

# EVENING FLIGHTS OF FEMALE NORTHERN PINTAILS FROM A MAJOR ROOST SITE<sup>1</sup>

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**Abstract.** We monitored evening flights of female Northern Pintails (*Anas acuta*) from Lacassine National Wildlife Refuge (NWR) in southwestern Louisiana during winters of 1991-1992 and 1992-1993. We analyzed the influence of female age, winter, and date within wintering period on three flight parameters: distance, duration, and departure time. Flight distance and duration increased with date within wintering period, and age differences in flight distance and duration were not consistent between winters. Females departed 12 min later, on average, on clear, moonlit evenings than on overcast, moonless evenings, and 4 min later when winds were light rather than heavy. After controlling for variation due to environmental conditions, immature females departed Lacassine NWR 1.3 min earlier, on average, than did adults. Flight parameters of females did not differ between hunting and non-hunting time periods. Estimated daily transit costs ranged from 27-54% of basal metabolic rate, 7-19% of daily energy expenditure, and 8-20% of daily dietary intake of rice (*Oryza sativa*). Our findings that flight distance and duration increased with date within wintering period were consistent with predictions of refuging theory, but alternative hypotheses also could explain these results. Evening flights of Northern Pintails roosting on Lacassine NWR were greater in distance and duration than those reported for most other species of wintering waterfowl. We recommend that proximity of refuges to feeding sites be considered in conservation and management plans for wintering Northern Pintails and other refuging waterfowl.

**Key words:** *Anas acuta*; Northern Pintail; evening flights; flight energetics; refuging theory; Lacassine National Wildlife Refuge; Louisiana.

## INTRODUCTION

Many waterfowl species concentrate on refuges in winter, particularly during hunting seasons (Chabreck et al. 1989, Baldassarre and Bolen 1994). Refuging theory predicts that individuals concentrated within a central place will increase distance traveled over time as easily accessed food resources near the central place are depleted (Hamilton and Watt 1970). Flight is energetically expensive for birds, with costs estimated as high as 15 times basal metabolic rate (BMR; King 1974, Prince 1979). Consequently, individuals roosting on refuges which provide limited feeding opportunities must weigh benefits of roosting

on refuges (e.g., increased survival) against foraging flight costs.

Northern Pintails (*Anas acuta*, hereafter pintails) roost diurnally on Lacassine National Wildlife Refuge (NWR) in southwestern Louisiana during winter, with peak numbers reaching 285,000 birds (Yakupzack 1988). Seventy-five percent of waterfowl use on Lacassine NWR occurs between 1 November and 31 January, with largest numbers found during hunting seasons (Tamisier 1976, Yakupzack 1988). Pintails spend little time feeding on the refuge, but rather spend over 8 hr sleeping during daytime hours (Tamisier 1976). Most pintails depart Lacassine NWR after sunset, apparently to forage nocturnally in rice (*Oryza sativa*) fields to the north (Tamisier 1976, Yakupzack 1988).

We used radio-telemetry to investigate three parameters of evening flights of female pintails using Lacassine NWR as a daytime refuge: flight

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distance, flight duration, and departure time. We examined variation in flight parameters attributable to winter (1991–1992 or 1992–1993), female age, and date within wintering period. We further tested for variation in flight parameters in relation to hunting versus non-hunting seasons, and variation in departure time in relation to environmental conditions. Finally, we examined whether temporal variations in flight distance and duration were consistent with predictions of refueling theory.

## STUDY AREA AND METHODS

Our study site included an area extending 80 km from the perimeter of Lacassine Pool (29°58'N, 92°54'W), a permanently flooded 6,793 ha freshwater impoundment located on Lacassine NWR (U. S. Fish and Wildlife Service [USFWS] 1977, Yakupzack 1988). The refuge is located in a transition zone marked by extensive marsh to the south and agricultural lands to the north (Tamsisier 1976, Chabreck et al. 1989). The area was described in detail by Rootes (1989).

We captured pintails from 30 September–27 October 1991 and from 4–25 October 1992 by rocket-netting over bait (Cox and Afton 1994). We aged females as immature or adult using cloacal and tail- and wing-feather characteristics (Hochbaum 1942, Carney 1964, Duncan 1985). We attached 21-g backpack-type radio transmitters (Dwyer 1972; Advanced Telemetry Systems, Inc., Isanti, MN) that had expected lives of 150 days and maximum ground-to-ground ranges of 7–9 km using truck-mounted, four-element, null-peak antennas. Our goal was to radio-tag equal numbers of immature and adult females each winter, but we consistently captured and tagged greater numbers of adults. In the final rocket-net shot in 1991–1992, numbers of captured immatures exceeded pre-planned sample sizes, and we randomly selected immatures to tag. In the final rocket-net shot in 1992–1993, we radio-tagged all captured immatures, and randomly selected adults to tag. We radio-tagged 155 females (58 immatures and 97 adults) in 1991–1992, and 152 females (44 immatures and 108 adults) in 1992–1993.

From 20 November 1991 to 9 February 1992 and 30 October 1992 to 22 February 1993, we obtained late afternoon (16:00–17:30 CST) locations of radio-tagged females on Lacassine NWR. We estimated locations by triangulation (Samuel and Fuller 1994) from two 11-m per-

manent towers, each supporting nine-element unidirectional antennas. We selected a maximum of three individuals daily from radio-tagged females located on Lacassine NWR (range of radio-tagged females on Lacassine NWR = 1–80), and continuously monitored selected birds for aerial movements from 0.5 hr before sunset until 1 hr after sunset. We followed females flying to their nocturnal destinations (hereafter direct observations) and then estimated their locations by triangulation using truck-mounted antenna systems. We used Lenth's maximum-likelihood estimator (MLE) to produce point locations in Universal Transverse Mercator system coordinates from all triangulations (White and Garrott 1990). We calculated MLEs on-site using laptop computers and LOCATE II software (Nams 1990). We estimated linear distance moved from origin and destination coordinates. We recorded times of departure and arrival to the nearest minute.

In selecting birds to monitor, we maximized the number of individuals included in the study and temporally segregated successive observations on individuals. We first divided winters into five time periods: (1) pre-hunting season (30 October–20 November 1992), (2) first hunting season (16 November–6 December 1991 and 21 November–5 December 1992), (3) time between split hunting seasons (7–27 December 1991 and 6–25 December 1992), (4) second hunting season (28 December 1991–5 January 1992 and 26 December 1992–9 January 1993), and (5) post-hunting season (6 January–9 February 1992 and 10 January–22 February 1993). We then preferentially selected in order: (1) birds not monitored previously, (2) birds not monitored previously during the present time period, and (3) birds monitored previously during the present time period.

During 1–24 January 1992 and 6 November 1992–9 February 1993, we also indirectly estimated flight distance of radio-tagged females. We did this by scanning for a randomly selected subset of radio-tagged birds ( $n = 30\text{--}80$ ) from permanent towers on Lacassine NWR during late afternoon (16:00–17:30), and then relocating them later that night (19:00–05:00). We used fixed-winged aircraft equipped with a pair of two- or four-element Yagi antennas to assist in locating birds (Gilmer et al. 1981). We estimated nocturnal locations using vehicle-mounted telemetry systems as described above, except for one

individual which we located aerially in an inaccessible area.

For analysis, we assumed that radio-tagged females were independent. We examined this assumption by estimating the frequency at which radio-tagged females flew in the same flock during direct observations. We liberally assumed that females flew in the same flock if they departed and arrived within 5 min of each other at destinations within 1 km. We considered three response variables for analysis: flight distance (km), flight duration (min), and departure time (min after sunset). For flight distance, we analyzed direct and indirect observations separately. We used repeated-measures, mixed-model ANCOVA (PROC MIXED, SAS 1996) with maximum likelihood estimation to assess relationships of response variables to several explanatory variables. We considered winter (1991–1992 or 1992–1993) and age (immature or adult) as fixed effects, and date within wintering period (days since 29 October; hereafter date) as the covariate. We tested all interactions in initial models, including those with date, to assess homogeneity of slopes (SAS 1991). The number of observations per individual varied greatly because of mortality and emigration from the study area (Cox, unpubl. data). Repeated measures also were irregularly spaced in time because the probability of a bird being monitored was conditional upon its survival and presence on Lacassine NWR in late afternoon. Therefore, we used likelihood ratio tests (Wolfinger 1992) from full models to evaluate the matrix structure of repeated measures as either simple (no correlation among repeated measures) or compound symmetry (equal correlation among successive repeated measures; SAS 1996), and maintained the appropriate structure throughout model-fitting. We used stepwise model-fitting procedures with  $-2$  log likelihood tests as criteria for deleting terms from models for each response variable (Wolfinger 1992), beginning with the highest-order interactions.

Tamisier (1976) indicated that departure times of waterfowl from Lacassine NWR may be influenced by environmental effects, primarily illumination and wind conditions. Consequently, we categorized cloud cover on-site each day at 0.5 hr before sunset as: (1) clear (CLR)—no clouds present, (2) partly cloudy to partly sunny (PCLPSN)—1–99% cloud cover, or (3) overcast (OVC)—100% cloud cover. We concurrently classified wind velocity as: (1) light— $\leq 8$  km

hr<sup>-1</sup>, or (2) heavy— $> 8$  km hr<sup>-1</sup>. We classified moon presence or absence from 0.5 hr before sunset until 1 hr after sunset using lunar phase, and rise and set times (Hoffman 1991–1993). We were unable to include environmental variables in the ANCOVA of departure time because of small samples relative to explanatory variables. Thus, we examined the influence of environmental variables on departure time in a separate ANOVA (PROC MIXED, SAS 1996). We were able to treat this analysis as a completely randomized design (Montgomery 1991) because repeated measures of departure times in our original ANCOVA were not correlated ( $P = 0.68$ ). We used variation due to trials (date treated as a class variable rather than a continuous covariate) as the error term for testing environmental effects, and considered variation due to birds as sampling error. We initially included all interactions among environmental variables, and eliminated terms as described above using  $-2$  log likelihood tests (Wolfinger 1992). We then used residuals from this final fitted model to refit our original ANCOVA model. This approach allowed us to test for effects of age, winter, and date after controlling for environmental effects.

To test for possible effects on departure time due to duck hunting, we replaced date with a categorical variable, hunting presence (first and second duck hunting seasons) or absence (pre-hunting season, time between split hunting seasons, and post-hunting season), and refit the model. We hypothesized that if duck hunting was an important factor influencing departure time, departure times should be similar between first and second hunting seasons, and among the three non-hunting seasons, but dissimilar between hunting and non-hunting time periods. We tested for hunting effects on flight distance (direct observations) and duration by replacing date with the categorical variable denoting presence or absence of duck hunting in final fitted models. We compared least-square means of significant ( $P < 0.05$ ) effects from all final models using Fisher's Protected LSD (PDIF option; SAS 1996).

For flight distance and duration, initial analyses indicated that residuals were not normally distributed. We subsequently applied square-root and natural logarithm transformations to flight distance and duration, respectively, to achieve normality. We omitted from analyses birds that failed to take flight ( $n = 9$  direct and  $n = 1$  indirect). On seven occasions, we temporarily lost birds during monitored flights, but later located

TABLE 1. Estimated intercepts (a) and slopes (b) ( $\pm$  SE) from final fitted mixed-model ANCOVAs describing relationships between response variables (Y; flight distance, flight duration, and departure time) and date within wintering period (X) for age and/or winter combinations for female Northern Pintails departing Lacassine NWR.

Response <sup>1</sup>	a <sup>2</sup>	b	P <sup>3</sup>
<b>Flight distance (km<sup>0.5</sup>)</b>			
Direct observations			
Immatures 1991–1992	2.60 $\pm$ 0.32 A	0.011 $\pm$ 0.003	<0.001
Adults 1991–1992	3.64 $\pm$ 0.27 B	0.011 $\pm$ 0.003	<0.001
Immatures 1992–1993	3.62 $\pm$ 0.27 B	0.011 $\pm$ 0.003	<0.001
Adults 1992–1993	3.14 $\pm$ 0.22 AB	0.011 $\pm$ 0.003	<0.001
Indirect observations			
1991–1992	6.78 $\pm$ 1.53 A	–0.036 $\pm$ 0.021	0.09
1992–1993	2.86 $\pm$ 0.21 B	0.022 $\pm$ 0.004	<0.001
<b>Flight duration (ln min)</b>			
Immatures 1991–1992	2.72 $\pm$ 0.20 A	0.004 $\pm$ 0.002	0.049
Adults 1991–1992	3.17 $\pm$ 0.17 B	0.004 $\pm$ 0.002	0.049
Immatures 1992–1993	3.03 $\pm$ 0.16 AB	0.004 $\pm$ 0.002	0.049
Adults 1992–1993	2.80 $\pm$ 0.14 A	0.004 $\pm$ 0.002	0.049
<b>Departure time (min after sunset)<sup>4</sup></b>			
1991–1992	21.98 $\pm$ 1.23	0.004 $\pm$ 0.020	0.83
1992–1993	21.98 $\pm$ 1.23	–0.047 $\pm$ 0.020	0.019

<sup>1</sup> To obtain untransformed predicted values for an age and/or winter group on a particular date, calculate  $a + b(X)$  and either square or antilog the result for flight distance and duration, respectively.

<sup>2</sup> Intercepts within flight parameter and type of observation groups followed by the same letter do not differ ( $P > 0.05$ ) as determined by Fisher's LSD.

<sup>3</sup>  $P$ -value testing slope ( $b = 0$  given  $Y = a + b(X)$ ).

<sup>4</sup> Estimates from mixed-model ANCOVA testing for age, winter, and date effects before controlling for environmental variables (see Methods).

them to obtain flight distance. Pintails departed Lacassine NWR prior to sunset on three of 196 (2%) occasions. We subsequently omitted these observations (20, 11, and 8 minutes before sunset) from analyses of departure time to meet normality assumptions.

We used Aschoff and Pohl's (1970) equation for non-passerines to estimate daily BMR (kcal day<sup>-1</sup>) of adult female pintails ( $\bar{x} \pm$  SE body mass at capture = 765  $\pm$  5.8 g,  $n = 234$ , Cox, unpubl. data), assuming equal lengths of active and rest periods. We estimated energetic cost of flight by multiplying flight duration by 12 times BMR (kcal; King 1974, Robbins 1993). To express flight costs in terms of amount of rice necessary to meet metabolic costs, we used 3.34 kcal g<sup>-1</sup> as an estimate of true metabolizable energy for rice (Reinecke et al. 1989).

## RESULTS

Pintails departed Lacassine NWR between 0.5 hr before sunset and 1 hr after sunset on 196 of 205 (96%) directly monitored trials. Radio-tagged females rarely traveled together in the same flock (1 of 164 [0.6%] possible trials). On 189 occasions, we attempted to locate pintails on Lacassine NWR the day after their evening flights were

monitored, and found that they had returned to Lacassine NWR from nocturnal destinations on 135 (71%) occasions.

### DIRECT OBSERVATIONS OF FLIGHT DISTANCE

We analyzed 198 flights of 108 females. Compound symmetry provided a better fit to these data than did a simple structure (likelihood ratio test from full model,  $P < 0.01$ ), indicating that repeated measurements on birds were correlated. The final fitted model indicated that flight distance increased with date ( $P < 0.001$ ), and that age differences in distance were not consistent between winters (age-by-winter interaction,  $P < 0.005$ ; Table 1). Flight distance increased at an estimated rate of 0.011  $\pm$  0.003 km<sup>0.5</sup> per day during winter ( $n = 198$ ; Table 1). When we replaced date with hunting presence or absence, we found that flight distance did not differ ( $P = 0.58$ ) in relation to duck hunting.

### INDIRECT OBSERVATIONS OF FLIGHT DISTANCE

We analyzed 176 observations of 91 females. Repeated measures of individual females also were correlated in this analysis (likelihood ratio

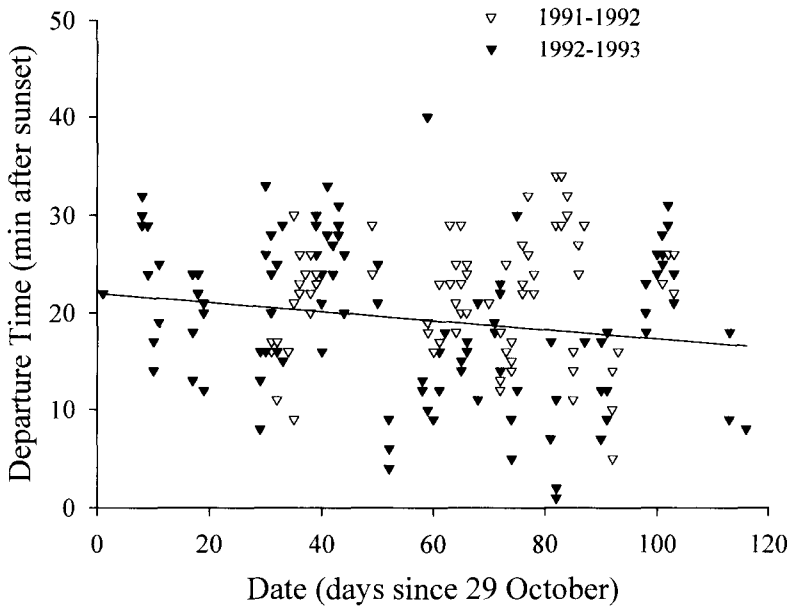


FIGURE 1. Relationship of departure time (min after sunset) of female Northern Pintails roosting on Lacassine National Wildlife Refuge to date within wintering period for each winter. Regression equation (winter 1992-1993 only) is given in Table 1.

test from full model,  $P < 0.01$ ). The final fitted model included only the date-by-winter interaction ( $P < 0.001$ ). Flight distance did not vary with date in 1991-1992 (Table 1), but increased  $0.022 \pm 0.004 \text{ km}^{0.5}$  per day in 1992-1993 ( $n = 176$ ; Table 1).

#### FLIGHT DURATION

We analyzed durations of 191 flights of 106 females. Compound symmetry described the relationship among repeated measurements better than simple structure (likelihood ratio test from full model,  $P < 0.005$ ), indicating that successive observations of individuals were correlated. Our final model indicated that flight duration increased with date ( $P < 0.05$ ) and that age differences in duration were not consistent between winters (age-by-winter interaction,  $P < 0.05$ ; Table 1). Flight duration increased  $0.004 \pm 0.002$  (ln min) per day during winter ( $n = 191$ ; Table 1). When we replaced date with hunting presence or absence, we found that flight duration did not differ ( $P = 0.48$ ) in relation to duck hunting.

#### DEPARTURE TIME

We analyzed 193 departure times of 106 individuals. Compound symmetry did not describe the relationship among repeated measures better

than simple structure (likelihood ratio test from full model,  $P = 0.68$ ), indicating that repeated observations on individuals were not correlated. Our final fitted model indicated that departure time varied with date, but the relationship was not consistent between winters (date-by-winter interaction,  $P < 0.005$ ). Females departed earlier in relation to sunset as winter progressed in 1992-1993, but departure times did not vary with date in 1991-1992 (Table 1, Fig. 1).

Our analysis of departure times in relation to environmental variables indicated that observations made on a given day were correlated ( $P < 0.005$  from full model); individual females apparently adjusted departure times similarly to conditions specific to a given evening. The final fitted model indicated that differences in departure time due to moon phase were not consistent among levels of cloud cover (moon-by-cloud cover interaction,  $P < 0.05$ ) and that departure times differed between levels of wind velocity ( $P < 0.005$ ). Females generally departed earlier as cloud cover increased (Table 2). Under PCLPSN conditions, departures were 3.4 min earlier, on average, on moonlit evenings as compared to moonless evenings (Table 2). Females departed Lacassine NWR earlier on evenings when winds were heavy ( $LS \bar{x} \pm SE = 18.0 \pm 1.0$  min post-

sunset) than when winds were light (LS  $\bar{x} \pm SE = 21.7 \pm 0.6$  min post-sunset).

Our final fitted model, using residuals from the analysis of environmental variables, indicated that departure times differed between ages ( $P < 0.05$ ). Date and winter main effects, and all interactions, were not significant ( $P > 0.05$  for all tests). After controlling for environmental effects, immatures departed Lacassine NWR 1.3 min earlier, on average, than did adults. When we replaced date with hunting presence or absence and refit the model, we again adopted a final fitted model that contained only age effects. After controlling for environmental effects, departure times did not differ ( $P = 0.66$ ) between hunting and non-hunting seasons, and all interactions were not significant ( $P > 0.05$  for all tests). These results indicate that the earlier apparent association between departure time and date in 1992–1993 was caused primarily by a higher proportion of cloudy, windy days from mid-December through January in 1992–1993 than in 1991–1992 (dates 50–90 in Figs. 2b and 2d).

## DISCUSSION

Our analysis of direct observations indicated that predicted one-way evening flight distances for various age and winter combinations ranged from 8.7 to 24.4 km, and predicted one-way evening flight durations ranged from 16.4 to 32.9 min. Females returned to Lacassine NWR following evening flights at a high rate (71%). Furthermore, our estimate of return rate probably is conservative because we selected birds for monitoring that habitually roosted on Lacassine NWR less often than expected by chance (see Methods). Assuming that return flights were similar in duration to departing flights, pintails spent 32.8–65.8 min day<sup>-1</sup> in flight to and from the refuge. We estimate BMR of adult females to be 67.6 kcal day<sup>-1</sup>, and foraging flight costs to be 18.4–36.8 kcal day<sup>-1</sup>. Therefore, transit costs were equivalent to 27–54% of BMR, and pintails would have to consume 5.5–11.0 g of additional rice per day to meet these costs.

Estimated daily energy expenditure (DEE) and food consumption by female pintails in California from 15 October–15 February ranged from 177–232 kcal and 51–69 g of rice and moist-soil seeds, respectively (M. Miller, unpubl. data). Assuming that these values are similar for females in southwestern Louisiana, transit costs were

TABLE 2. Least-square means  $\pm$  SE of departure time (min after sunset) by moon and cloud cover categories for female Northern Pintails departing Lacassine NWR during winters 1991–1992 and 1992–1993.

Moon	Cloud cover <sup>1</sup>	Estimate <sup>2</sup>
Not present	CLR	23.5 $\pm$ 1.4 A
Not present	PCLPSN	22.6 $\pm$ 1.3 A
Not present	OVC	13.1 $\pm$ 1.1 B
Present	CLR	24.6 $\pm$ 1.2 A
Present	PCLPSN	19.2 $\pm$ 1.1 C
Present	OVC	15.9 $\pm$ 1.2 B

<sup>1</sup> CLR = clear, PCLPSN = partly cloudy to partly sunny, and OVC = overcast.

<sup>2</sup> Means followed by the same letter do not differ ( $P > 0.05$ ).

equivalent to 7–19% of DEE and 8–20% of total daily intake. The maximum one-way difference in flight duration among ages and winters was 12.8 min (adults versus immatures on 9 February 1992), which amounts to 14.4 kcal or 4.3 g of rice per day for transit costs. Using 58–61 g as an estimate of daily food consumption during 15 January–15 February (M. Miller, unpubl. data), maximum differential flight duration among ages and winters represents 7% of total daily food intake. Although these estimated costs do not seem excessive, we believe that they are not trivial. Our estimates of flight distance and duration for female pintails were greater than for most other species of wintering waterfowl, although comparative studies of flight duration are limited (Table 3). When additional flight activity due to disturbance is considered, which may be substantial (Tamisier 1976, Chabreck et al. 1989, Rave and Cordes 1993), it is likely that energy expenditure for flight constitutes an important component of DEE for pintails roosting on Lacassine NWR.

We conclude that departure times of female pintails are influenced primarily by environmental conditions. This conclusion is based on several results: (1) departure times measured on the same individual on different dates were not correlated, (2) departure times of different individuals measured on the same evening were correlated, and (3) after controlling for environmental effects, departure times did not differ between winters or among dates, but differed slightly (1.3 min) between ages. The significant cloud cover-by-moon interaction suggests that light conditions in late evening serve as a proximate cue for departures. Although not quantified, Tamisier (1976) reported that bright moonlight

TABLE 3. Mean flight distances and durations reported for wintering waterfowl.

Species	Distance (km)	Duration (min)	Authority
<i>Anser caerulescens</i>	23.0 <sup>a</sup>	78.0	Davis et al. 1989
<i>Anser caerulescens</i>	—	25.1 <sup>b</sup>	Frederick and Klaas 1982
<i>Branta canadensis</i>	—	9.4	Austin and Humburg 1992
<i>Aix sponsa</i>	1.4	—	Parr et al. 1979
<i>Aix sponsa</i>	0.6	—	Costanzo et al. 1983
<i>Anas rubripes</i>	5.6 <sup>a</sup>	—	Morton et al. 1989
<i>Anas penelope</i>	10.0–20.0+ <sup>a</sup>	—	Lebret 1959
<i>Anas platyrhynchos</i>	6.4–40.0 <sup>a</sup>	7.4–34.0 <sup>a</sup>	Jorde et al. 1983
<i>Anas acuta</i>	17.4–48.8 <sup>a</sup>	32.8–65.8 <sup>a</sup>	This study
<i>Aythya valisineria</i>	23.4 <sup>a</sup>	—	Howerter 1990

<sup>a</sup> Estimate restricted to daily flights between roosts and feeding sites.

<sup>b</sup> Calculated from estimates presented in Frederick and Klaas (1982) assuming mean of 11 hr daylight in Nebraska from October–December.

was responsible for delaying departure times of pintails and Green-winged Teal (*Anas crecca*) from Lacassine NWR. In Texas, evening foraging flights of mixed flocks of ducks, primarily pintails and Green-winged Teal, began 10–15 min earlier than normal under completely overcast conditions (Baldassarre and Bolen 1984). Wood Ducks (*Aix sponsa*) and scaup (*Aythya* spp.) also delay evening flights with decreasing cloud cover (Blackbill 1952, Hein and Haugen 1966, Tabberer et al. 1973, Scott and Parr 1978).

Females generally departed Lacassine NWR earlier as wind velocity increased. These findings are consistent with those of Tamisier (1976), who reported earlier departure times for pintails and Green-winged Teal from Lacassine NWR on windy, cloudy, or rainy days, and Miller (1985), who noted earlier evening flights of pintails from refuges in California on rainy, windy days. Windy conditions in winter are associated with passage of cold fronts, which, in turn, are characterized by marked changes in barometric pressure and surface temperatures (Schroeder and Buck 1970). We speculate that earlier departures under windy conditions allow pintails additional foraging time in preparation for, or in response to, increased thermoregulatory costs.

Flight parameters did not differ between hunting and non-hunting seasons. However, because females consistently departed well after sunset throughout winter, even prior to initiation of hunting, pintails really were not exposed to hunting during evening flights because legal hunting ended at sunset. Our results of no hunting effects would have been more conclusive if we had found that pintails maintained consistent pre-sunset departure times between non-hunting and hunt-

ing seasons. Thus, we are reluctant to conclude, as did Tamisier (1976), that hunting does not influence activity patterns of pintails roosting on Lacassine NWR. Pintails may adopt post-sunset departures in response to disturbance from agricultural harvesting, which is high in October when pintails arrive in the study area (Bagent et al. 1987), or in anticipation of, rather than in response to, shooting pressure. Pintails roosting on refuges in the Sacramento Valley of California, which arrive there 6–8 weeks earlier than in southwestern Louisiana, adjusted departure times from pre-sunset prior to hunting to post-sunset once hunting began, and maintained post-sunset departures thereafter (Fig. 7 in Miller 1985). Miller et al. (1995) speculated that high survival of adult female pintails in the Sacramento Valley of California was due, in part, to reacquaintance with refuge areas between arrival and hunting seasons. Whether post-sunset departure from refuge areas (and nocturnal feeding) is a learned response to disturbance that is retained between winters or a naturally occurring phenomenon (Tamisier 1976) can be tested only with rigorous, long-term, experimental (non-observational) research.

Flight distance and duration increased among dates within winters for all combinations of female ages, winters, and types of observations, except indirect observations of flight distance in 1991–1992. Using indirect observations, our analysis of the relationship between flight distance and date in 1991–1992 had reduced power because of the short time interval (24 days) over which we obtained these observations. Restricted observation dates in 1991–1992 also decreased power for testing main effects and inter-

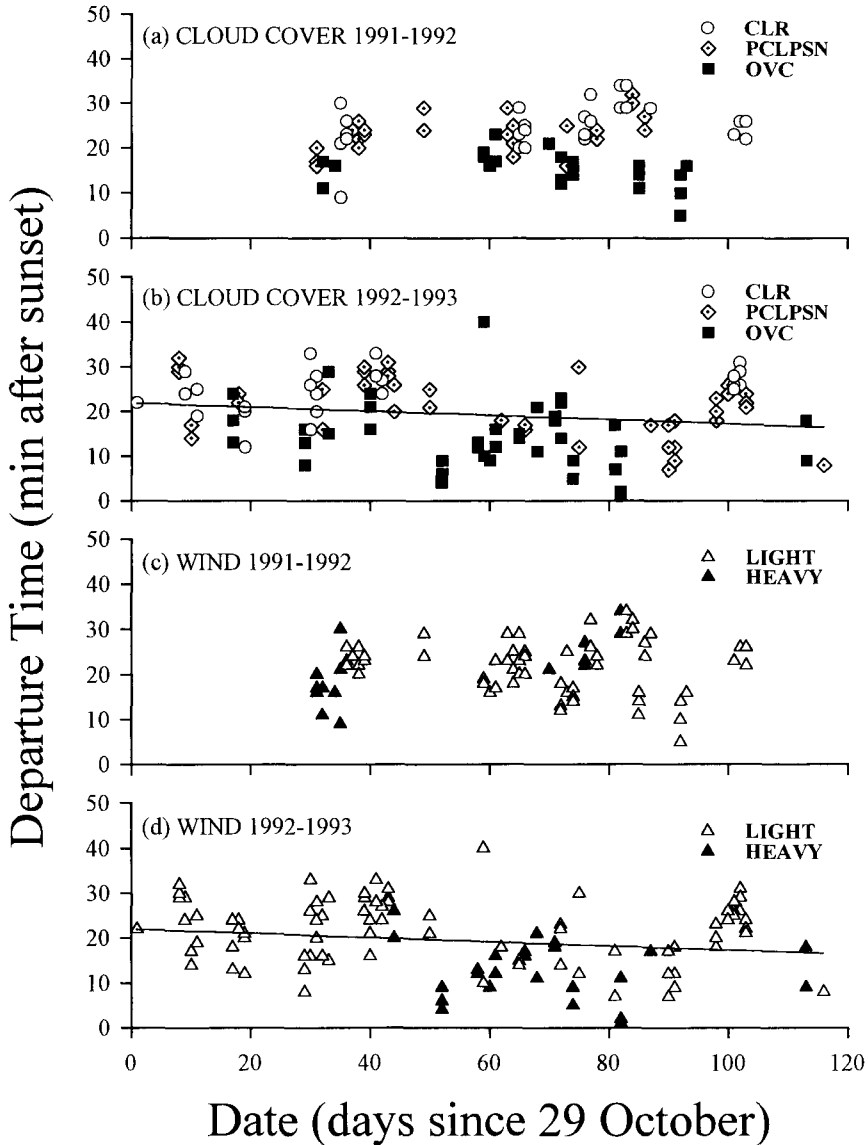


FIGURE 2. Relationship of departure time (min after sunset) of female Northern Pintails roosting on Lacassine National Wildlife Refuge to date within wintering period for each winter. Graphs (a) and (b) show levels of cloud cover, while graphs (c) and (d) show levels of wind velocity. Fitted regression line on graphs (b) and (d) is from the date-by-winter effect from mixed-model ANCOVA (see text and Table 1).

actions involving winters using indirect observations. The agreement between direct and indirect observations of flight distance in 1992-1993 is consistent with our observations (Cox, unpubl. data) that female pintails infrequently made additional flights at night, and suggests that reliable estimates of flight distance could be ob-

tained using less labor-intensive indirect methods.

Our results of increased flight distance and duration during winters are consistent with predictions of refueling theory when food resources are depleted preferentially near the central place or core area (Hamilton and Watt 1970). However,



hunting leases and commercial hunting operations are more prevalent near Lacassine NWR than in more distant (> 20 km) portions of the study area (R. Helm, LDWF, pers. comm. and Cox, unpubl. data). Because agricultural fields leased to hunters often are flooded artificially to attract ducks, nearby areas probably are more likely to be flooded earlier in winter than more distant areas. Thus, greater flight distance and duration by pintails later in winters may be in response to availability of naturally flooded habitat from heavy rains in December and January rather than food depletion. Alternatively, increases in flight distance and duration within winter may result partly from increased *zugunruhe* (nocturnal restlessness; Farner 1955) associated with spring migration. Rigorous testing of refuging theory would require temporal and spatial quantification or manipulation of food availability throughout the range of distances flown, which was beyond the scope of our study. We conclude that while our results are consistent with predictions of refuging theory, alternative hypotheses could explain these findings.

Pintails flew relatively long distances to obtain food, suggesting that potential benefits of roosting on Lacassine NWR were great. Accordingly, transit costs of pintails and other refuging waterfowl, along with evaluation of relative importance of specific benefits of roosting on refuges, should receive further research. If food availability on and near refuges is a potentially important determinant of flight distance and duration, flight energetics may become an increasingly important component of DEE of refuging waterfowl in the future if habitat losses continue on wintering areas. We recommend that proximity of refuges and feeding areas should be considered in management plans for pintails and other wintering waterfowl.

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