

# TIMING OF REPRODUCTION IN TWO POPULATIONS OF WILLOW PTARMIGAN IN NORTHERN CANADA

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**ABSTRACT.**—We examined extrinsic and intrinsic factors that might influence the timing of clutch initiation and determined the relationship between timing and reproductive success in two populations of Willow Ptarmigan (*Lagopus lagopus*) in northern Canada. The mean date of clutch initiation varied up to 16 days over 8 yr and appeared to be related to the timing of snow melt. In one population females laid more synchronously when the onset of breeding was late, but in the other they did not. Laying was not correlated with population density or with proportion of yearling hens in the population. Older hens paired with adult males initiated nesting earlier than yearlings or adult hens paired with yearling males. Females that switched mates from one year to the next laid at the same time as those paired with their previous mates. The timing of clutch initiation or hatch was consistent for individual females from one year to the next in one population, but not in the other. Body size, estimated by wing length, was not correlated with time of laying, but hens with larger body mass laid earlier. Females that nested early laid larger clutches than those laying late. In only 1 yr of 6, a year with very high nest predation, late-nesting hens lost a lower proportion of their clutches. Early-nesting hens hatched more eggs from successful nests than late-nesting hens, but the number of young that fledged and subsequently returned to the population was similar for hens nesting in early, middle, and late reproductive periods. We suggest that hens capable of laying early do so to renest if their clutches are destroyed by predators. Received 29 April 1987, accepted 11 January 1988.

TIMING of reproductive events within a breeding season may affect individual fitness and the number of young produced in the population. In birds, females that lay early often have larger clutches than those laying later (e.g. Winkler and Walters 1983), and those that initiate laying late may fledge fewer young (O'Donald et al. 1974). Timing of nesting may also be related to predation rate on clutches. In some species predation is higher on clutches initiated early (e.g. Findlay and Cooke 1982); in others it increases through the season (e.g. Robertson 1973, Wiklund 1984). For any population the optimal time to lay depends on a variety of intrinsic and extrinsic factors that may vary among years.

Birds that breed in northern environments are considered to be constrained by the time available to reproduce successfully. Early laying may be prevented by a lack of snow-free habitat (Barry 1962, Holmes 1966, Sealey 1975) or a food shortage (Perrins 1970, Greenlaw 1978, Ewald and Rohwer 1982). Late laying may be constrained by insufficient time for development of young before migration or onset of winter conditions (Barry 1962, Findlay and Cooke 1982).

Within the limits set by environmental factors, initiation of laying may be influenced by other extrinsic factors such as population density (Moss et al. 1984) or by intrinsic factors such as the age or experience of either mate (Nol and Smith 1987), the physical condition of a female, genetic effects (e.g., van Noordwijk et al. 1981), or interactions among these factors.

We documented the timing of reproduction in two subarctic populations of Willow Ptarmigan (*Lagopus lagopus*) in Canada. We examined both extrinsic and intrinsic factors that may influence when an individual female began to lay. These include spring weather, population density, age of hen, body size and mass, and experience with mate. Second, we examined the influence of time of clutch initiation on a hen's reproductive success within a season.

The Willow Ptarmigan is a territorial, usually monogamous grouse with a holarctic distribution. Females begin to breed as yearlings and are single-brooded, but may renest up to 3 times if the first clutch is lost. Populations undergo cyclic fluctuations with a period of 4–11 yr (Watson and Moss 1979, Myrberget 1984, Hannon and Barry 1986).

## METHODS

Populations of Willow Ptarmigan were studied at Chilkat Pass (CP) in northwestern British Columbia (59°50'N, 136°30'W) and La Perouse Bay (LPB) 40 km east of Churchill, Manitoba (58°24'N, 94°24'W). Hannon worked on a 2.5-km<sup>2</sup> area (enlarged to 4.5 km<sup>2</sup> in 1985 and 1986) of subalpine tundra at CP in 1979–1981 and 1984–1986. This area has been described by Weeden (1960) and Hannon (1983, 1984). Martin conducted studies on 10 km<sup>2</sup> of subarctic tundra from 1981 to 1984. Martin (1984) and Martin and Cooke (1987) described this study area and field methods, and Jefferies et al. (1979) described the vegetation. Field seasons in both areas were from mid-April to early August.

Study methods were similar in both areas. More than 90% of the resident birds were captured before incubation and uniquely color-banded. Ptarmigan were classified as yearlings (hatched the previous season) or adults (2+ yr) based on pigmentation of the 8th and 9th primaries (Bergerud et al. 1963). Sexes were distinguished by differences in voice, plumage, and wing length.

Nests were found by using pointing dogs, searching around roosts of territorial males, or following radio-marked hens (1985 and 1986 at CP only). Clutch size was recorded and most nests were visited 2–3 times/week until hatch. We present data from first nests only (i.e. the first completed clutch of each hen). At hatch, or when encountered thereafter, chicks were captured, weighed, and marked with numbered metal tags attached to the patagium. Chick age was determined from wing length (Westerkov 1956). This method was accurate for chicks up to 9 days of age (unpubl. data). Unknown hatch dates were estimated by subtracting the modal age of chicks in a brood from capture date. The date of laying of the first egg was calculated by backdating from hatch date; we subtracted 21 days for incubation and 1 day/egg in the clutch. The majority of hens at both sites that had nests that we found early in laying laid 1 egg/day (40/56) and incubated 20–22 days from the date the last egg was laid (70/83). For nests of radio-marked hens and nests found during laying, the date of the first egg was determined directly. We controlled for annual variation in laying or hatching dates by expressing date of laying or hatch each year relative to the overall mean date of laying of first egg or hatch (van Noordwijk et al. 1981). This was called the adjusted laying or hatch date. Dates are expressed as "day numbers," with 1 January as day 1. The number of chicks fledged/brood was estimated as the highest number of flying chicks recorded from broods 15–25 days old. The juveniles began to fly at 11–12 days of age in both populations.

Sample sizes for clutch-initiation dates were small at CP until 1985 and 1986. We obtained a larger sample of hatch dates, and in some analyses we used hatch

dates and did not analyze clutch-initiation dates. At LPB a large sample of clutch-initiation dates was available, but nest-predation rates were high. Thus, sample sizes for date of hatch were reduced. Because initiation dates and hatch dates were highly correlated (CP:  $r = 0.96$ ,  $P < 0.01$ ,  $n = 114$ ; LPB:  $r = 0.97$ ,  $P < 0.01$ ,  $n = 81$ ), we used these dates interchangeably. We used variance of date of clutch initiation or hatch date as a measure of nesting synchrony.

Nest-initiation dates for each year were divided into early, middle, and late periods. The middle period was defined as dates within  $\pm 0.5$  SD of the mean initiation date. Early and late periods were dates before and after the middle period, respectively. Data from the 2 sites, all years, or age classes were combined if they were homogeneous. One-way analysis of variance and the Scheffe range test were used to compare variable means from the 3 periods (Sokal and Rohlf 1981).

At CP from 1979 to 1984 only a few nests were located, and most were found in late incubation; thus, the rate of predation would be underestimated. These data were omitted. In 1985 and 1986 most nests were found during laying. At LPB most nests were located early in incubation or during laying. We subtracted the date of clutch initiation from the date the clutch was found to give an index of nest exposure to potential predation while under our observation. We then compared the distributions of exposure indices between areas, among years, and within years among reproductive periods (early, middle, late) with a Kruskal-Wallis test. If the data were homogeneous, we assumed that indices of exposure were similar and that comparisons of nest-predation frequency among years were valid.

At CP mean maximum, mean minimum, and overall mean temperature, and number of days with snow or rain in May were calculated from meteorological data collected at Mule Creek Highway Camp, approximately 4 km south of the study area. We measured snow depth to the nearest 5 cm at 65 stations, 100 m apart on CP each year on 29 or 30 April or 1 May. We recorded the date annually when approximately two-thirds of the ground was free from snow, called snow melt. Similar meteorological data were collected at LPB from the weather station at Churchill, Manitoba, 30 km west of the study area. Snow depths were not taken at LPB, and we used snow depth on 30 April at the Churchill weather station. Snow melt was not recorded at LPB.

Parametric statistical tests were used on continuous data that were distributed normally and had homogeneous variances; otherwise, nonparametric tests were used. Two-way contingency analyses were done with G-tests using a William's correction (Sokal and Rohlf 1981). When minimum expected values in any cell were less than 5, sampled randomization tests ( $n = 1,000$ ) were used to test for independence and  $G_{min}$  values reported (Sokal and Rohlf 1981).

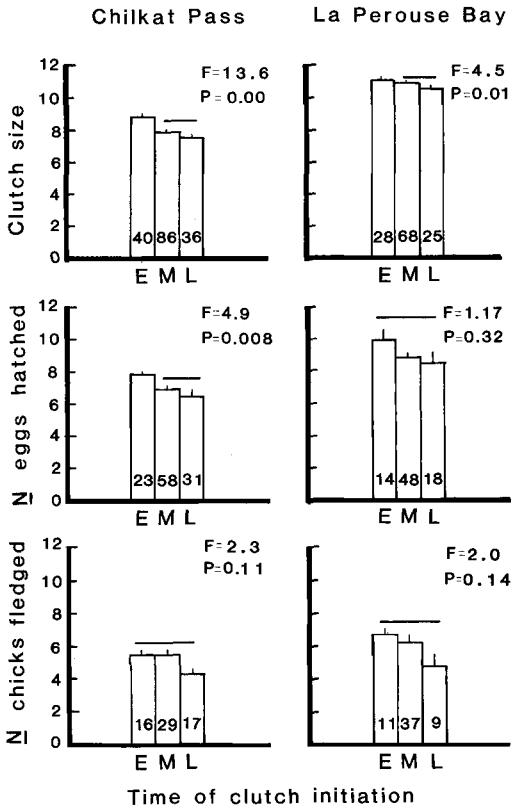


Fig. 1. Mean adjusted clutch size of all nests initiated, and number of eggs hatched and fledged from successful nests for clutches in early (E), middle (M), and late (L) reproductive periods. Numbers in bars denote sample sizes, vertical lines are standard errors, and horizontal lines connect means that are not different.

RESULTS

POTENTIAL FACTORS INFLUENCING TIMING OF LAYING

*Year.*—The mean date of clutch initiation varied significantly among years at both CP and LPB (Table 1, one-way ANOVA). At CP the mean date of clutch initiation varied by 11 days over 6 yr and at LPB by 15 days over 4 yr. The variation in mean date of hatch reflected the variation in mean date of clutch initiation, except that hatch dates in 1985 and 1986 did not differ from each other at CP (Table 1). In 1985 early nests were destroyed at a higher rate than later nests (see below), which would have resulted in a later mean hatching date. In 1981 and 1984, when work was done at both sites, clutch-ini-

TABLE 1. Mean date of first egg and mean date of hatch of first nests of Willow Ptarmigan by year. Asterisks and crosses denote means that do not differ (ANOVA) from each other.

	Date of first egg			Date of hatch		
	$\bar{x}$	var	n	$\bar{x}$	var	n
Chilkat Pass						
1979	147.6*	3.4	6	177.5*	4.8	42
1980	154.5	8.3	17	183.2	7.8	47
1981	152.1	14.4	13	179.5	7.8	51
1984	148.4*	4.8	8	176.5*	7.8	23
1985	157.2	11.3	51	186.9+	7.0	24
1986	158.6	11.1	68	186.5+	10.7	73
	F = 34.1, P = 0			F = 99.6, P = 0		
La Perouse Bay						
1981	152.6	7.9	23	184.0	9.9	14
1982	150.0	10.2	38	181.3	4.9	25
1983	163.4	5.4	43	193.2	3.8	29
1984	148.5	9.2	35	179.5	8.2	28
	F = 224.8, P = 0			F = 167.8, P = 0		

tiation dates did not differ between sites (1981:  $t = -0.44, P = 0.66$ ; 1984:  $t = -0.14, P = 0.89$ ), but mean hatch dates were 4.5 and 3 days later, respectively, at LPB (1981:  $t = 5.25, P = 0$ ; 1984:  $t = -3.84, P = 0.0004$ ). The mean clutch size at LPB was about 3 eggs larger than at CP (Fig. 1) which may account for the later hatch at LPB despite similar initiation dates.

*Weather.*—The mean date of hatch was positively and most highly correlated with the date of snow melt at CP. It was correlated negatively with the mean maximum temperature in May and the number of days with rain in May, and positively with the number of days with snow in May (Table 2). At CP birds did not hatch more synchronously in years with late snow melt ( $r_s = 0.38, n = 6, P > 0.05$ ), nor was mean initiation date correlated with variance in initiation date ( $r_s = 0.70, n = 6, P > 0.05$ ).

The mean date of clutch initiation correlated most highly with the number of days of snow in May at LPB, and less so with the mean minimum temperature. No correlations were significant, however, because of the small sample size (with  $n = 4, r_s$  would have to equal 1 to be significant) (Table 2). Variance in the date of clutch initiation was negatively (but not significantly) correlated with the mean laying date and indicated higher synchrony in late years ( $r_s = -0.96, P > 0.05, n = 4$ ).

*Breeding density and age structure of females.*—Female density at CP declined from about 46/

TABLE 2. Spearman rank correlation matrix ( $r_s$ ) of weather factors with mean date of hatch and mean date of clutch initiation of Willow Ptarmigan. Bold-face values differ from zero at  $P < 0.05$ .

	Mean hatch at Chilkat Pass ( $n = 6$ )	Mean initia- tion at La Perouse Bay ( $n = 4$ )
Snow melt	<b>0.96</b>	—
Snow depth	0.53	0.40
Maximum temperature	<b>-0.93</b>	-0.40
Minimum temperature	-0.06	-0.80
Mean temperature	-0.82	-0.40
Days of snow	<b>0.92</b>	0.95
Days of rain	<b>-0.85</b>	-0.74

km<sup>2</sup> in 1979 and 1980 to 20/km<sup>2</sup> in 1985 and 1986. The mean date of hatch each year did not correlate with the density of females ( $r_s = -0.53$ ,  $P > 0.05$ ,  $n = 6$ ). The density of hens declined from 9/km<sup>2</sup> in 1981 to 6.8 in 1982–1984 at LPB. Mean initiation dates at LPB were not correlated with population density ( $r_s = 0.32$ ,  $P > 0.05$ ,  $n = 4$ ). Breeding densities at LPB were much lower than at CP, in part because there was more standing water at LPB.

The proportion of yearling females in the population at CP varied from 33% to 64% over 6 yr and did not correlate with the mean hatch date ( $r_s = -0.47$ ,  $P > 0.05$ ,  $n = 6$ ). At LPB the proportion of yearling hens in the population varied from 37% to 53% and was not correlated with the mean date of clutch initiation ( $r_s = -0.80$ ,  $P > 0.05$ ,  $n = 4$ ).

*Age of female and experience with mate.*—We compared four categories of age pairing (Table 3). Adult females paired with adult males initiated clutches about 1 day earlier than other pair/age combinations (Table 3). Females that remated with their previous mates did not lay earlier than hens that changed mates (CP and LPB combined, only hens paired with adults included; same mate:  $\bar{x} = 147.0$ , SE = 0.55,  $n = 28$ ; changed mate:  $\bar{x} = 147.6$ , SE = 0.41,  $n = 51$ ;  $t = 0.84$ ,  $P = 0.40$ ).

*Individual female effects.*—To examine whether individual females initiated clutches consistently early or late among years, we correlated their clutch-initiation dates in year  $x$  with their clutch-initiation dates in year  $x + 1$  (dates were adjusted for year effects). At LPB hens did not initiate clutches at a consistent time from year to year ( $r = 0.16$ ,  $P > 0.05$ ,  $n = 22$ ). We had insufficient data to do this at CP, so we exam-

TABLE 3. Mean data of clutch initiation of adult and yearling female Willow Ptarmigan when paired with adult and yearling males (dates adjusted for year, areas combined). Asterisks denote mean dates that do not differ from each other. Y = yearling, A = adult, M = male, F = female.

Category	$\bar{x}$	var	$n$
YF × YM	148.2*	8.8	69
AF × YM	148.9*	10.1	22
YF × AM	148.4*	9.8	77
AF × AM	147.3	8.8	123
$F = 3.37$ , $P = 0.02$			

ined consistency of hatch date. Dates of hatch for individual females were positively correlated with their dates of hatch in the following year ( $r = 0.45$ ,  $P < 0.05$ ,  $n = 23$ ). At LPB this relationship was not significant ( $r = 0.39$ ,  $P > 0.05$ ,  $n = 13$ ).

*Body mass and size of female in spring.*—Female body mass increases rapidly during the prelaying period (Hannon and Roland 1984). Thus, we used analysis of covariance with date of weighing (adjusted for year effects) as a covariate and compared body mass of hens laying in early, middle, and late periods. Adult and yearling masses were not significantly different and were combined. At CP hens that laid early were significantly heavier than those that laid in middle or later periods (Table 4). At LPB there was no significant difference in mass, although hens that laid in early and middle periods tended to be heavier than those laying later (Table 4). We used wing length as an index to body size. The wing lengths of yearlings were significantly shorter than those of adults at both sites (CP:  $t = 2.36$ ,  $P = 0.02$ ; LPB:  $t = 2.61$ ,  $P = 0.01$ ). The mean wing lengths of adults and yearlings at both sites were similar for birds in early, middle, and late clutch-initiation periods (Table 5). Thus, although heavier hens were

TABLE 4. Mean body mass (g) of hen Willow Ptarmigan laying in early, middle, and late reproductive periods (ANCOVA). Asterisks denote mean masses that do not differ from each other.

	Chilkat Pass			La Perouse Bay		
	$\bar{x}$	SE	$n$	$\bar{x}$	SE	$n$
Early	528.9	7.7	25	659.5*	12.9	9
Middle	504.9*	4.9	62	654.4*	6.6	34
Late	511.4*	4.8	64	640.1*	6.6	34
$F = 3.5$ , $P = 0.03$			$F = 1.6$ , $P = 0.22$			

TABLE 5. Mean wing lengths (mm) of adult and yearling hen Willow Ptarmigan that initiated laying in early, middle, and late periods.

	Chilkat Pass			La Perouse Bay		
	$\bar{x}$	var	<i>n</i>	$\bar{x}$	var	<i>n</i>
Yearlings						
Early	180.5	17.5	22	190.5	40.9	10
Middle	179.8	20.9	49	190.0	37.5	33
Late	180.4	18.6	42	191.3	22.8	42
	$F = 0.30, P = 0.74$			$F = 0.44, P = 0.64$		
Adults						
Early	183.9	5.2	7	191.5	22.7	6
Middle	181.8	22.9	22	192.9	24.2	22
Late	181.4	22.8	25	191.1	24.2	20
	$F = 0.77, P = 0.47$			$F = 0.71, P = 0.49$		

observed to lay earlier, they were not larger. We believe that the condition of females, rather than their size, is relevant to the timing of reproduction.

#### RELATIONSHIP BETWEEN DATE OF CLUTCH INITIATION AND REPRODUCTIVE SUCCESS

*Nest predation.*—We found no differences in indices of exposure between 1985 and 1986 at CP ( $H = 0.37, P = 0.54, n = 109$ ) or between early, middle, and late periods within years (1985:  $H = 1.26, P = 0.54, n = 43$ ; 1986:  $H = 3.64, P = 0.16, n = 66$ ). There was no difference in indices of exposure among years at LPB ( $H = 1.16, P = 0.76, n = 137$ ), or among reproductive periods ( $H = 0.48, P = 0.78, n = 137$ ). Exposure indices did not differ between sites ( $H = 0.04, P = 0.83, n = 294$ ). Thus, the distributions of times that nests were under observation and exposed to predation did not differ between areas, years, or reproductive periods.

Nests were destroyed at a much higher rate in 1985 than in 1986 at CP (1985: 65%,  $n = 49$ ; 1986: 14%,  $n = 72$ ;  $G = 32.5, df = 1, P < 0.0001$ ). Predation varied over the 3 time periods in 1985 but not in 1986 (Table 6). In 1985 at CP, nests initiated in the early and middle periods suffered more predation than those initiated late ( $G_{\text{ran}} = 5.2, df = 1, P = 0.03$ ). We do not believe the use of radio collars increased predation in 1985 because nest failure was also high for females that were not radio-marked. Telemetry also was used in 1986, when predation was much lower. At LPB nest predation was similar in each year ( $G = 2.48, P = 0.48, df = 3, n = 121$ ),

TABLE 6. Percentage of first clutches of Willow Ptarmigan destroyed in each period of initiation.

Initiation period	Chilkat Pass				La Perouse Bay	
	1985		1986		1981-1984	
	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>
Early	86	14	13	15	46	28
Middle	68	25	20	35	31	68
Late	33	9	6	17	28	25
	$G = 6.3, P = 0.04$		$G = 1.5, P = 0.47$		$G = 2.5, P = 0.29$	

and data were combined. Nest predation did not differ among the 3 time periods at LPB (Table 6).

*Reproductive output.*—At both sites the clutch sizes of hens nesting early were larger than those nesting in the middle or late periods (clutch size adjusted for year effects; Fig. 1). The number of eggs that hatched in successful first nests was higher from early than from later nests at CP; the trend was similar, but nonsignificant, at LPB (Fig. 1). The number of chicks fledged (adjusted for year effects) from successful nests did not differ with respect to timing of clutch initiation at either site (Fig. 1), although the trend was for later nests to fledge fewer chicks.

Adults produced heavier chicks at hatch than did yearlings at CP ( $t = 2.87, P = 0.005$ ), but not at LPB ( $t = 1.47, P = 0.15$ ). There was no difference at either site between the mass of chicks from nests initiated in the 3 periods (Table 7), although there was a trend for young hatched late by adults to be heavier.

Chicks returned to the study areas in subsequent years from 34 broods for which we knew hatch dates at CP and 25 at LPB. There was no difference in the likelihood of young returning from nests with eggs hatching in the 3 reproductive periods at either site (Table 8).

#### DISCUSSION

From year to year female Willow Ptarmigan encounter large weather variations at the onset of the breeding season. The mean date of clutch initiation varied over years and was correlated most strongly with variations in snow melt. The timing of snow melt was correlated with the date of egg laying in Willow Ptarmigan in Norway (Myrberget 1986). Cold springs with late

TABLE 7. Mean body mass (g) of Willow Ptarmigan chicks hatched from nests initiated in early, middle, and late time periods.

	Yearlings			Adults		
	$\bar{x}$	var	n	$\bar{x}$	var	n
Chilkat Pass						
Early	14.0	0.8	12	14.5	0.6	9
Middle	14.7	0.9	21	14.9	0.7	23
Late	14.4	1.3	14	15.4	0.8	11
	$F = 2.20, P = 0.12$			$F = 2.95, P = 0.06$		
La Perouse Bay <sup>a</sup>						
		$\bar{x}$		var	$\bar{n}$	
Early		15.1		1.3	13	
Middle		15.1		1.1	43	
Late		14.7		1.3	15	
		$F = 1.03, P = 0.36$				

<sup>a</sup> Adults and yearlings pooled.

snow melt have been implicated in delays in nesting in other grouse (e.g. Braun and Rogers 1971, Zwickel 1977, Smyth and Boag 1984), in waterfowl (Barry 1962, Abraham 1980, Pehrsson 1986), and in passerines (Slagsvold 1976).

Delayed nesting in cold, late springs could be due to a lack of suitable nest sites (e.g. Findlay and Cooke 1982) or insufficient food for clutch formation (Perrins 1970, Ewald and Rohwer 1982). In years when females must wait for snow to clear before they nest, one would predict higher synchrony. This was the case at LPB, but the opposite trend was observed at CP. During late springs at CP, the heterogeneity of local conditions may be higher (e.g. differences of snow melt within the study site; Zwickel 1977) or the response of individual females may be more variable, possibly related to early-spring body condition. Our data were not sufficient to discriminate among these alternatives.

Breeding density and the age structure of the population were not related to the mean date of clutch initiation, although this should be interpreted with caution because the sample size was small. Myrberget (1986) found a similar relationship for Willow Ptarmigan in Norway. Red Grouse (*L. l. scoticus*) in Scotland hatched earlier in years of high population density (Moss et al. 1984), but without data on spring weather we cannot reject the possibility that the seasonal phenology was also early when their population was at high density.

Adult females, when paired with adult males, initiated nests on average 1 day earlier than yearlings. In an earlier analysis of CP data Hanon and Smith (1984) found a nonsignificant

TABLE 8. Percentage of Willow Ptarmigan broods that had chicks return from eggs hatched in the early, middle, and late reproductive periods ( $n$  = number of broods).

	Chilkat Pass		La Perouse Bay	
	% return	n	% return	n
Early	26	43	50	12
Middle	17	110	31	39
Late	11	38	41	17
	$G = 3.20, P = 0.20$		$G = 1.63, P = 0.45$	

trend for adult-adult pairs to lay earlier than other pair groups. Adult females mated with the same males as the previous year did not lay earlier than those mated with different males. Thus, it was not experience with a specific male per se, but possibly the previous breeding experience of an adult male combined with the adult hen's experience, that afforded earlier laying.

In some species individual females tend to lay at the same time each year relative to the population mean (e.g. Moss et al. 1981, van Noordwijk et al. 1981, Findlay and Cooke 1982). We found a significant relationship in laying date between years at CP but not at LPB. Female consistency in the time of laying may vary with location, age, body condition, or experience of individuals and their mates. Our sample sizes were not sufficient to test for the potential confounding effects of these factors.

Egg predation varies significantly from year to year in some populations (e.g. Myrberget 1984, this study), and in years of high predation it might vary with respect to initiation date. First clutches initiated in the early and middle periods suffered higher predation than clutches initiated later in only 1 of the 6 yr of study: the year of highest predation. Findlay and Cooke (1982) found that the earliest clutches of Lesser Snow Geese (*Anser caerulescens caerulescens*) suffered the highest predation. Predation declined as the density of nests in the colony increased. Either predators were satiated, or as the numbers of geese increased, it was easier to repel predators. We believe this mechanism is unlikely to operate in a noncolonial species like the Willow Ptarmigan. Nests are difficult to locate because of the crypticity and reduced odor of incubating hens (Hudson 1986). Late clutches may be partially protected from predation by increased cover during incubation, but this ef-

fect may be significant only in years of heavy predation pressure. In 1985 we sighted 3 times as many foxes (*Vulpes vulpes*), the major nest predator (unpubl. data), as in 1986 (Hannon and Gruys in press).

A disadvantage accrues to first nests laid late in the season. Fewer chicks were fledged than in earlier periods. Furthermore, the efficiency of producing fledged chicks from eggs laid late was lower, particularly at LPB. In fact, the number of chicks fledged from late-hatching eggs at LPB was similar to CP, even though the clutch size was about 3 eggs larger (Fig. 1). This may produce directional selection for earlier laying and may contribute to the higher hatching synchrony observed at LPB (7–10 days) than at CP (13–18 days) (Martin and Hannon 1987). At CP individuals that initiate laying later recruit fewer young (Martin and Hannon 1987). In the present analysis, with an additional year's data from CP, the relationship was not significant, although there was a trend for late-hatching broods to have fewer recruits.

There may also be a disadvantage in laying too early in the season. Despite larger clutches and more hatchlings, early nesters produced similar numbers of fledged chicks as hens nesting in the middle period. Thus, early nesters lost more chicks than those nesting in the middle period. A weak trend toward poor survival of early-hatched chicks was reported in Red Grouse (Moss et al. 1981). Both juvenile ptarmigan (Table 6) and Red Grouse (Moss et al. 1984) hatched early in the season did not weigh noticeably less. Reduced survival of early-hatched young may result from poor weather conditions, inadequate food supply, or perhaps higher predation pressure. More early-hatched Lesser Snow Geese goslings were killed by predators than those hatched later (Findlay and Cooke 1982).

If our measure of recruitment reflects survival and not differential dispersal, young hatched in the early and middle periods may survive better once fledged than those hatched later, but the earliest young to hatch do not appear to have an advantage over those hatched in the middle period. Lesser Snow Geese hatched from early-initiated nests had higher recruitment rates than those hatched later (Cooke et al. 1984), and a similar trend was noted for young Blue Grouse (*Dendragapus obscurus*) (Zwicker 1983). Early-laying ptarmigan hens that lose their nests may have a higher probability of renesting,

however, than those that nest later (Martin and Hannon in prep). Because predation on first nests was about 34% at LPB and 14–65% at CP, the ability to renest is a substantial benefit. At LPB 38–59% of pairs that successfully hatched eggs did so only because they had renested (Martin 1984, 1985).

Variation in the timing of snow melt appeared to be the most important extrinsic factor influencing the timing of reproduction in Willow Ptarmigan. Environmental "noise" may have obscured other more subtle influences caused by intrinsic or extrinsic factors. More data and larger sample sizes may be required to delineate these effects on timing of clutch initiation. The two sites are separated by a distance of about 2,500 km and represent quite different habitats (Martin and Hannon 1987), although they are located at similar latitudes. Despite habitat differences, the response of hens from the two populations to environmental, extrinsic, and intrinsic factors were remarkably similar. We suggest that most of the relationships we observed between the timing of laying and reproductive success are species-specific and not simply population responses to local conditions.

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Dr. Jonathan Becker was appointed Chapman Fellow for the period October 1987 though September 1988. He is studying the small arboreal birds from the early Neogene of North America.

Dr. Angelo Capparella was appointed Chapman Fellow for the period September 1987 through August 1988. He is studying the phylogeny and diversification of the woodcreepers (Dendrocolaptidae) using allozyme biochemistry.

Chapman grants for 1987, totalling \$44,868, with a mean of \$575, were awarded to: Stephen S. Albano, social organization of the Southern African Ostrich, *Struthio camelus australis*; Todd W. Arnold, factors affecting clutch size and egg size in American Coots; William N. Beckon, how to preserve the most endangered species—a few large refuges or many small ones?; Steven R. Beissinger, experimental brood manipulations and the mate desertion threshold in Snail Kites; Craig L. Berman, tactics of intraspecific brood parasitism in the House Sparrow (*Passer domesticus*); Robert E. Bleiweiss, a DNA-DNA-hybridization-based phylogeny of hummingbirds; Janet S. Boe, colony site and nest site selection by Eared Grebes in Minnesota; Eleanor Brown, comparative eco-ethology of Cracticidae; Carolee Caffrey, cooperative breeding in western American Crows; Kevin J. Cash, brood reduction in Swainson's Hawk; Gonzalo Castro, time and energy budgets of the Sanderling at four latitudes; Glen Chilton, discrimination of dialects by female White-crowned Sparrows; Nigel J. Collar, threatened birds of the Americas and Sao Tome birds; Donald A. Croll, diving and energetics of the Common Murre; Timothy M. Crowe, systematics of African galliforms, hornbills, bustards and larks; Robert L. Curry, social organization and breeding biology of the Bahama Mockingbird; Brent J. Danielson, hummingbird foraging memory in a variable environment; Mark K. Decker, relatedness of individuals within feeding groups of communally roosting Black Vultures; Toni Linn DeSanto, physiological and ecological factors influencing prey selection in the White Ibis; John McA. Eadie, brood parasitism in a precocial bird; David Enstrom, delayed plumage maturation in Orchard Orioles (*Icterus spurius*); Patricia Escalante, speciation in the genus *Geothlypis*; David C. Fleck, acorn tannin concentrations and possible effects on Florida Scrub Jay caching; Charles M. Francis, hatching asynchrony and growth rate of White-bellied Swiftlets; Scott R. Freeman, rates of speciation in the Icterinae; Theodora J. Glenn, avian habitat utilization of the native fan palm oases on the San Andreas Fault; Rosemarie Gnam, breeding biology of the Bahama Parrot (*Amazona leucocephala bahamensis*); Cheri L. Gratto, endocrinological analysis of subarctic sandpipers; Gary R. Graves, systematic studies of Colombian birds; Michael T. Green, ecological constraints on the vocalizations of birds—test of the degradation hypothesis; Rogier Gruys, mortality in a wintering ptarmigan population; Lisa Guminski, the breeding behavior of the White-cheeked Pintail in the Bahamas; Wesley M. Hochachka, intraseasonal variation in parental effort in Song Sparrows; Stephen B. Holmes, behavior and reproduction in Zebra Finches treated with Fenitrothion; H. D. Jackson, breeding biology of the Rufous-cheeked Nightjar; Susan Jackson, digestive physiology of seabirds in relation to foraging ecology; Douglas A. James, community ecology of shrubland birds in northern Michigan, and a study of the Aplomado Falcon at AMNH; Frances C. James, study of Red-winged Blackbirds at AMNH; Torgeir Johnsen, the influence of testosterone and territorial experience on male behavior and reproductive biology in the Red-winged Blackbird; Deborah Ann Johnson, ecological segregation of Western and Clark's grebes; L. Scott Johnson, singing strategies and polygyny in House Wrens using natural nest cavities; Ian L. Jones, the function and evolution of social signals of *Aethia* (Alcidae); Nedra K. Klein, geographic variation and systematics of the Yellow Warbler; Natasha B. Kotliar, a hierarchical concept of patchiness—implications for the foraging behavior of nectivorous birds; Timothy C. Lamey, egg-

(continued on p. 394)