

FREE-LIVING WILLOW PTARMIGAN ARE DETERMINATE EGG-LAYERS¹

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Abstract. Egg-laying behavior of free-living Willow Ptarmigan (*Lagopus lagopus*) was studied at Chilkat Pass, B.C. to learn if females were indeterminate egg-layers in natural conditions. Eggs were removed from clutches of experimental birds during laying, usually beginning with the third egg. All birds were determinate egg-layers and there was no difference in the number of eggs laid by control ($\bar{x} = 8.11$ eggs, $n = 19$) and experimental ($\bar{x} = 8.00$ eggs, $n = 20$) females. Number of eggs did not cue the cessation of laying because females started incubation with 2-3 eggs left in the nest.

Key words: Willow Ptarmigan; *Lagopus lagopus*; determinate laying; clutch size.

INTRODUCTION

Removal of eggs from nests of laying birds can induce extended egg-laying. Birds that respond to egg removal during laying by producing extra eggs in the same nest are *indeterminate* egg-layers, whereas birds that do not lay more than a normal clutch size are *determinate* egg-layers (Cole 1917, Kennedy and Power 1990, Kennedy 1991). Birds that respond to egg removal during laying by immediately producing a replacement clutch of normal size in a new nest are *continuation* egg-layers (Sowls 1955, Arnold 1992), whereas birds that delay production of a second clutch are *renest* egg-layers.

Clutch size in some birds may be limited by food available to the female during egg production (egg formation hypothesis; Winkler and Walters 1983). Maternal nutrition is thought to be particularly important for waterfowl and grouse that lay relatively large clutches (Winkler and Walters 1983, Ankney et al. 1991) of eggs that are rich in yolk (Sotherland and Rahn 1987). Indeterminate and continuation egg-laying are strong evidence for rejecting the egg formation hypothesis (Arnold 1992).

Kennedy (1991) classified the Willow Ptarmigan (*Lagopus lagopus*) as an indeterminate egg-layer because studies of captive birds (Höst 1942, Moss et al. 1981) have shown that females will lay supernumerary eggs. Höst (1942) removed eggs daily from captive ptarmigan during laying

and found females would lay up to 27 ($\bar{x} = 16.8$) eggs, whereas free-living birds generally laid 8-9 eggs. Captive birds may show extended egg-laying because they have ad libitum food that is unavailable to free-living birds (Rohwer 1984). If Willow Ptarmigan show extended egg-laying under natural conditions, maternal nutrition is unlikely to be the factor that limits clutch size. I examined egg-laying behavior in Willow Ptarmigan to learn whether free-living females are indeterminate egg-layers.

METHODS

Willow Ptarmigan were studied at Chilkat Pass in northwest British Columbia (59°50'N, 136°30'W) during 1992. Features of this study area and general methodology have been described by Hannon (1984) and Martin et al. (1989). Conditions in 1992 were not unusual compared to previous years, although density of breeding pairs was low and snow melt was late. Female ptarmigan were captured on territories prior to clutch initiation and classed as yearlings or adults by comparing pigmentation patterns on the primary wing feathers (Bergerud et al. 1963). Each bird was uniquely color-banded and radio-marked.

Willow Ptarmigan lay their clutches in shallow scrapes on the ground at the rate of about 1 egg/day; 85% of females begin incubation after laying the penultimate egg (Schieck 1988). If the entire clutch is depredated during laying or incubation, the female abandons the nest. Ptarmigan can renest but only first nests were used in this study. The mean clutch size of first nests in Chilkat Pass is 8.1 eggs (Martin et al. 1989, range = 5-11 eggs).

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Telemetry was used to locate females daily and to find nests. When a female's nest was first found, it was marked nearby with flagging tape and I returned within 12 hr to count the eggs. Date of first egg was interpolated for nests found during laying (assuming a laying rate of 1 egg/day). A few nests ($n = 9$) were not found until the female had begun incubation, and in these cases, the eggs were floated in water to estimate stage of incubation (Westerkov 1956); the date of first egg was calculated by back-dating (Hannon et al. 1988). After a nest was found, it was visited daily to mark and measure newly laid eggs. Eggs were numbered on the blunt end with a felt marker, and length and width were recorded with Vernier calipers to the nearest 0.1 mm.

Females were assigned to one of two treatments based on number of eggs that had been laid before the nest was found. If a female had previously laid six or more eggs, the clutch was treated as a *control* nest. When control nests were visited, eggs were removed briefly and replaced in the nest bowl. If a female had laid five or fewer eggs, the clutch was treated as an *experimental* nest. If a female had laid 3–5 eggs, 1–3 eggs were removed at once so that two eggs were left in the nestbowl. If a female had laid only 1–2 eggs, I waited until the female had laid three eggs before manipulating the clutch. I delayed clutch manipulation because Willow Ptarmigan that are disturbed early in laying usually abandon their nest (S. J. Hannon, pers. comm.). Experimental nests were visited daily, and eggs were removed as they were laid to keep clutch size at two eggs. If the female was on the nest or had not yet laid the latest egg, I returned later in the same day to remove the egg.

Eggs were stored in a shed at ambient temperature and rotated twice per day. Incubation was considered to have started when females were found on the nest twice within 24 hr. Onset of incubation was a good indication that laying was about to cease and I immediately replaced all eggs removed from that specific nest. I returned two days after incubation had been initiated to ascertain final clutch size.

A better experimental design would have been to find nests on the first day of laying, and randomly assign them to control and experimental treatments. It was not possible to find all nests at the start of laying because females spend only about 1 hr per day on the nest and do not lay at a predictable time of day. However, search time

was equivalent for each female per day, and there was an equal probability of finding a nest on each day of laying. Presumably, females whose nests were found early in laying should not differ in any consistent way from females whose nests were found when the clutch was almost complete.

RESULTS

Female Willow Ptarmigan consistently laid one egg a day at a laying interval that varied from 24–26 hr. The estimate of laying interval is imprecise because each nest was visited only once per day. There was no time of day that laying females could reliably be found on the nest. In the sample of 45 nests that were found at different stages of laying, only one female skipped a day during laying and in no nest did more than one egg appear within 24 hr. Females initially left the nest covered with vegetative matter but began to leave the eggs exposed when laying neared completion. I did not observe partial clutch loss due to depredation in any nest.

The assignment of female ptarmigan to treatment groups was effectively random. There was no significant difference between treatments in proportion of yearling females, timing of clutch initiation, or egg volume (Table 1).

Twenty-two clutches were found late in laying and treated as control nests. Of these, three were depredated during laying (at seven, eight, and nine eggs) and were omitted from further analysis. Final clutch size of the remaining 19 clutches ranged from 6–10 eggs (Fig. 1).

Eggs were removed from 23 experimental clutches. One female abandoned her nest after two of four eggs were removed, two clutches were depredated during laying (at 8 and 10 eggs) and one female abandoned her nest after the removed eggs were returned. The first three clutches were not considered further because laying was incomplete. Clutch size at start of manipulation varied among experimental nests. Egg removal began in 10 (50%) clutches of three eggs, seven (35%) clutches of four eggs, and three (15%) clutches of five eggs.

All 20 experimental females acted as determinate egg-layers because they produced clutches of 5–11 eggs (Fig. 1). Four experimental nests were depredated after eggs were returned but before I was able to assess final clutch size. However, only three (18.8%) of the other 16 females laid an additional egg before I counted the final

TABLE 1. Nesting data for Willow Ptarmigan in the control (19 females, 154 eggs) and experimental (20 females, 159 eggs) treatments.

	Percent yearlings	Julian date of first egg ^a		Egg volume ^b (cm ³)		Clutch size	
		\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Control	32.6	156.84	0.63	19.57	1.06	8.11	0.26
Experimental	40.0	156.15	0.51	19.63	1.37	8.00	0.30
χ^2	0.19						
U (χ^2 approx.)		0.43				0.06	
<i>t</i>				-0.40			
<i>P</i>	0.65	0.51		0.69		0.80	

^a Julian date 156 = 5 June.^b Volume = $k(\text{length})(\text{width})^2$, where $k = 0.49$ for Willow Ptarmigan (Myrberget 1977).

clutch size. The conclusions do not change if any or all of the four females laid an additional egg. There was no significant difference in mean clutch size among experimental females if egg removal began at three, four, or five eggs (H, χ^2 approx. = 0.55, $P = 0.77$). There was no significant difference in mean clutch size of control and experimental females (Table 1).

DISCUSSION

Free-living Willow Ptarmigan in this study were determinate egg-layers. The number of eggs laid

by control and experimental birds (Fig. 1) was identical to the mean (8.1 eggs, Martin et al. 1989) and range (5–11 eggs) of clutch size previously reported for this population. Females did not use egg number as a stimulus to stop laying. Experimental females laid a total of 6–10 eggs but all began incubation with only 2–3 eggs left in the nestbowl. Moss and Watson (1982) reported a similar finding in female Red Grouse (*L. l. scoticus*). If Willow Ptarmigan relied upon tactile (Winkler and Walters 1983) or visual stimuli (Steen and Parker 1981) to stop laying, they should have laid indeterminately in this study.

Kennedy (1991) reported that the schedule of egg removal can influence egg-laying experiments: early removal leads to indeterminate egg-laying whereas late removal produces determinate egg-laying. Timing of egg removal had no effect on mean clutch size in this study, but may partly explain why free-living Willow Ptarmigan laid determinately. Follicle development and yolk synthesis occur quickly in Willow Ptarmigan (Thomas 1986); the ovarian hierarchy usually contains two rapidly developing follicles (Thomas 1982). Egg removal began after the third egg was laid, and some manipulations may have started after half the clutch had been ovulated. Nonetheless, most ptarmigan in the experiment continued to lay for an extended period after egg removal; one experimental female laid an egg per day for seven days before finally starting to incubate.

The timing effect described by Kennedy (1991) may be associated with the rising levels of prolactin which suppress follicular development (Meijer et al. 1990), and are associated with the onset of incubation. Prolactin levels are low in Willow Ptarmigan (H. C. Pedersen and P. J.

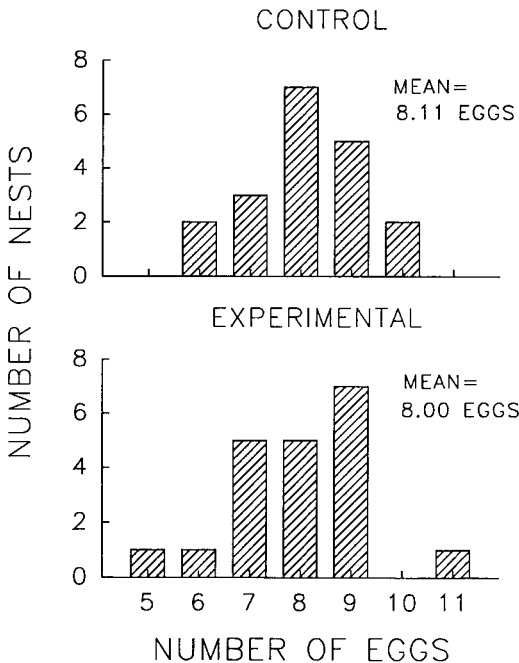


FIGURE 1. Final clutch size in control and experimental nests of free-living Willow Ptarmigan. Eggs were removed from experimental nests during laying.

Sharp, pers. comm.) and Ruffed Grouse (*Bonasa umbellus*, Etches et al. 1979) at the stage of laying when I began to remove eggs, possibly because females do not begin incubation until they have laid the penultimate egg of their large clutch.

The timing of egg removal in this study could have been advanced in the earliest manipulations by only one day, to after the second egg was laid. Kennedy (1991) suggested that egg removal should begin with the first egg. However, Willow Ptarmigan, and perhaps other birds, will not continue to lay eggs in the same nest if the entire clutch is depredated during laying. Removal of the first egg in Willow Ptarmigan would be a test for continuation egg-laying, and not indeterminate egg-laying.

Egg-laying experiments are also sensitive to the amount of the clutch that is removed during laying: American Coots (*Fulica americana*) respond to partial clutch removals by laying an average of one additional egg but lay complete continuation clutches if they suffer total clutch loss (Arnold 1992). Removal of a clutch of eggs during incubation causes a sharp decline in the plasma prolactin of Ruffed Grouse (Etches et al. 1979) and Mallards (*Anas platyrhynchos*, Hall 1987), which may lead to nest abandonment (Armstrong and Robertson 1988). Birds may lay determinately if prolactin continues to rise after partial clutch loss, whereas total clutch loss may lead to continuation laying because the decline in prolactin restarts the laying cycle.

The determinate egg-laying of free-living Willow Ptarmigan in response to partial clutch removals is a marked contrast to the extended egg-laying reported for captive ptarmigan (Höst 1942, Moss et al. 1981). Daily removal of eggs from captive ptarmigan (Höst 1942, Moss et al. 1981) probably simulated total clutch loss, and females may have shown extended egg-laying not as indeterminate egg-layers (as classified by Kennedy 1991), but as continuation egg-layers. The consequences of natural nest abandonment or total clutch loss in free-living ptarmigan (1985–1992, S. J. Hannon, unpubl. data) are inconclusive: 5 of 22 (22.7%) females did not lay more eggs, 7 of 22 (31.8%) delayed at least five days before reneating, and 10 of 22 (45%) females laid possible continuation clutches. The total number of eggs laid in first and continuation clutches was less than the maximum clutch size of first nests in 6 of 10 females (7–11 eggs), but 4 of 10 females laid at least 12–15 eggs.

It is not currently possible to evaluate the egg formation hypothesis because free-living Willow Ptarmigan may be determinate egg-layers for reasons other than maternal nutrition. Indeterminate or continuation egg-laying is good evidence for rejecting the egg formation hypothesis (Arnold 1992), and some free-living Willow Ptarmigan may be capable of extended egg-laying in response to total clutch loss during laying. Free-living Willow Ptarmigan are capable of extended egg-laying in renests (Martin et al. 1989, Milonoff 1989), but reneat egg-laying does not address the egg formation hypothesis. Females could use the reneating interval (Parker 1981) to forage for the nutrients required for a second clutch.

Kennedy and Power (1990) suggested that indeterminacy could be adaptive if it allowed birds to maximize incubation efficiency by adjusting clutch size to natural changes in egg number. Neither egg removal nor addition are likely to act as strong selection pressures on Willow Ptarmigan. Conspecific removal of eggs has not been observed and partial nest predation is rare at Chilkat Pass; 98–100% of the eggs laid in first nesting attempts are still present at hatch (Martin et al. 1989, this study). Intraspecific nest parasitism is also rare in Willow Ptarmigan. I observed no egg dumping. Martin (1984) reported one of 30 nests was parasitized in a two-year study and Schieck and Hannon (in press) reported three of 49 nests were parasitized in a three-year study. These studies used laying rates of more than 1 egg per day to indicate parasitism (Clawson et al. 1979), and the estimates have been corroborated by DNA fingerprinting (J. R. Freeland, unpubl. data). The low frequency of nest abandonment observed in this study indicates that Willow Ptarmigan are insensitive to changes in egg number. Free-living Willow Ptarmigan may be determinate egg-layers because the rarity of natural egg removal and addition create only weak selection for indeterminacy.

Free-living Willow Ptarmigan at Chilkat Pass are poorly adapted to cope with natural changes in egg number because females function as determinate egg-layers for a large portion of the egg-laying period. If females could lay indeterminately in response to earlier egg removals, they would only be able to compensate for partial clutch loss that occurred before the third egg was laid. The critical test of the egg formation hypothesis (Winkler and Walters 1983) in free-liv-

ing Willow Ptarmigan will be to remove entire clutches early in laying. If free-living birds are capable of extended egg-laying in continuation nests, nutrient availability can be rejected as a constraint on clutch size.

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