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Effects of predation, body condition and temperature on incubation rhythms of white-tailed ptarmigan *Lagopus leucurus*

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The effects of predation risk, body condition of females, and microclimate at the nest site on timing and length of incubation recesses at 30 nests of white-tailed ptarmigan *Lagopus leucurus* were examined. Incubation patterns in 1994 (an early year) were also compared to those of 1995, an unusually late spring with low temperatures. Data on incubation schedules were obtained by placing programable temperature data-loggers in nests and by direct observation of incubating females. Some egg depredation was associated with movements of hens to and from nests, but there were no apparent differences in risk between crepuscular recesses and daytime recesses. Ptarmigan showed high nest attentiveness (>90%) in both years of the study but took significantly more recesses of longer duration in 1995 than in 1994. This suggests that the amount of recess time was affected by body condition of the female which was lower during incubation in 1995. The overall number of recesses per day did not vary according to cover at the nest site; however, females with nests that had no overhead cover did not leave during the warmest part of the day. It is suggested that timing of recesses in this population of ptarmigan is related to microclimate and body condition, rather than being a strategy to avoid predation.

Key words: body condition, incubation, *Lagopus leucurus*, predation, temperature, white-tailed ptarmigan

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To hatch eggs successfully, incubating birds must balance their own somatic requirements to forage away from the nest, and the need to protect eggs from predators and from extremes of temperature (Drent 1975, Skutch 1976). In addition to the energetic cost of providing heat to eggs, incubation may be particularly stressful for female Galliformes because most males do not share incubation duties or bring food (Johnsgard 1983). Grouse have longer incubation periods (21-27 days) than most passerines and the risk of predation on ground nests is typically high (Johnsgard 1983). In ptarmigan as in many other grouse species, the greatest attrition in potential fecundity is loss of eggs during incubation (Martin,

Hannon & Rockwell 1989, Braun, Martin & Robb 1993). Together, these factors probably impose strong selection pressure on the behaviour of female grouse during incubation. To date, most studies about patterns of incubation in wild birds address passerines (e.g. Morton & Pereyra 1985, Haftorn 1988) or waterfowl (review in Afton & Paulus 1992) breeding in temperate habitats. Observations of incubating grouse in the wild are mainly anecdotal (e.g. Zwickel & Lance 1965, McCourt, Boag & Keppie 1973, Maxson 1977 but see Erikstad 1986). Giesen & Braun (1979) described the general behaviour of female white-tailed ptarmigan *Lagopus leucurus* during incubation but did not monitor nests continuously.

Generally, little is known about energetic and behavioural trade-offs for grouse during incubation especially in harsh environments.

Timing and length of incubation recesses in birds may be influenced by ambient temperature, body condition of females, and the risk of predation on eggs and adults. The importance of ambient temperatures has been emphasized for small-bodied passerines and shorebirds which may take more recesses during the warmest part of the day (Zerba & Morton 1983, Cartar & Montgomerie 1985) and adjust the length of recesses to rate of egg-cooling (Haftorn 1988). Larger birds, such as waterfowl, are able to accumulate and store nutrient reserves for incubation and, for these species, body condition rather than ambient temperature is believed to be the most important factor determining schedules of recesses (Afton 1980). Female Canada geese *Branta canadensis* leave the nest more frequently as body mass declines during incubation (Aldrich & Raveling 1983). Similarly, willow ptarmigan *L. lagopus* females with a low body mass before laying spent more time off the nest during incubation (Erikstad 1986). Predators that hunt by vision, may track movements of incubating females to and from nests which makes leaving the nest risky. Crepuscular recesses in low light levels may be a strategy to avoid predation by avian predators (Giesen & Braun 1979, Angelstam 1984).

In this paper we examine the extent to which predation risk, body condition and ambient temperatures at nest sites influence timing of incubation recesses in an energetically costly environment. We studied white-tailed ptarmigan breeding in an alpine environment characterized by large diel fluctuations in temperature, intense solar radiation, and hypoxia (Martin, Holt & Thomas 1993). If incubation constancy of ptarmigan is dependent on body reserves accumulated before laying, we predict that females should take more or longer recesses in 1995, an unusually cold and late season compared to 1994. If hens schedule recesses according to ambient temperature, they should leave during mid-morning or mid-afternoon hours when exposed eggs will not cool or heat rapidly.

Methods

White-tailed ptarmigan are the smallest species of grouse in North America, with females averaging 325 g in late summer (Braun et al. 1993). We studied

white-tailed ptarmigan in 1994 and 1995 on and near Mt. Evans, Colorado (39°34-40'N, 105°35-53'W) in alpine habitat at 3,350-4,250 m. a.s.l. A mean clutch of six eggs is laid in a ground nest and incubation periods range from 24 to 27 days (Martin et al. 1993). Predation rates on first nests vary between 40 and 70% annually, but females may lay a replacement clutch if the first clutch is destroyed early in the season. Details about the general biology of the species and study area were summarized by Braun et al. (1993).

We captured ptarmigan and affixed 3.8 g radio-transmitters shortly after birds arrived on study areas. We relocated birds subsequently throughout the breeding season and recorded laying date, clutch size, and nesting success for most females. Field methods and data collection protocols followed Artiss & Martin (1995). Each year, females were captured during incubation using noose carpets. An index of body condition was calculated using the residual of a regression of mass on wing length. Because body mass declined throughout incubation, we only used mass of females captured during days 3-7 of incubation to compare individuals between years. We placed programable temperature data loggers ('HOBOS', Onset Inst., MA., USA) in nests which recorded temperatures (range: -37° to +45°C) every 3.2 minutes and allowed us to determine to an accuracy of one minute the time hens left, or returned to, nests. Because data loggers responded more quickly than eggs to changes in temperature, we could not equate the minimum logger temperature with minimum egg temperature in the nest bowl. However, changes in data logger temperatures should be proportional to those of eggs. Nest sites were visited every four days to exchange data loggers. Timing of nest predation was unrelated to the timing of our visits and we do not suspect that predators followed us to nests. Eight hens that were radio-marked in spring 1995 but not checked again until late summer had similar hatching success to those hens whose nests we located and visited. Thus, our activity did not appear to increase the overall predation at nests (see also Hannon, Martin, Thomas & Schiek 1993).

To measure ambient temperatures of nest sites (i.e. temperatures experienced by eggs lying exposed in nests), we placed a data logger in the nest bowl within a week after it was vacated by the female in 1994 and let it run for four days. Mean temperatures for each hour of the day at each nest site were calculated. We had insufficient HOBOS to measure temperatures

at all nests simultaneously, so we analyzed temperature profiles over two clear days with similar temperature profiles: 17 and 23 July, 1994.

In 1995, we observed the behaviour of females during morning and evening recesses. One hour before the hen left the nest, observers stationed themselves behind boulders about 50 m from the incubating hen. The timing of recesses we observed during these periods did not differ from those recorded by the data loggers in our absence and we do not believe our presence affected behaviour of hens. We followed hens after they left the nest and recorded the location of feeding sites using a compass and UTM coordinates (accurate to 10 m). An individual was classified as 'not eating' in a 30-second period if it did not peck at the ground during that time.

Data were analyzed using SAS (1988) and SPSS (1995). The total recess time per day was log-transformed for statistical tests, but was untransformed in some figures for clarity. For the five hens monitored both in 1994 and 1995, data from both years were included as independent observations. Weather data were obtained from a station on Mt. Evans (3,243 m). The maximum temperature recorded by the weather station during 17 and 23 July, 1994 was 21 and 22°C respectively.

Results

Timing of recesses

We recorded incubation recesses during a total of 369 days at 14 nests in 1994 and 16 nests in 1995. Laying dates of first clutches in 1994 (mean date 3 June)

Table 1. Timing (24 hrs) and length (minutes) of nest recesses taken by white-tailed ptarmigan and female body mass (g) during incubation. Means are shown with standard deviations in parentheses.

	1994	1995	1994-95
Dawn recess, (N)	133	208	341
Time	5.00 (0.10)	5.16 (0.12)	5.13 (0.18)
Length	24.2 (4.6)	30.0 (11.2)	24.9 (10.6)
Dusk recess, (N)	134	220	354
Time	20.1 (0.33)	20.1 (0.32)	20.1 (0.59)
Length	28.1 (7.4)	37.7 (16.8)	31.2 (21.5)
Day recess, (N)	103	257	360
Time	13.7 (3.4)	12.9 (3.4)	13.4 (3.78)
Length	17.4 (5.4)	20.9 (9.13)	19.6 (6.7)
Recesses/day	2.65 (0.85)	3.33 (1.2)	3.07 (1.1)
Recess minutes/day	61.5 (17.7)	88.2 (37.5)	77.8 (31.6)
Incubation mass*	405 (N = 13)	376 (N = 17)	

* Females weighed during days 3-7 of incubation.

were the earliest, on average, of any year during an 8-year study in contrast to those in 1995 which were the latest recorded (26 June). Incubating hens spent most of the 24-hour period on the nest; overall incubation constancy was 95.7% in 1994 and 93.9% in 1995. Recesses could be classified into three types: dawn, dusk, and daytime (Table 1). Almost invariably, hens took crepuscular recesses (dawn, dusk) each day; only two dawn and three dusk recess opportunities

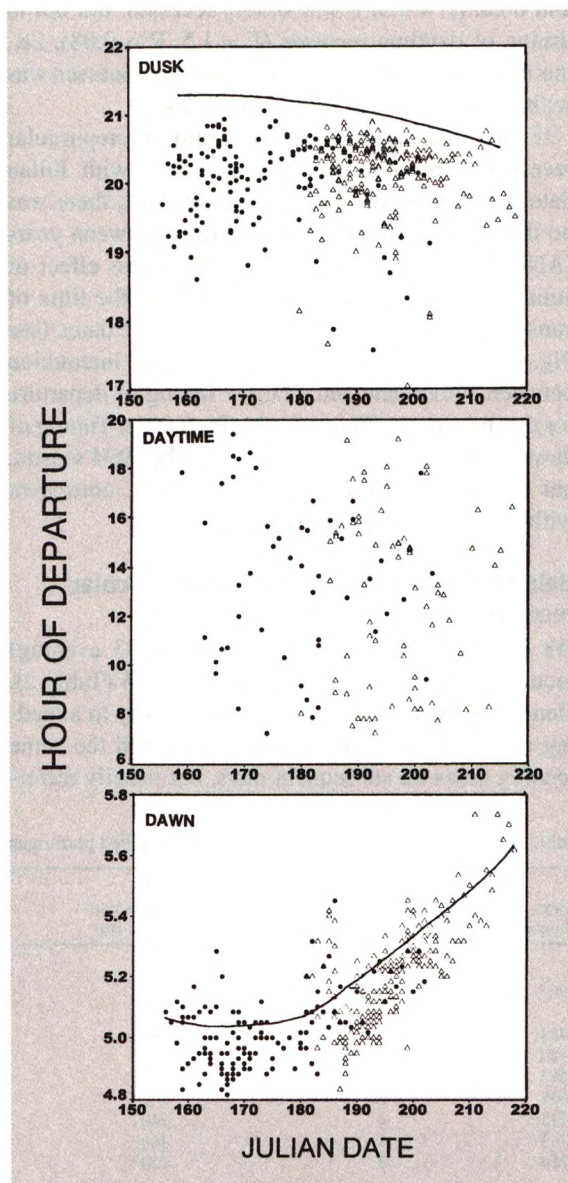


Figure 1. Times of departure for crepuscular and daytime incubation recesses by female white-tailed ptarmigan on different dates. Lines for crepuscular recesses are times of civil twilight. Symbols: 1994 (●), 1995 (△). Note the different scales on the y-axes.

were missed (<1%). The latest evening recess we observed was at 22:05 hrs and hens did not leave nests at night. Between 0 and 5 daytime recesses were taken daily and were typically of shorter duration than crepuscular recesses (see Table 1). While crepuscular recesses occurred within narrow time limits, timing of daytime recesses was much more variable (see Table 1, Fig. 1). There were significant overall differences (1-way ANOVA) between females (N = 30) in the timing of dawn ($F = 18.6$, $P < 0.001$) and dusk ($F = 3.5$, $P = < 0.001$) recesses, but not in timing of daytime recesses ($F = 1.5$, $P = 0.08$), i.e., the majority of the variation in daytime recesses was within, rather than among, individuals.

If light intensity is a cue for timing of crepuscular recesses there should be a relationship with Julian date (i.e. daylength). For recesses at dusk, there was no difference in the time of departure between years (ANCOVA $F_{1,353} = 0.01$, $P = 0.93$) and no effect of Julian date ($F_{1,353} = 2.33$, $P = 0.13$), but the time of sunset also varied little over this range of dates (see Fig. 1). In contrast, there was a significant interaction between Julian date and year for timing of departure for dawn recesses ($F_{1,340} = 71.94$, $P < 0.001$). Timing of dawn recesses did not change during the 1994 season, but increased with Julian date in 1995, consistent with the shorter days (see Fig. 1).

Behaviour observations during crepuscular recesses

We observed 36 crepuscular (3 dawn, 33 evening) incubation recesses of 10 females in 1995 (Table 2). Hens flew from the nest site all or part way to a feeding area 50-800 m away. Some hens used the same feeding areas on subsequent days, but usually differ-

ent sites were used, separated by as much as 850 m. A majority of the incubation recess (mean 88%) was spent feeding voraciously, mostly on leaves of *Salix*. The remainder of the time was spent preening, dust-bathing, and walking. Females usually returned to the nest by flying most of the way back, and walking the last 10-30 m. Interestingly, the male had a role in the timing of the recesses of 7 of 10 females (see Table 2). Within a minute after hearing their mate give a territorial 'challenge-call' (Schmidt 1988), hens became alert, left their nest, and flew to him. On other occasions, females initiated the recess by flying from the nest and were subsequently joined by their mate at the feeding site. Males stayed within 5 m of females during recesses, remained vigilant and did not feed. They usually followed hens in the flight back to the nest site.

Timing of predation events

About two-thirds of predation events (21 of 33) recorded by data loggers in nests occurred during the night between 22:30 and 04:30 hrs (Fig. 2) and the distribution was significantly different from random (Rayleigh Test: $R = 13.56$, $P = 0.002$). The three predation events at dawn were almost certainly associated with nest recesses as they occurred within minutes of the hen's 'normal' recess time. In one predation at dusk, the data logger indicated that the hen was killed on the nest minutes after starting to rewarm the eggs after a recess. The other three predations at dusk and five during the day could not be linked with certainty to recesses.

Effect of body condition

The body condition index of females was significant-

Table 2. The behaviour of female and male white-tailed ptarmigan during incubation recesses and the distances to feeding sites.

Ring Number	Number of recesses observed	Mean distance to feeding site (m)	Maximum distance between sites (m)	Percent time feeding	Male behaviour*
5067	4	660	150	88	called (2) joined (1)
5438	5	580	300	91	called (2) joined (2)
5480	4	375	600	85	-
5497	5	360	750	85	called (4)
5695	2	75	150	92	called (2)
5733	4	240	200	82	-
5743	1	400	-	83	called (1)
5786	3	170	320	90	-
5903	3	470	300	87	called (1) joined (2)
5910	5	390	850	89	called (2)

* Called: male called and then female flew to him, joined: female flew from the nest silently and male subsequently joined her. Numbers in parentheses give the frequencies in which the behaviours were observed. If male behaviour is not recorded, the female was alone during the recess.

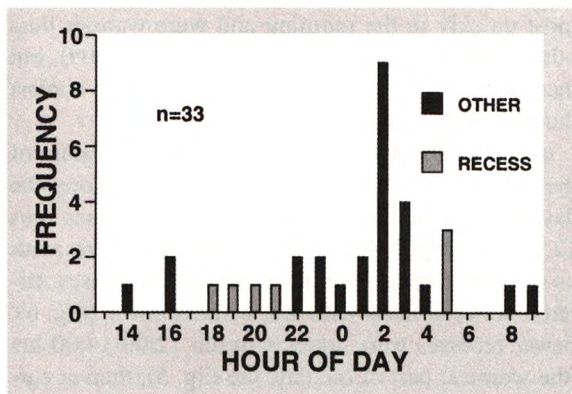


Figure 2. Frequency of predation events on eggs of white-tailed ptarmigan during crepuscular recesses and at other times.

ly lower in 1995 than in 1994 ($t = 2.3$, $df = 28$, $P = 0.046$) and body mass also declined by about 11% during incubation (K.L. Wiebe, unpubl. data). To investigate the relationship between body condition and the number and duration of incubation recesses, we included year as a category in ANCOVAs and day of incubation as the covariate. Number of recesses increased during incubation in both years ($F_{1,359} = 56.5$, $P < 0.001$; Fig. 3). There was no interaction between slopes for the two years ($F_{1,359} = 0.46$, $P = 0.50$) but significantly more recesses were taken in 1995 than in 1994 ($F_{1,359} = 13.78$, $P < 0.001$). Females added daytime recesses to crepuscular recesses only part way through incubation in 1994, but included daytime recesses at the beginning of incubation in 1995. The relationship between total recess time per day (logged) and day of incubation differed between years (ANCOVA interaction: $F_{1,357} = 4.53$, $P = 0.03$). Total time off the nest per day did not change during incubation in 1994 ($r^2 = 0.006$, $N = 133$, $P = 0.35$) but

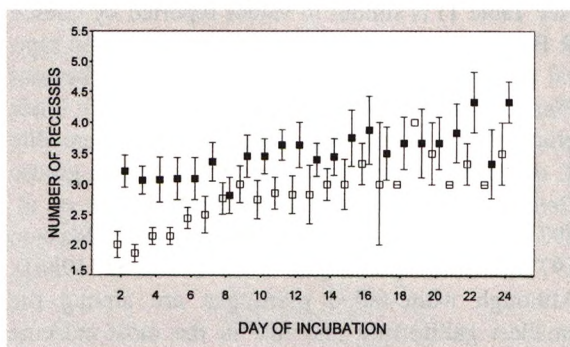


Figure 3. Number of recesses taken by female white-tailed ptarmigan according to stage of incubation in 1994 (□) and 1995 (■). Means are given with standard errors.

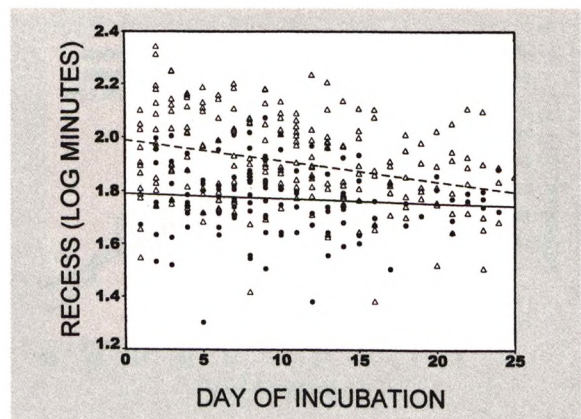


Figure 4. Total recess time (log minutes) of female white-tailed ptarmigan by stage of incubation in 1994 (●) and 1995 (△). The interaction between the slopes of the lines fitted by ANCOVA was significant.

decreased during 1995 ($r^2 = 0.09$, $N = 221$, $P < 0.001$) although the overall time off the nest at all stages was greater in 1995 than in 1994 (Fig. 4). The lower constancy in 1995 probably resulted from lower body mass rather than increased energetic costs during incubation because mean ambient temperatures during incubation in 1994 (11.2°C) were similar to those during incubation in 1995 (10.5°C).

Number of recesses per day in both years increased during incubation but the total time off the nest did not, indicating that the length of recesses became shorter as incubation progressed. Associated with shorter recesses, temperatures in the nest bowl when the female was absent were higher in late compared to early incubation (ANCOVAs on dawn $N = 266$, dusk $N = 271$, and day $N = 202$ recesses separately: year effects non-significant, day of incubation significant $P < 0.01$ in all cases).

Nest site and microclimate

We examined the effect of ambient temperatures during the day on the timing of recesses because the time females left their nests for daytime recesses showed no pattern with respect to Julian date (see Fig. 1) or day of incubation (ANCOVA: $F = 0.68$, $P = 0.411$). Temperature profiles at nests showed extreme variation, ranging from -2°C at night to $\geq 45^\circ\text{C}$ around noon. When nests were classified according to type of cover, and their surface temperatures plotted at hourly intervals (Fig. 5), bare nests without any overhead cover reached the coldest and warmest temperatures during a 24-hour period. A one-way ANOVA showed that at 12:00 hrs, bare nests were warmer

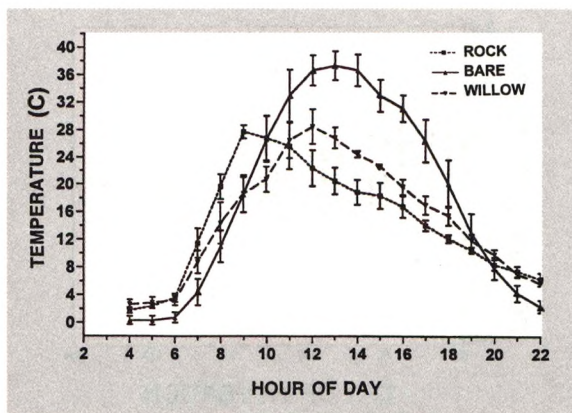


Figure 5. Diel temperature variation in unattended rock ($N = 6$), bare ($N = 6$) and willow ($N = 5$) nests of white-tailed ptarmigan. Means are given with standard errors.

than other nest types ($F_{2,15} = 9.47$, $P = 0.003$) and they remained warmer until about 18:00 hrs. In contrast, eastern-facing nests sheltered by rocks heated up

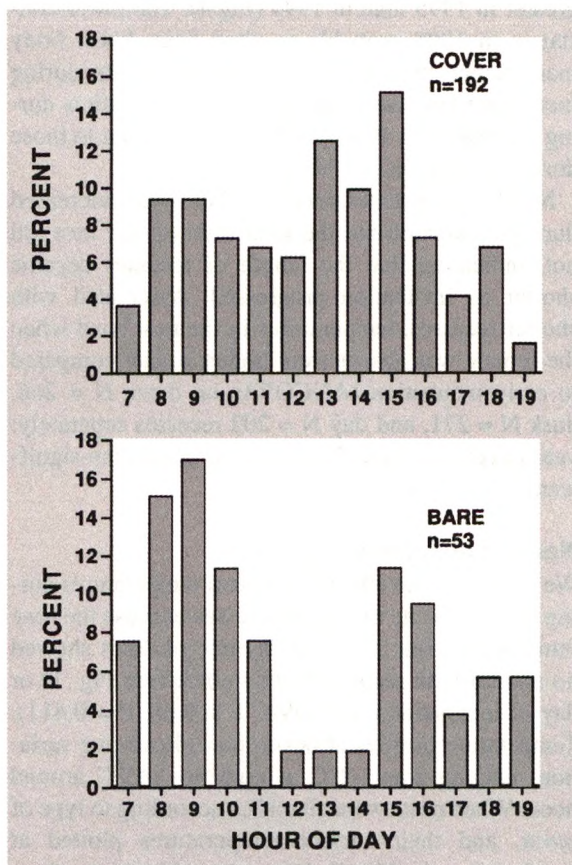


Figure 6. Hourly distribution of daytime incubation recesses by female white-tailed ptarmigan at bare nests with no overhead cover and at rock or willow nests with overhead cover. Only recesses from days when there was only one daytime recess are included.

most quickly in the morning and were warmer than other nests at 09:00 hrs ($F_{2,15} = 6.9$, $P = 0.009$), but thereafter declined in temperature and were coolest during the majority of the day.

In only 15 of 360 cases (5.7%) did temperature of the nest increase when a hen left the nest during the day. The mean time of these 'warm' recesses was 12.24 ± 1.25 (SD) hrs, and all occurred at nests with no overhead cover. Timing of daytime recesses differed between nests with and without cover (Fig. 6). Fewer recesses were taken between 12:00-14:00 hrs (the warmest part of the day, see Fig. 5), than at earlier or later times at bare nests compared to nests with cover ($\chi^2_2 = 13.9$, $P = 0.001$). Although timing of recesses differed between types of nest sites, the overall number of recesses per day did not differ between nests with and without cover (ANCOVAs with day of incubation as a covariate: $F_{1,301} = 0.19$, $P = 0.65$). Total amount of recess time per day did not differ according to nest type either ($F_{1,300} = 0.26$, $P = 0.11$).

Discussion

Incubation recesses in white-tailed ptarmigan appear to be of two types. 'Core' crepuscular recesses are taken almost invariably each day while supplementary daytime recesses are probably in response to declining body reserves. Crepuscular and daytime recesses have been previously documented for white-tailed ptarmigan (Giesen & Braun 1979, Schmidt 1988), but their pattern and regularity during the incubation period was unknown. A relatively small number (2-7) of recesses per day seems typical of most galliforms (Johnsgard 1983). A high incubation constancy of 95% by female ptarmigan in this study (see Table 1) is similar to values reported by Giesen & Braun (1979) based on nest visits and is also typical of other galliforms (e.g. ring-necked pheasant *Phasianus colchicus*: 96% (Westerskov 1958); black grouse *Tetrao tetrix*: 86% (Robel 1969); capercaillie *T. urogallus*: 96% (Pulliainen 1971); spruce grouse *Dendragapus canadensis*: 93% (McCourt et al. 1973); ruffed grouse *Bonasa umbellus*: 96% (Maxson 1977); willow ptarmigan: 96% (Erikstad 1986)). Although white-tailed ptarmigan are among the smallest galliformes and live in the most extreme environmental conditions, they are able to achieve a similar level of nest attentiveness to other Tetraoninae living in more benign habitats.

Incubation constancy

Predation risk may be an important factor selecting for high nest attentiveness. Longer recesses are associated with longer egg-development times (Westerkov 1958, Aldrich & Raveling 1983, Webb 1987) and, since eggs in the nest are more vulnerable than chicks, hens should try to reduce the incubation period by reducing recess time. The need to minimize development time of eggs may be especially critical for ptarmigan in hypoxic conditions at high altitude where incubation periods are longer than for ptarmigan at lower elevations (Martin et al. 1993). High incubation constancy among cryptic birds is also important if moving on and off nests attracts attention of predators or leaves the eggs exposed to view (Inglis 1977). Most nest losses occurred at night for white-tailed ptarmigan and was not linked to recesses, but a few predation events were associated with leaving the nest (see Fig. 2). Therefore, hens should minimize the number, as well as length, of recesses for a strategy of passive nest defence.

An overall strategy of maximizing incubation constancy at the expense of maintaining body reserves is consistent with the observation that, on average, hens lost 11% of body mass during incubation (K.L. Wiebe, unpubl. data). Although ptarmigan fed voraciously during recesses (see Table 2) compared to three species of geese which spent only 14-77% of the recess feeding (review in Thompson & Raveling 1987), hens were apparently in a negative energy balance. Although mass of a female declines during incubation, body condition at hatching may be important for the survival of both hens and chicks. In 1995 when hens had a lower body condition index, they took more recesses and had lower overall incubation constancy than in 1994. Thus, it appears that females are unwilling to let their body reserves fall below a certain threshold.

The relationship between time off the nest and stage of incubation is more complex. Although hens in both years took more recesses as incubation progressed as would be expected when body mass was declining, the length of recesses became shorter so that total time off the nest remained constant in 1994, or even declined in 1995. Thus, overall attentiveness did not decrease during incubation in contrast to Canada geese (Murphy & Boag 1989). Fluctuations in temperature are more detrimental to eggs as incubation progresses (Webb 1987) so perhaps ptarmigan regulate egg temperatures more precisely as incubation proceeds which is a special challenge in an

alpine environment characterized by extremes of temperature.

Timing of recesses

If ptarmigan try to minimize the number and length of recesses, what explains the time those recesses occur? Rewarming eggs is costly, and eggs cool faster than they warm (Drent 1975); to minimize energy for rewarming eggs, birds should take more and longer recesses during the warmest part of the day. Some passerines (Haftorn 1988), waterfowl (Thompson & Raveling 1987) and grouse (Naylor, Szuba & Bendell 1988) do spend more time away from the nest in the warmest part of the day, but we did not observe this. In fact, dawn recesses were taken during the time of day when temperatures were coldest (see Fig. 5), and these recesses were also longer than daytime recesses (see Table 1). Embryos are generally more tolerant of cold temperatures than even short exposures above 40°C (Webb 1987). This explains why ptarmigan avoided mid-day recesses at exposed nests where temperatures could reach 45°C or more (see Fig. 5). Paradoxically, heat stress rather than cold stress may explain timing of incubation recesses in exposed nests of alpine birds (Zerba & Morton 1983). The low variance in the length of crepuscular recesses suggested that ambient temperatures during the incubation period had little effect on the total time off the nest. Similarly, Erikstad (1986) reported that length of recesses in willow ptarmigan was not associated with ambient temperature.

Angelstam (1984) and Erikstad (1986) suggested that crepuscular recesses in grouse may reduce the chance of being detected by a predator while they move on and off the nest. However, on our study area the most important predators were those that hunt by scent (mammals) rather than those that rely on vision (avian). That most depredations occurred at night (see Fig. 6) is consistent with the nocturnal activity of the main predators in our area: coyote *Canis latrans*, red fox *Vulpes vulpes*, and long-tailed weasel *Mustela erminea* (Giesen & Braun 1979). Nevertheless, 7 of 33 (21%) predation events occurred during crepuscular periods, and at least four of these were associated with movements from the nest site. Sample size was small but the number of predation events was similar for each of the dawn, dusk and day periods (see Fig. 6) and number of recesses in each period was also similar (see Table 1). This suggests that crepuscular recesses were not overwhelmingly safer than activity during daylight. If ptarmigan are optimizing the light

level at which they leave the nest in order not to be seen, then light levels at the time of departure for dawn and dusk recesses should be similar, and the timing of recesses should follow the changing day lengths throughout the season. We found that the time of departure for crepuscular recesses was related to day length, but dawn recesses were darker on average than dusk recesses (see Fig. 1).

Incubation strategies and life history

The timing of core recesses at dawn and dusk may simply be the result of foraging constraints and the physiology of hunger and digestion. Hens must fast during the night because it is too dark to forage and, because ambient temperatures are coldest during the night, females will be most hungry in the morning and will feed as soon as light levels allow. Likewise, it should be best to forage in the evening to have energy reserves to last through the night; evening departures at the nest may occur when it is relatively light because the sun is setting and it soon becomes too dark to forage. Supplementary recesses may be added at any time during the day based on hunger (body condition), their timing adjusted to avoid overheating or chilling of the eggs. Length of an incubation recess is probably related to hunger and amount of time required to fill the crop, and may be constrained by ambient temperature at the nest site especially at later stages of incubation. Predation risk has an ultimate effect on incubation patterns by selecting for high nest attentiveness but probably does not affect the time of departure from nests. Body condition and nest site have more proximate effects on timing and number of recesses in white-tailed ptarmigan. The need to incubate eggs almost constantly to protect them from predators and from extremes of temperature may constrain other aspects of the life history of this species. It may be more costly to form eggs in the alpine (Martin et al. 1993, Wiebe & Martin 1995) and clutch size may be limited by the need to retain sufficient body reserves to last through incubation, or to renest. Thus, there may be an energetic trade-off between clutch mass and nest attentiveness.

Females should also choose nest sites which minimize energy demands during incubation. It is unclear (see Fig. 5) which type of nest site provides the best thermal environment. Although bare nests sometimes reached lethal temperatures for embryos during mid-day, they were warmer than other sites in the afternoon and evening and may have offered overall energy savings for hens. Further information about costs

of thermoregulation in white-tailed ptarmigan, and trade-offs between cover and predation risk will help elucidate strategies of nest site selection and incubation in this species.

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