim Delta, Alaska 1994–1995.

we flushed each female at close range to determine nesting status. When we located the nest of a marked hen, we did not visit it again until the anticipated 4th-day of incubation. In 1994, if the renest was still active at 4 days of incubation we removed the eggs. We estimated the distance between successive nest attempts using locations plotted and digitized from 1:15,000 color infra-red aerial photographs.

We defined renesting interval as the number of days between the date of egg removal and the date the first egg was laid in a subsequent nest. Some second nests were destroyed by predators before the fourth day of incubation, so we used the midpoint of the interval between nest discovery and the projected fourth day of incubation as the start of the renesting interval assuming a mean clutch size of six eggs. We calculated the mean (\pm SE) clutch sizes and interval between attempts for second and third nests separately. We investigated the relationship between renesting interval among first and second nests, weight at capture, nest initiation date of first nests, and year using analysis of covariance (Steel and Torrie 1980, SAS Institute 1990). We examined two models. Renesting interval and weight at capture were the dependent variables and year, nest initiation date, and their interaction were the independent variables. We did not examine this relationship for third nest attempts because of low sample size (n = 3). We examined interactions between all factors and covariates, and interactions with low (P > 0.05) type III sums



FIGURE 2. Relationship between weight during early incubation and initiation date of first nests for female Northern Pintails on the Yukon-Kuskokwim Delta, Alaska 1994–1995.

of squares were dropped from the models. We determined the relationship among female weight at capture, nest initiation date, and year using linear regression. We used stepwise logistic regression to examine the influence of first nest initiation dates, weight at capture, and year on the probability of renesting (SAS Institute 1990). Variables were added to the model if they provided significant ($P \le 0.05$) improvement to log-likelihood scores.

RESULTS

We marked 51 females, 23 in 1994 and 28 in 1995. Of these, 12 females (6 each year) either moved off the study area and could not be observed or were outfitted with transmitters that failed. Twenty-two females renested at least once (56 ± 8%; n = 10 in 1994 and n = 12 in 1995) and 3 renested twice on the study area. Only nest initiation date explained sufficient variation in renesting propensity to be used in the model predicting probability of renesting ($\chi^2_1 = 4.3$, P = 0.04; Fig. 1).

The analysis of covariance of weights of females at capture indicated that initiation date of the first nest and year were important explanatory variables ($F_{2,47} = 14.7$, P < 0.001). Weight of females at capture was related to initiation date of the first nest ($F_{1,47} = 15.9$, P < 0.001) and year ($F_{1,47} = 12.0$, P < 0.001; Fig. 2), but there was no difference in the relationship between weight and initiation dates between years ($F_{1,47} = 0.01$, P = 0.9). Mean renesting interval



FIGURE 3. Interval between first and second nest attempts of Northern Pintails on the Yukon-Kusko-kwim Delta, Alaska 1994–1995.

between first and second nests was 11.4 ± 1.0 days (n = 22; range 7-26 days; Fig. 3). Mean interval between second and third nests was 11.3 \pm 1.5 days (n = 3). The interval between first and second nests was not related to female age or weight, year, or initiation date of first nests $(F_{3,18} = 2.0, P = 0.16)$. The median distance between renests and preceding nest sites was 276 m (range 33-6,098 m; n = 22; Fig. 4). Mean clutch sizes for first and second nests were 8.2 \pm 0.2 eggs (n = 51) and 6.3 \pm 0.2 eggs (n = 15). Within females, clutch sizes declined 2.3 ± 0.4 eggs between first and second nests (n = 15). Weights of females during early incubation were not correlated with clutch size of second nests. $(F_{1,14} = 0.04, P = 0.85).$

DISCUSSION

Renesting interval increases and propensity to renest declines with increasing nest age at the time of destruction for several species of dabbling and diving ducks (*Anatini* and *Aythyini*; Sowls 1955, Gates 1962, Krapu et al. 1983, Doty et al. 1984). We controlled for the effect of nest stage at destruction, so we could examine the influence of year, female condition and nesting date on renesting propensity and interval. Because all first nests 'failed' early in incubation, our estimates of renesting propensity likely are higher and our estimates of renesting interval likely are shorter than would be found for wild pintails with a range of nest destruction times.

We found no difference in renesting interval due to female age, weight, year, or initiation date of first nests. However, our sample size was small (n = 22). Our mean renesting interval of 11.4



FIGURE 4. Distance between first and second nests of Northern Pintails on the Yukon-Kuskokwim Delta, Alaska 1994–1995.

days was similar to that previously reported by Duncan (1987) for captive reared pintails ($\bar{x} =$ 9.6 \pm 0.6 days; n = 25). The period of rapid ovarian follicle growth (RFG) occurs just prior to ovulation when the daily nutritional demands of egg production increase quickly (Alisauskas and Ankney 1992). Several females began RFG within 2 days of nest destruction given our minimum renesting interval of 7 days, Esler's (1994) estimate of 4.25 days for RFG in pintails, and approximately 24 hours for the secretion of albumen, membranes, and shell (Sturkie 1965). We may have overestimated the mean renesting interval if we missed some nesting attempts and classified some third nesting attempts as second nests. Thus, the three long intervals we observed (>15 days; Fig. 1) may represent more than one renesting attempt. Regardless of this potential bias our estimate is less than the mean 19.8 days Duncan (1987) reported for color-marked females. Swanson et al. (1986) found shorter renesting intervals and larger clutch sizes early in the nesting season when food availability for captive Mallards (Anas platyrhynchos) was higher. The short renesting interval we measured suggests that foraging conditions were not limiting for renesting pintails on our study area.

Duncan (1987) found that, among wild freeranging pintails in southern Alberta, only 5 of 127 (4%) color-marked and 0 of 17 radio-marked hens renested. In that study, nests were destroyed at various stages of incubation, and detection and emigration rates of color-marked hens were unknown. Additionally, recent studies (Pietz et al. 1993, Rotella et al. 1993, Ward and Flint 1995) indicate that backpack transmitters have deleterious effects on nesting propensity of waterfowl. Sowls (1955) considered pintails the most persistent renester among dabbling ducks in southern Manitoba, where at least 19 of 62 (31%) marked hens renested. He also did not estimate the detection or emigration rates of color-marked females.

Our estimate that 56% of females renested is similar to Duncan's (1987) finding that 50% of captive female pintails renested, but we believe our estimate is low. Pintail hens frequently were away from the nest early in the laying cycle and nest success was low during this study (Flint and Grand 1996a). Also, none of the renests were detected until at least four eggs had been laid. Consequently, predators may have destroyed some nests during laying or early incubation before we found them. Additionally, we were unable to monitor hens that left the study area or those with failed transmitters. One hen with a failed transmitter was observed renesting, and some hens (n = 3) moved over 5 km to renest. We assumed that transmitters failed at random and distances moved were unrelated to renesting.

Renesting propensity declined among birds that initiated first nests later. Krapu et al. (1983) found that Mallards renested less frequently when wetlands and associated foods for nesting hens were less abundant. Thus, our high estimate of renesting propensity implies that, at least early in the renesting period, foraging conditions were not limiting for renesters on our study area. Early nesting pintails had greater productivity as a result of larger clutches, greater nest success, more time to renest, and better duckling survival (Esler and Grand 1994, Flint and Grand 1996a, Grand and Flint 1996).

We found that weights of pintail hens captured in early incubation of their first clutch declined at later nest initiation dates. However, weight at capture was not related to either renesting interval or propensity to renest. Esler and Grand (1994) found that renesting pintails did not rely on stored reserves for egg formation. Furthermore, they found that reserves at the end of laying were small and invariant with respect to nest initiation dates. Therefore, our results suggest that larger females nest earlier.

Distances between first nests and renests in this study were similar to those previously published for pintails. In studies of color-marked females, Duncan (1987) found that hens move approxi-

mately 300 m between nest attempts (range 100-750 m), and Sowls (1955) found the mean distance of 258 m (range 78-1,372) between nest attempts. We were able to document large movements by three hens because we used radio telemetry. These movements (> 5 km) were much greater than the median and created a highly skewed distribution of movement distances. Sowls' (1955) mean distance probably suffers from the same skewed distribution. The fact that most renests were within several hundred meters of the original site suggests that a large proportion of the nests found on our study area are renests (Flint and Grand 1996a). Therefore, annual differences in nest density may represent differences in early nest success and habitat conditions, as opposed to changes in size of the breeding population.

Clutch size declined in renests, while egg size did not vary between first nests and renests (Flint and Grand 1996b). Thus, there is a decline in nutritional investment in renests. Also, nest success and duckling survival declined for later nesting birds (Flint and Grand 1996b Grand and Flint 1996). Renesting pintails rely upon foods for nutrients required for egg production (Esler and Grand 1994), and Krapu and Swanson (1975) demonstrated that egg production was lower among pintails on deficient diets. Given that reserves were not used by renesting pintails, either ultimate factors such as declining nest success and duckling survival, or foraging conditions, may limit clutch size for renesters.

Calverly and Boag (1977) concluded that arctic nesting pintails had lower reproductive potential than their prairie nesting counterparts due to low nesting effort, smaller clutch size, and lack of renesting. Flint and Grand (1996a) demonstrated that this conclusion was not appropriate with regard to clutch size and nest success for pintails nesting on the subarctic Yukon-Kuskokwim Delta. Our results clearly demonstrate that subarctic nesting pintails commonly renest. Further, with regard to renesting interval and propensity, our results are most similar to those of captive pintails with unrestricted diets, suggesting that Yukon-Kuskokwim Delta nesting pintails are not limited in their renesting ability

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