

## ECOLOGICAL AND PHYSIOLOGICAL EFFECTS ON EGG LAYING INTERVALS IN PTARMIGAN<sup>1</sup>

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**Abstract.** Birds lay eggs at different rates and at different times of the day. Some species also show skipped days during the laying sequence, "laying gaps," but patterns of egg laying have not been well studied. We compared timing of laying during the day, laying gaps, and laying rates (number of eggs/day) for White-tailed Ptarmigan (*Lagopus leucurus*) and Willow Ptarmigan (*L. lagopus*). Both species tended to lay eggs near midday, but Willow Ptarmigan had fewer laying gaps and faster laying rates than White-tailed Ptarmigan. The variation in laying rates among individuals was greater for White-tailed Ptarmigan which had a bimodal distribution of inter-egg intervals, long ( $\bar{x} = 44$  hr) and short ( $\bar{x} = 26$  hr). Laying gaps were not associated with spring body condition but severe spring storms seemed to cause some laying delays. The patterns and frequency of gaps observed within and between species may be the result of nutrient constraints on egg formation in conjunction with physiological mechanisms which control a time-window for egg laying.

**Key words:** *Lagopus lagopus*; *Lagopus leucurus*; egg-laying interval; egg-laying time; nutritional constraints; arctic; alpine.

### INTRODUCTION

Few studies have investigated variation in egg laying intervals within species of free-living birds and underlying factors responsible for laying patterns. Egg laying rates may influence the timing and duration of breeding, both important determinants of reproductive success in birds (Daan et al. 1988). The timing of breeding within a season may affect the ability of parents to provision young (Perrins 1970), and fledging date may affect survival or recruitment of juveniles (Arcese and Smith 1985, Martin and Hannon 1987, Nilsson 1989, Hochachka 1990). For ground-nesting precocial birds, the greatest attrition in fecundity often occurs when eggs are lost to predators (Myrberget 1984, Martin et al. 1989). Thus, a short egg-laying period should minimize the time eggs are vulnerable to predation (Clark and Wilson 1981) and maximize the possibility of renesting should the first clutch be destroyed. Birds can reduce the egg-laying period by laying fewer eggs (Milonoff 1989) or by reducing the intervals between eggs. Because fewer eggs result in an immediate and certain reduction in fecundity, there should be intense se-

lection to reduce laying intervals when predation rates on nests are high.

Despite the potential consequences of laying interval for reproductive success in birds, most information about laying patterns across species comes from anecdotal reports on few individuals (reviews in Astheimer 1985, Schubert 1990). Passerines are generally believed to lay one egg every 24 hr at dawn (Skutch 1952, Perrins 1979, Schifferli 1979) although eggs are sometimes laid at midday (Muma 1986, Weatherhead et al. 1991). Galliformes and Anseriformes tend to have intervals of one to two days (e.g., Robinson 1980, Schubert and Cooke 1993, Watson et al. 1993), while Falconiformes, Ciconiiformes, Gruiformes and many Charadriiformes lay an egg every two to three days (e.g., Allen 1980, Ratcliffe 1980, Meanley 1985, Bortolotti and Wiebe 1993). Gaps during the egg-laying sequence have been studied most intensively in Blue Tits (*Parus caeruleus*) in which 20-40% of breeding females skip a day while laying their clutch (Kluijver 1951, Dhondt et al. 1970, Nur 1984, Nilsson and Svensson 1993).

Three major hypotheses may explain interruptions during laying, or "laying gaps." If laying intervals of birds are regular but between 24-48 hr, and the observer visits nests daily, "gaps" in laying may be reported as an artifact of the frequency of nest checks because a new egg will not appear in the nest every exact 24 hr period (Schu-

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bert and Cooke 1993). Second, if there is true variation in laying intervals for an individual bird, the nutrient constraint hypothesis suggests gaps occur because of the inability to accumulate sufficient nutrient reserves for daily egg production (Lack 1968, Winkler and Walters 1983). Individuals with limited food resources, or species with nutritionally poor food, would be expected to take longer to form eggs than individuals or species with more abundant food. In support of nutrient constraints, some researchers have reported a correlation between laying gaps and days of poor weather when foraging is difficult (Bryant 1975, Dhondt et al. 1983). Nilsson and Svensson (1993) also found fewer laying gaps in Blue Tits experimentally supplemented with extra food.

The physiological/hormonal mechanism hypothesis suggests laying gaps result from an interaction of the development time for individual eggs, with an "open period" during which ovulation of follicles can be stimulated. The open period lasts 8–10 hr in the domestic chicken (*Gallus domesticus*), during which a surge of luteinizing hormone can cause ovulation (Sharp 1983). When follicles take longer than 24 hr to mature, laying occurs later each day, until follicle maturation is so late in the day that it is beyond the open period. As a result, ovulation of the follicle would be delayed until the beginning of the open period the following day (Sharp 1983, Lillpers and Wilhelmson 1993), causing a laying gap. Timing of open periods in chickens is influenced proximately by daylengths and light intensity (Phillips et al. 1985). However, we suggest that the timing of "open periods" in wild birds may be determined ultimately by diel patterns of predation, weather, or food availability. The hypothesis of an open period predicts that eggs will be laid at a restricted time during the day and that food availability for the hen need not affect laying rates.

White-tailed Ptarmigan (*Lagopus leucurus*) in the alpine and Willow Ptarmigan (*L. lagopus*) in the arctic are ground-nesting grouse which often have high levels of nest predation, 60–80% of all nesting attempts (Wiebe and Martin 1994) and short breeding seasons. Martin et al. (1993) noted variation between the species in egg laying rates. We examine patterns of (1) timing of laying during the day, (2) inter-egg intervals, and (3) laying rates within and between species. We investigated whether physiological mechanisms or nutrient constraints might be operating in each spe-

cies by relating the duration of the laying period to measures of female quality and environmental factors.

## METHODS

White-tailed Ptarmigan were studied from 1987 to 1994 on and near Mt. Evans in Colorado (39°34–40'N, 105°35–53'W, 3,500–4,700 m altitude) and Willow Ptarmigan from 1981 to 1985 at La Perouse Bay in Manitoba (58°24'N, 94°24'W, 0.75 m altitude). The two congeneric species have similar life histories and hatch precocial young, but Willow Ptarmigan have larger body size, and lay nearly twice as many eggs as White-tailed Ptarmigan (mean clutch size for White-tailed = 6.0, Willow = 10.8; Martin et al. 1989, Robb et al. 1992). Details of the study sites and general biology of the species are in Martin (1984a) and Braun et al. (1993).

Females were weighed and measured in the pre-laying period and an index of spring body condition was calculated as the residual from a regression of mass vs. wing length and days before laying (Robb et al. 1992). Indices of body condition were calculated separately for yearlings and adults because yearlings had shorter wings on average than older birds. Birds were classified as yearlings or  $\geq 2$  years by the pigmentation on their primaries (Bergerud et al. 1963, Braun and Rogers 1971). Most birds in both populations were color-banded and of known age. Females were followed throughout the breeding season using either radio transmitters (Mt. Evans) or tracking dogs (La Perouse Bay). We calculated laying dates and clutch sizes following Martin et al. (1989).

Finding nests during laying was difficult because females only spend a short time at the nest site to lay an egg. Once a nest was found, we attempted to visit it once a day to record the laying intervals of subsequent eggs. One nest, when two eggs appeared in a Willow Ptarmigan nest on the same day, was considered egg-dumping (Martin 1984b) and was excluded from analyses. During nest visits, presence or absence of the female on the nest was noted and whether the eggs were cold or warm. To ensure an accurate laying rate for an individual female, we only used clutches when we knew the exact day of laying for the first and last eggs in a sequence of at least three successive eggs. Laying rates were calculated as the number of eggs (minimum of three) divided by the number of days during which

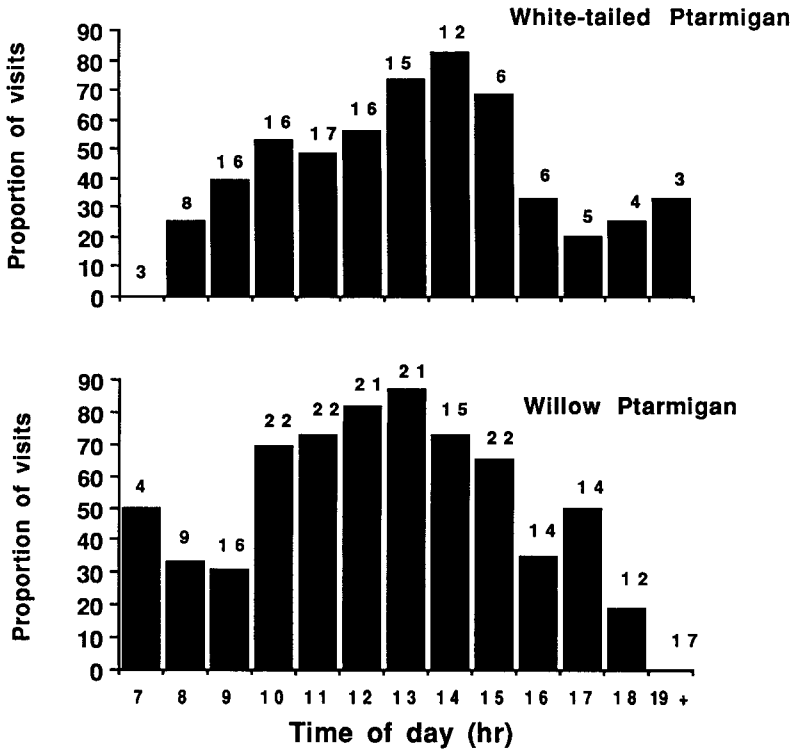


FIGURE 1. Proportion of our visits to the nest during which a female White-tailed or Willow Ptarmigan was observed laying an egg. Number of visits per time interval are shown. Time interval “7” means 07:00–08:00 hr, etc.

those eggs were laid. In cases where the laying rate of a female was recorded in two years, ( $n = 2$  for Willow, 4 for White-tailed) we included both observations in the analyses; the statistical tests did not change when only one observation per female was included.

In 1994, we placed programmable temperature data loggers (“HOBOS,” Onset Inst., Mass., USA) in nests of laying hens at Mt. Evans, Colorado. These data loggers recorded the temperature in the nest bowl every 3.2 min allowing us to determine when the hen was on the nest, and intervals between successive eggs. Nests with data loggers were visited daily to confirm an egg was laid during the time a hen was on the nest. The laying time was calculated as the midpoint of the 30–60 min interval the hen was present and thus have an error of  $\pm 15$ –30 min.

RESULTS

LAYING TIMES DURING THE DAY

Female ptarmigan laid eggs between 07:00 and 19:00 hr (Fig. 1). For both species, the proba-

bility of finding a female laying an egg peaked around 13:00 to 14:00 hr and these distributions were significantly different from random (Rayleigh Test: White-tailed,  $w = 38.2$ , Willow,  $w = 37.8$ ,  $P < 0.05$ ). However, the peak of laying was gradual, protracted over about 6 hr in mid-day. Repeatabilities of laying times for White-tailed Ptarmigan with multiple records ( $n = 11$ ) was not high; the mean difference among laying times within females was  $3.8 \text{ hr} \pm 0.76 \text{ SE}$  and as high as 8 hr.

INTER-EGG INTERVALS AND LAYING GAPS

Using HOBO temperature loggers in nests, we obtained 21 laying intervals for nine females (Table 1). The distribution of these intervals was bimodal; 14/21 (67%) were between 24 and 30 hours (mean = 26.3, SE = 0.42) and 7/21 (33%) were between 40 and 47.5 hours (mean = 43.7, SE = 1.12). Individual females were not characterized by having either short or long intervals. All six females with long intervals ( $\geq 40$  hours)

also had a short interval ( $\leq 30$  hours) in the same clutch. Two long intervals in succession were rare but did occur in a few White-tailed Ptarmigan during bouts of severe weather. Missed days during laying did not occur with more frequency in the beginning or end of the laying sequence. When we classified the gaps as occurring either during beginning (first half) or end (last half) of clutches of White-tailed Ptarmigan, we found almost exactly equal frequencies of skips in each; 47% at beginning vs. 53% at end (G-test:  $G = 0.053$ ,  $df = 1$ ,  $P > 0.1$ ). Our data are few, but there appeared to be a relationship between timing of laying during the day and the subsequent laying interval. In all three cases when an egg was laid after 15:00 hr, there was a laying gap before the next egg. However, there was a laying gap in only 3/17 (18%) of cases when an egg was laid before 15:00 hr.

#### LAYING RATES

We obtained laying rates for 31 White-tailed Ptarmigan and 36 Willow Ptarmigan (including nests with and without HOBOS). For White-tailed Ptarmigan, we were more likely to detect a laying gap when we observed a longer sequence of eggs ( $\chi^2 = 5.8$ ,  $P = 0.05$ ), but the number of eggs observed was not associated with clutch size or female age and condition so our analyses of these factors should not be biased. Because the distribution of laying rates in both species was not normal and was not continuous (Fig. 2), we classified rates as "fast" if a female laid one egg per day, i.e., rate = 1, and "slow" if more than one day was required to lay an egg, i.e., rate < 1. Fast or slow laying rates were not associated with nesting attempt (Fisher exact test: White-tailed  $P = 0.15$ , Willow  $P = 0.63$ ) or with year (Fisher exact: White-tailed  $P = 0.16$ , Willow  $P = 0.50$ ) so we pooled the observations. Proportionately more White-tailed Ptarmigan had slower laying rates (61%,  $n = 31$ ) than did Willow Ptarmigan (8%,  $n = 36$ ;  $\chi^2_1 < 0.001$ ). Willow Ptarmigan females had a maximum of one gap, if any, during laying despite the fact that their clutch sizes were larger than White-tailed Ptarmigan and, on average, we observed more eggs in sequence; Willow Ptarmigan: mean = 6 eggs observed in sequence, range 3–12, White-tailed: mean = 4 eggs, range 3–7. Some White-tailed Ptarmigan had multiple gaps during laying (rates < 0.75 eggs/day in Fig. 2).

For the White-tailed Ptarmigan, we attempted

TABLE 1. Inter-egg intervals (hours) according to position in the laying sequence for nine White-tailed Ptarmigan.

Clutch size	Egg number			
	1–2	2–3	3–4	4–5
6		30	40	25.5
6	28	42	25	25
6			47.5	28
6			42	26
5				24
5	24	25		
5		28	46	
5	42	28	26	
5		47	26	

to identify whether gaps were related to female quality or to environmental factors. Wing length, a correlate of female size, was not associated with fast or slow laying rates (ANOVA:  $F_{1,30} = 0.49$ ,  $P = 0.48$ ). There was also no relationship between laying rates and female spring body condition (ANOVA:  $F_{1,27} = 0.05$ ,  $P = 0.82$ ) or with the body condition index classified into three equal groups, low (poor condition), medium, and high (Fisher exact test:  $P = 0.88$ ). Older and more experienced females did not have faster laying rates than yearlings (Chi square test:  $\chi^2_1 = 0.75$ ,  $P = 0.38$ ) and laying rates were not associated with clutch size (ANOVA:  $F_{1,30} = 1.96$ ,  $P = 0.17$ ).

There was a positive relationship between clutch initiation date and egg-laying rate (fast vs. slow) for White-tailed Ptarmigan (ANOVA:  $F_{1,30} = 4.72$ ,  $P = 0.04$ ) but a visual inspection of the data suggested this relationship was only present in one year, 1992, when there were severe spring storms. When the 1992 data were removed, the relationship was no longer significant ( $F_{1,21} = 2.2$ ,  $P = 0.15$ ). The few Willow Ptarmigan nests with laying gaps ( $n = 5$ ) were laid earlier than nests without gaps (ANOVA:  $F_{1,32} = 5.57$ ,  $P = 0.02$ ). We also analyzed rates of egg laying using adjusted clutch initiation dates. Willow Ptarmigan laying early relative to the population had slower laying rates than birds laying later (ANOVA:  $F_{1,32} = 7.96$ ,  $P = 0.008$ ) but not White-tails ( $F_{1,30} = 1.96$ ,  $P = 0.17$ ). To distinguish whether slow rates early in the spring were the result of laying dates per se, or storms which were more likely to occur in spring, we looked at the timing of laying gaps compared to the timing of bad weather. While not every one-day skip in White-tailed Ptarmigan was associated with spring storms, low

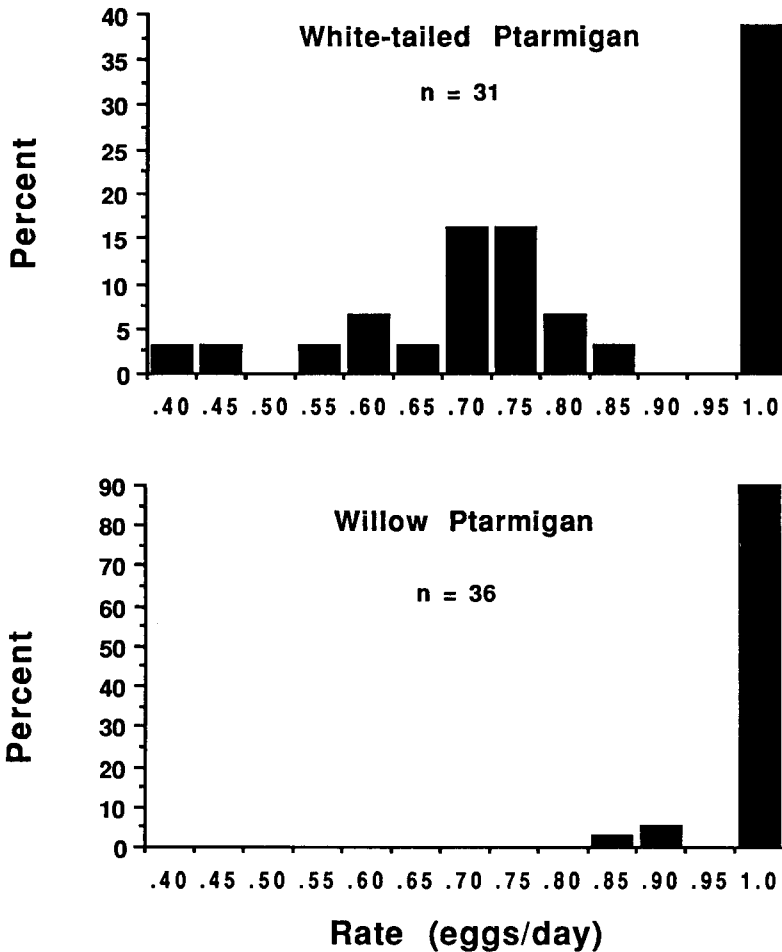


FIGURE 2. Egg laying rates of female White-tailed and Willow Ptarmigan.

temperatures and heavy snowfall seemed to be a factor in all cases with inter-egg intervals greater than 48 hr, and in cases with successive "long" inter-egg intervals of 40–48 hr (Fig. 3). For Willow Ptarmigan, two of three one-day laying gaps occurred with snowstorms early in the season.

## DISCUSSION

### INTER- AND INTRASPECIFIC COMPARISONS OF INTRA-EGG INTERVALS

Intraspecific variation in egg laying behavior could result from physiological or nutritional constraints, or potentially be a strategy of adaptively varying resource allocation patterns and investment. Variable inter-egg intervals within and among species of wild gallinaceous birds may

not be uncommon (Table 2) and it appears that North American galliformes, in general, are not restricted to laying at a certain time of day consistent with our observations (Fig. 1). Our use of data loggers in nests allowed continual monitoring of nest temperatures, and calculation of precise inter-egg intervals. We found that reporting an "average interval" was somewhat meaningless because the distribution of laying intervals was bimodal. Variable laying intervals confirmed that laying gaps were real for our populations, and not an artifact of our sampling methods.

### NATURAL SELECTION AND EGG LAYING RATES

Likely there are both costs and benefits to laying many eggs quickly. Egg formation requires high

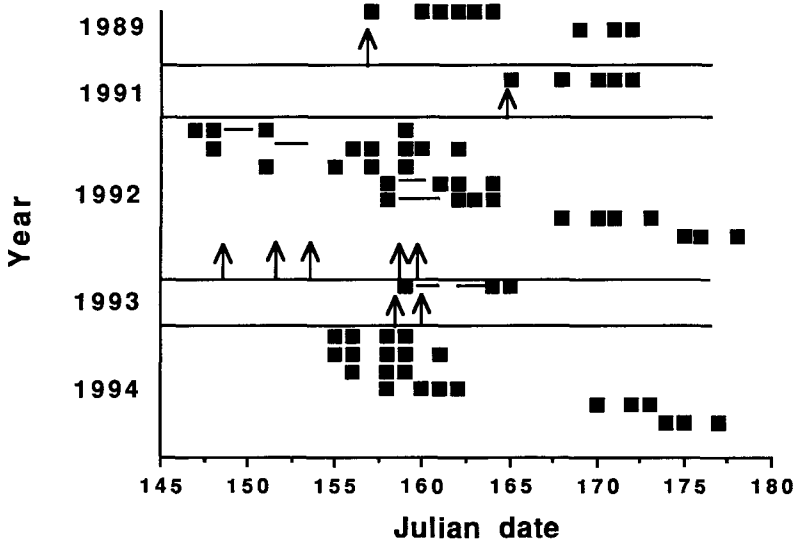


FIGURE 3. Julian dates on which eggs of White-tailed Ptarmigan were laid, and dates on which spring snow storms occurred. Years are separated by horizontal lines and snow storms are marked with arrows. The laying pattern of an individual female is on a single line with each square being an egg laid on that day. Spaces represent laying gaps. Dashes within the laying sequence mean an egg was laid during that time, but the exact day was not known. Julian date of 1 = January 1.

levels of protein and calcium to be mobilized either from body reserves or from the diet while the follicle is passing through the oviduct (King 1973). A new follicle will not be released into the oviduct until the previous follicle (egg) has been

laid (Welty 1983). An inter-egg interval of 24 hr seems to be the physiological maximum rate birds can achieve; domestic chickens selected for fast and prolonged egg laying with unlimited food (i.e., no nutrient costs) do not lay more than one

TABLE 2. Egg-laying intervals and laying times for North American galliformes. Note that the methods and rigor of data collection in these studies vary.

Species	Mean inter-egg interval (hours)	Laying time	Source
Gray Partridge ( <i>Perdix perdix</i> )	26.5		McCabe and Hawkins 1946
Spruce Grouse ( <i>Dendragapus canadensis</i> )	34-48 34 (24-144)	afternoon	McCourt et al. 1973 Robinson 1980
Blue grouse ( <i>Dendragapus obscurus</i> )	36 48-60		Caswell 1954 Zwickel 1992
Willow Ptarmigan ( <i>Lagopus lagopus</i> )	24-26 24	all day all day-peaks midday	Sandercock 1993 This study
Rock Ptarmigan ( <i>L. mutus</i> )	36 (24-48)	all day	Watson 1972 Holder and Montgomerie 1993
White-tailed Ptarmigan ( <i>L. leucurus</i> )	26 and 44 (24-192)	all day-peaks midday	This study
Ruffed Grouse ( <i>Bonasa umbellus</i> )	36		Bump et al. 1947
Greater Prairie-Chicken ( <i>Tympanuchus cupido</i> )	24 (24-72)		Schroeder and Robb 1993 Lehmann 1941
Bobwhite ( <i>Colinus virginianus</i> )	28.8	all day	Klimstra and Roseberry 1975

egg per day (Lillpers and Wilhelmson 1993). In wild birds, energetic and foraging costs would be expected to slow laying rates, while predation or short breeding seasons would select for faster laying. Eggs of precocial species have relatively larger yolks than eggs of altricial species and require a greater caloric input (Ricklefs 1977, Carey et al. 1980). Laying rates of populations in the wild may thus be a compromise based on energy intake, predation risk, and time constraints.

High predation rates on ptarmigan nests (Braun et al. 1993) and the fact that renesting ability declines with calendar date should select for early laying and a reduced time eggs are in the nest. Clearly, physiological and hormonal mechanisms in both species of ptarmigan allow some individuals to lay at the physiological maximum of one egg per day for the entire clutch (see Fig. 2), but why don't all females do so?

#### NUTRIENT CONSTRAINTS

Our results for White-tailed Ptarmigan do not support a simple link between food supply and laying rates. The presence of laying gaps was not associated with our measure of female body condition in the pre-laying period, or other possible reproductive correlates such as clutch size, age, or nesting attempt. Laying gaps did not occur more frequently later in the laying sequence (c.f., Nilsson and Svensson 1993) as would be expected if females were depleting body reserves during laying. Birds may depend on both stored body reserves "capital" and food during laying "income" for egg formation (see Drent and Daan 1980; Ankney et al. 1991; Wiebe and Bortolotti, in press). Spruce Grouse *Dendragapus canadensis* (Naylor and Bendell 1988) and galliformes in general (Thomas 1988) seem to rely heavily on food intake during laying to form eggs. If ptarmigan are similar, perhaps females that could not forage efficiently during spring storms had laying gaps (Fig. 3). Nevertheless, many single-day laying gaps in White-tailed Ptarmigan could not be easily explained by weather events or nutritional constraints on the date the gap occurred (Fig. 3).

#### PHYSIOLOGICAL MECHANISMS

We observed a significant clustering of laying times around midday in both ptarmigan populations consistent with the physiological hypothesis, but some females also laid in the early morning and late afternoon hours (Fig. 1). The vari-

ation in laying times suggests the open period for ptarmigan may be quite broad (c.f., 8–10 hr span in chickens). Another explanation is that individual females have open periods at different times of day, so that laying times among females might vary but the times for a given female should be similar. We do not believe this is the case because mean laying times within White-tailed Ptarmigan females differed on average by nearly four hours, and some by as much as eight hours.

If the minimum time it takes to develop successive follicles is greater than 24 hr, laying will occur progressively later each day until a mature follicle is no longer in synchrony with the "open period." Then, a laying gap will occur. If first eggs are laid early in the day, laying gaps should occur only after a few eggs are laid. In nine clutches of White-tailed Ptarmigan, the first eggs were laid between 10:00 and 18:00 hr (similar to Fig. 1), so we would expect laying gaps to occur at any point in the laying sequence (Table 1). While this physiological mechanism predicts laying gaps even in the absence of nutrient constraints, food availability or energetic costs presumably affect egg development time in the oviduct. If this is the case, hens (or species) with slow egg development times would get out of synchrony with the open period sooner and more often, and would therefore have more laying gaps than hens with egg formation times closer to 24 hr (Lillpers and Wilhelmson 1993). Although we did not measure exact inter-egg intervals for Willow Ptarmigan, the fact that gaps did not occur despite larger clutches and longer sequences of eggs compared to White-tailed Ptarmigan suggests their inter-egg intervals may be closer to 24 hr. Sandercock (1993) reported intervals of 24–26 hr for Willow Ptarmigan, and only one laying gap for 45 females, similar to our results.

#### EXPLAINING LAYING PATTERNS IN PTARMIGAN

We suggest that a combination of nutrient constraints and physiological mechanisms explains patterns of inter- and intraspecific variation in laying rates in ptarmigan. While food supply and weather in the alpine and arctic might appear similar, alpine ptarmigan may have increased energetic costs due to hypoxia and its physiological correlates as suggested by Martin et al. (1993); thus, it may take longer for some individuals to form an egg at high altitude. High daily energy allotments to egg formation result in a

more rapid depletion of body reserves (King 1973) or require more time spent foraging. Perhaps because of high energy costs, White-tailed Ptarmigan in the alpine invest relatively less in clutch volume than Willow Ptarmigan (clutch volume as percent of body mass = 35% in White-tails vs. 47% in Willows; Martin et al. 1993). Shorter summer day lengths in the alpine compared to the arctic may reduce the time for White-tailed Ptarmigan to forage. Future research is needed to quantify energetic costs of egg formation in alpine versus arctic habitats, and to document how these might affect patterns and timing of follicle development in wild birds.

Although an open period controlled by hormones helps to explain laying schedules in ptarmigan, ecological factors may offer an ultimate explanation for why the open period has the timing it does. We have little data on levels of predation risk during the day, but data-loggers in nests of seven incubating females in Colorado showed that all clutches were depredated between 23:00–07:00 hr at night. This pattern would select for laying during the day to avoid crepuscular and nocturnal periods of high predator activity. Other factors that need to be considered when forming a general explanation for egg-laying in birds are trade-offs between body mass (including egg mass in the oviduct) and predation risk, and diel patterns of weather and optimal foraging time.

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