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NESTING SUCCESS OF NORTHERN PINTAILS ON THE COASTAL YUKON-KUSKOKWIM DELTA, ALASKA[1]

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Abstract. We studied nesting chronology and success of Northern Pintails (*Anas acuta*) on the coastal Yukon-Kuskokwim Delta, Alaska during the summers of 1991–1993. We found a total of 795 nests during three annual searches of a 27.4 km^2 area. Minimum nest density averaged 9.67 nests per km^2. Nesting success varied among years and ranged from 43.12% in 1991 to 10.74% in 1993 (average 23.95%). Most nest loss was the result of predation and tidal flooding. Daily nest survival probability declined with nest initiation date in all three years and also varied with nest age in 1992. Clutch size averaged 7.63 ± 0.067 (SE) eggs per nest and was larger than reported for other populations of Northern Pintails. Clutch size declined during the 44–47 day nesting interval at a greater rate than reported for other populations of Northern Pintails. We conclude that sub-arctic and prairie nesting Northern Pintails have similar reproductive potentials.

Key words: Alaska; clutch size; initiation date; nest predation; nesting success; Northern Pintail; productivity.

INTRODUCTION

Historically, most of the continental population of Northern Pintails (*Anas acuta*) nested in the mixed prairie region including Saskatchewan, Alberta, Manitoba, and North and South Dakota (Bellrose 1980). The continental population of Northern Pintails (hereafter pintails) has been declining for many years (Hestbeck 1995a). However, the number of pintails counted in Alaska has remained relatively stable over the same period, resulting in an increasing proportion of the continental population being counted in Alaska. Within Alaska, the Yukon-Kuskokwim Delta (YKD) represents a major breeding area for pintails and supports approximately 15% of the spring continental population (U.S. Fish and Wildlife Service, Laurel, MD, unpubl. data).

One measure of productivity for pintails is the number of ducklings produced. Productivity can be estimated as the product of the proportion of hens that hatch a clutch (i.e., hen success) and clutch size. Variation in nesting success and clutch size potentially leads to differences in productivity among nesting populations. Egg production (i.e., clutch size) is correlated with levels of stored nutrients (Mann and Sedinger 1993, Esler and Grand 1994). Birds breeding at high latitudes are constrained by short breeding seasons and undergo long migrations that may deplete stored reserves, and thus, may have lower productivity than their temperate breeding conspecifics. Smith (1970) showed a lower percentage of juveniles in the fall harvest during dry years when more pintails were found at higher latitudes. Calverly and Boag (1977) concluded that arctic nesting pintails had lower reproductive potential than their prairie nesting counterparts due to a lower percentage of hens attempting to nest, smaller clutch size, and lack of renesting. Further, Derksen and Eldridge (1980) found little evidence of breeding by pintails on the Alaskan Arctic Coastal Plain.

The YKD represents a major sub-arctic breeding area for pintails and the productivity of this population remains unknown. Our goals in this study were to determine the clutch sizes, initiation dates, and nesting success of pintails nesting on the YKD. We compare our results among years and to those from other populations to assess potential differences in productivity.

STUDY AREA

This study was conducted along the lower Kashunuk River drainage (61°20'N, 165°35'W) on the outer coastal fringe of the Yukon Delta National Wildlife Refuge. The study area is predominantly flat sedge meadows with nearly pure stands of *Carex raminskii* (Tande and Jennings 1986). The study area is highly interspersed by small tidal sloughs and elevations are extremely

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low (Kinchloe and Stehn 1991). Nearly the entire study area floods on periodic storm tides. Most ponds on the study area are small (<10 m across) and shallow (<1 m depth).

METHODS

Nest searches were conducted from mid-May through mid-July 1991–1993. All slough banks and dry grassflats in a 27.4 km^2 area were systematically searched on foot by a single observer or a single observer and a dog. Intensive nest searches started within four days of first nest initiation in 1992 and 1993, and 10 days after first nest initiation in 1991. The entire area was searched a minimum of three times; additionally, new nests were frequently discovered during revisitation of previously located nests. Nest locations were plotted on 1:15,000 aerial photos and marked with a 1 m lathe stake placed 5 m north of the nest to facilitate relocation. The number of eggs, nest location, date, and status (active or destroyed) were recorded. Eggs were individually numbered and candled (Weller 1956) to determine the stage of embryonic development (± 2 days). Active nests were revisited at seven-day intervals until hatch or nest failure. During revisits the number of eggs and stage of development of embryos were recorded. Nest visitation intervals were modified so that each nest was visited just prior to and just after its projected hatch date.

Nest initiation dates were calculated for active nests found during egg laying by subtracting one day for each egg observed in the nest (Bellrose 1980). Nest initiation dates for nests found during incubation were calculated by subtracting the incubation period ($\bar{x} = 24$ days) plus the clutch size from the hatch date for nests that ultimately hatched, and by subtracting the stage of embryo development (number of days of incubation) plus the clutch size from the date the nest was found for nests that ultimately failed. Successful nests were defined as hatching one or more eggs. This difference in methodology for determining initiation date for successful and unsuccessful nests removed potential observer bias in egg candling for successful nests. Nests found destroyed, abandoned, or hatched were only used in estimating nest density. Nests abandoned due to our activity (i.e., hen flushed during laying with <5 eggs, nest abandoned on next visit), were only used to estimate initiation dates and nest density. Clutch size for nests that survived to incubation was defined as the total number of eggs laid into a nest. Nest age was defined as the number of days since the laying of the first egg.

ANALYSIS

Nesting success was determined by calculating a daily survival rate (DSR) of nests (Bart and Robson 1982). This technique uses maximum likelihood procedures to estimate a constant DSR and makes no assumptions about the timing of nest loss during observation intervals. We tested for variation in DSR across years following the methods of Sauer and Williams (1989). We examined variation in DSR within years due to nest age and initiation date using the technique of Klett and Johnson (1982) as modified by Grand (1995). We used the estimated DSR for each year as an initial estimate and then calculated the conditional probability that a nest was destroyed on each day of an observation interval, given that it was destroyed by the end of the interval. Similarly, the exposure of failed nests was partitioned across observation intervals. We then summed the exposure and mortalities for all nests (both successful and unsuccessful) within five-day nest age (AGE) and 10-day initiation date (INIT) groups (Grand 1995). For example, a nest was found at six days of age and visited again at 13 days. Data from this nest were partitioned into two age classes, the five to nine day block and the 10–14 day block for the given initiation date. Using these partitioned estimates, a separate DSR was calculated for each AGE and INIT group as:

$$\mathrm{DSR} = 1 - \frac{\sum \text{mortalities}}{\sum \text{exposure days}}.$$

Variation in DSR by nest AGE, INIT, and the interaction of AGE and INIT was examined using multiple regression with exposure days as a weighting factor (Klett and Johnson 1982, Grand 1995). We corrected for AGE related variation in DSR by calculating the product of survival probabilities for all AGE groups (Johnson 1979, Klett and Johnson 1982, Grand 1995). We corrected for INIT related variation in DSR by taking an average of the probability of nest success within each INIT group weighting by the proportion of nests initiated during each INIT block.

Because number of eggs laid declined with nest initiation date, clutch sizes across years were compared with analysis of covariance (ANCOVA) using year as a factor and initiation date as a covariate. To account for annual variation in phenology among years, nest initiation dates for each year were adjusted to a mean initiation date of zero prior to testing. To compare our clutch size data to other populations we re-analyzed Duncan's (1987) data from Alberta, Petrula's (1994) data from interior Alaska, and unpublished data from North Dakota (J. T. Lokemoen, unpubl. data). To account for geographic differences in nesting chronology, nest initiation dates for each location and year were adjusted to a mean initiation date of zero prior to testing. Adjusted mean clutch size and the slope of the relationship between clutch size and initiation date were compared among locations using ANCOVA, with location as a factor and initiation date as a covariate. The mean clutch size and slope from the YKD were compared to all other locations, when the overall ANCOVA was significant, with t-tests using Bonferroni adjustments for pairwise comparisons (Neter et al. 1985). In our case, we performed three pairwise comparisons. Therefore we used a critical value corresponding to t_{df} ($\alpha/6$) (i.e., $\alpha = 0.00833$).

RESULTS

We located 795 pintail nests during the three years of study. First nests were initiated about 15 May each year and nest initiation continued for about 46 days (Fig. 1, Table 1). Minimum nesting density ranged from 7.19 to 13.43 nests per km^2 (Table 1). Mean clutch size, adjusted for initiation date, averaged 7.63 ± 0.067 (SE) and was not significantly different among years on the YKD ($F = 0.18$, df = 2, 336, $P = 0.83$; Table 1). Clutch size declined with nest initiation date at a rate of 0.0870 eggs per day (Fig. 2). This rate of decline was not different among years on the YKD ($F = 1.59$, df = 2, 334, $P = 0.206$). Clutch size varied with nesting location ($F = 19.94$, df = 4, 963, $P = 0.0001$) and was higher on the YKD than for all other locations ($t > 3.57$, $P < 0.0004$). Additionally the slope of the relationship between clutch size and initiation date varied with location ($F = 6.30$, df = 4, 963, $P = 0.0001$) and declined at a greater rate for pintails nesting on the YKD than for all other locations ($t > 2.46$, $P < 0.00714$).

Daily nest survival probability, assuming constancy, was 0.9668, 0.9522, and 0.9169, for 1991, 1992, and 1993, respectively. This DSR differed across the three years of the study ($\chi^2 = 41.84$, df = 2, $P < 0.0001$); thus, years were not pooled.

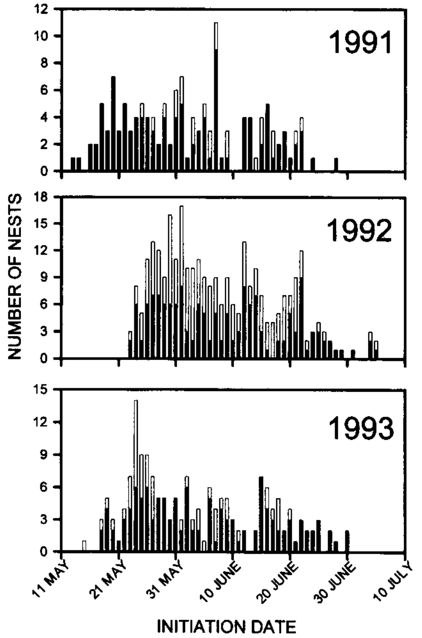

FIGURE 1. Distributions of nest initiation dates for Northern Pintails nesting on the Yukon-Kuskokwim Delta, 1991–1993. Solid bars represent initiation dates back calculated based on egg candling. Open bars represent initiation dates back calculated based on nests found during egg laying, or successful nests for which the hatch date was known.

In 1991, DSR varied by INIT ($F = 10.03$, df = 1, 30, $P = 0.0035$, Fig. 3), but not AGE ($F = 0.57$, df = 1, 30, $P = 0.4562$). Accounting for variation in INIT yields an estimate of nesting success for 1991 of 43.1%. In 1992, DSR varied by both INIT ($F = 13.05$, df = 1, 30, $P = 0.0010$, Fig. 3) and AGE ($F = 5.68$, df = 1, 30, $P = 0.0233$). Accounting for variation in both INIT and AGE yields an estimate of nesting success for 1992 of 18.0%. In 1993, DSR varied by INIT ($F = 39.69$, df = 1, 30, $P = 0.0001$, Fig. 3) but not AGE ($F = 2.91$, df = 1, 30, $P = 0.0973$). Accounting for variation in INIT yields an estimate of nesting success for 1993 of 10.7%. Most nest loss occurred as a result of predation and tidal flooding (Table 2). The proportion of successful nests in which loss of one or more eggs occurred during incubation was 18.9%, 36.6%, and 90.0% for 1991, 1992, and 1993, respectively. Additionally, the number of eggs lost during incubation from successful nests varied among years ($F = 27.11$, df = 2, 202, $P = 0.0001$, Table 1).

TABLE 1. Number of nests, nesting densities, mean clutch size, and initiation dates for Northern Pintails nesting on the Yukon-Kuskokwim Delta, Alaska.

Parameter	Year		
	1991	1992	1993
Number of nests	197	368	230
Minimum nest density[a]	7.19	13.43	8.39
Mean nest initiation	2 June (0.936)[b]	6 June (0.587)	4 June (0.869)
n	138	296	172
Nesting interval[c]	47	44	47
Clutch size	7.65 (0.179)	7.69 (0.130)	7.01 (0.201)
n	87	167	84
Partial clutch loss[d]	0.34 (0.096)	0.95 (0.155)	3.20 (0.572)
n	74	112	18

[a] Number of nests per km^2.
[b] Mean (SE).
[c] Number of days between earliest and latest initiation dates.
[d] Number of eggs lost from successful nests.

DISCUSSION

NESTING SUCCESS

Although success rates vary annually, average nesting success of pintails on the YKD (this study) was higher than in interior Alaska (Petrula 1994) or the prairies (Duncan 1987, Klett et al. 1988). Nesting success in the prairies over an 18-year period averaged 11.5% and never exceeded 19% (Klett et al. 1988). Nesting success in interior Alaska averaged only 3.8% between 1989 and 1991 (Petrula 1994). Our results indicate that during years of poor nesting success, nesting success of pintails breeding on the YKD was similar to their prairie nesting counterparts. In some years, however, YKD nesting pintails were more successful.

While we believe that our estimates of nesting success are unbiased, they may not be representative of the YKD as a whole. Our study site was not randomly selected, but was chosen for its abundance of slough bank and sedge meadow habitats which we knew were preferred nesting habitat. Concurrent measurement of nesting success on a small sample of nests at a study site 10 km east of our location suggests substantially lower success at other locations (C. R. Ely, unpubl. data). Thus, nesting success can vary greatly within geographic areas, indicating that much of the production from an area may come from localized "hot spots." Further work is needed to determine the consistency of productivity at given locations, nesting success at other locations on the YKD, and habitat characteristics that influence nesting success.

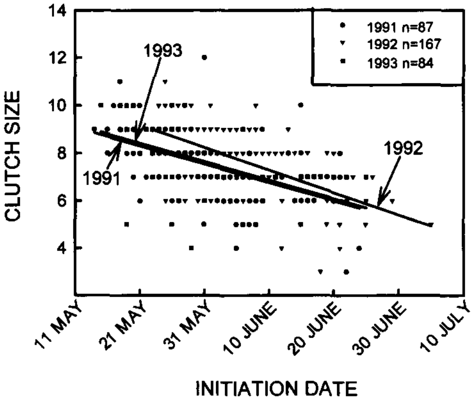

FIGURE 2. Regression of clutch size across nest initiation dates for Northern Pintails nesting on the Yukon-Kuskokwim Delta, 1991–1993.

SOURCES OF VARIATION IN NESTING SUCCESS

Within years. Nesting success varied with initiation date in all three years studied (Fig. 3). In general, nesting success was highest for nests initiated early in the season and declined to near zero at the end of the season. Pintail nests represent approximately 25% of the waterfowl nests on our study area (pers. observ.) and our study area is adjacent to a large Black Brant (*Branta bernicla nigricans*) colony (>5,000 pairs). Nests initiated early in the season are synchronous with other species of waterfowl and may benefit from predator swamping. A majority of other waterfowl species nesting on the study area (e.g., geese and eiders) have nest initiation intervals of less than two weeks. Late-nesting pintails are initiating nests after most other waterfowl nests have

TABLE 2. Fates of Northern Pintails nests on the Yukon-Kuskokwim Delta, 1991–1993.

	Year					
	1991		1992		1993	
Status	*n*	%	*n*	%	*n*	%
Predated	71	36.0	197	53.5	160	69.6
Flooded	30	15.2	4	1.1	21	9.1
Abandoned[a]	8	4.1	36	9.8	15	6.5
Found abandoned[b]	7	3.5	11	3.0	11	4.8
Human caused abandonment[c]	7	3.5	6	1.6	1	0.4
Hatched	74	37.6	112	30.4	20	8.7
Other[d]	0	0.0	2	0.5	2	0.9

[a] Includes nests abandoned after suffering partial predation.
[b] Hen not present when nest was found, no activity at nest after detection.
[c] Hen flushed during laying (<5 eggs), nest abandoned by next visit.
[d] Final nest fate unknown because nest could not be relocated.

hatched. Thus, the decline in nesting success with initiation date may have been a result of increased predation pressure due to declining alternative prey (i.e., other waterfowl nests).

Among years. The cause of the decline in nesting success from 1991 to 1993 was most likely a result of increased predation rates in 1992 and 1993 (Table 2). While classification of the cause of nest failure was difficult and may be biased, consistent methods across years should yield an adequate index of cause-specific nesting failure. We frequently could not determine the species of predator responsible for nest destruction; however, arctic foxes (*Alopex lagopus*), Glaucous Gulls (*Larus hyperboreus*), and Mew Gulls (*Larus canus*) were known to destroy nests. In cases where the nest predator was known, we observed that fox predation typically resulted in total clutch destruction, whereas gull predation more frequently resulted in partial clutch loss. Many nests that ultimately failed were known to have suffered partial predation prior to destruction and we believe this is typical of gull predation. Both the proportion of successful nests suffering partial clutch loss and the average number of eggs lost from successful nests increased from 1991 to 1993, and we interpret this as indicative of increased gull predation during the study. Thus, we believe that the decline in nesting success across years was a result of increased predation by gulls. We have no data on gull numbers and do not know if this apparent increase in predation was a result of a functional or numerical change in gull populations.

Variation in the proportion of nests lost to flooding across years was likely caused by differences in the relative timing of flooding. Peak high tides occur approximately every 14 days. The occurrence of a near-peak high tide combined with low barometric pressure and onshore winds flooded most of the study area at least once each season. However, the proportion of nests lost due to tidal flooding varied depending on the time of flooding relative to nesting chronology. In 1992, a flood event occurred just after the main peak in hatching and losses to flooding were low. Conversely, flood events in 1991 and 1993 occurred during the peak of hatching and destroyed a much higher proportion of nests. The influence of flood tides rarely exceeds 15 km inland (Adams 1952 as cited in Hansen 1961); thus, flooding may be a major cause of nest destruction in some years along the coastal fringe of the YKD where a majority of pintails nest. In all years nests flooded early in incubation were observed to hatch, suggesting that pintail eggs are highly resistant to extreme, short-term cooling.

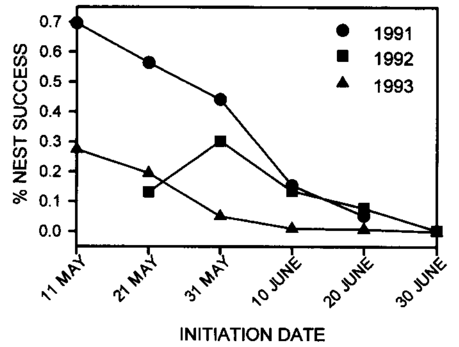

FIGURE 3. Relationship between nest initiation date and nesting success for Northern Pintails nesting on the Yukon-Kuskokwim Delta, 1991–1993.

CLUTCH SIZE

The average clutch size measured on the coastal YKD was larger than for pintails nesting in both interior Alaska and the prairie regions. Recent studies indicate that egg production in pintails is limited by the amount of endogenous reserves (Mann and Sedinger 1993, Esler and Grand 1994). The larger clutch size laid by YKD nesting pintails implies that they initiate laying with larger stored reserves. Pintails use stored lipid reserves during spring migration (Mann and Sedinger 1993) and the migrational costs for birds breeding in Alaska must be greater than for birds breeding in the prairies. Therefore, the larger clutch size found on the YKD suggests that pintails are able to more than compensate for the additional costs of migration to high latitudes.

The rate of decline in clutch size with initiation date that we measured is greater than that reported for any other nesting population of pintails. As a check, we compared our slope to that determined from a sample of laying hens collected on the YKD in 1990–1991 where clutch size and initiation date could be determined without error. This slope was -0.1065 ± 0.0381 (SE) eggs per day and was not different from that measured in our sample of nests (D. Esler, unpubl. data). The reason for the more rapid decline in clutch size with initiation date on the YKD is not known. The relatively short breeding season at high latitudes could result in a steeper decline in clutch size by laying date. However, the nesting interval that we measured (Table 1) is greater than the 38-day interval reported by Petrula (1994) for interior Alaska. Without knowing the cause of the seasonal decline in clutch size for pintails it is difficult to speculate on why different populations have different slopes; however, comparisons across populations may serve as a method of testing hypotheses regarding the seasonal decline in clutch size (Rohwer 1992).

PRODUCTIVITY

Calverly and Boag (1977) suggested that arctic nesting pintails have lower reproductive potential than prairie nesting pintails. Our results indicate that this reduction in productivity may not hold for sub-arctic nesting pintails on the YKD for the following reasons: (1) Nesting success on the YKD was, on average, greater than in the prairies. (2) Clutch sizes of pintails nesting on the YKD were larger than those reported from the prairies. (3) Nearly all (97%) hen pintails collected in areas adjacent to our study site showed evidence of having attempted reproduction (D. Esler and J. B. Grand, unpubl. data). (4) Renesting is common in Alaska as evidenced by the proportion of collected hens showing evidence of renesting (31%) (Esler and Grand 1994).

The duration of nesting on the YKD was several weeks shorter than found in the prairies (Duncan 1987), which must limit the opportunities for hens to renest. We estimated hen success from nesting success using the equation given by Cowardin and Johnson (1979). We used nesting success estimates of 0.2395 for the YKD (this study) and 0.115 for the prairies (weighted average of the estimates from Klett et al. 1988) and assumed all hens attempted at least one nest on both the YKD and the prairies. We allowed prairie nesting birds to renest >5 times, but restricted YKD birds to 2 nesting attempts. The estimates of hen success were 25.2% for the prairie region, as opposed to 37.8% for the YKD. Thus, the higher nesting success that we measured on the YKD may result in greater productivity on a per hen basis than in the prairies, even after accounting for the shorter breeding season on the YKD. Our data support Hestbeck's (1995b) conclusion that, in recent years, productivity of pintails breeding at high latitudes is equal to pintails breeding in the prairies. We conclude that pintails nesting on the YKD are at least as productive as their prairie nesting counterparts.

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