

Egg loss among spruce grouse inhabiting lodgepole pine forests

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The loss of eggs from clutches deposited in simulated and natural nests of spruce grouse was investigated during the spring of 1983 in lodgepole pine forests of southwestern Alberta. Two-thirds of all clutches, both in simulated and natural nests, were partially or completely lost. Density of simulated nests had no impact on proportional loss. Evidence suggests that nests under a conifer-dominated canopy, in an area lacking extensive shrub coverage, and at distances greater than 15 m from trails were the most vulnerable to egg predators. We conclude that red squirrels were the principle predator destroying these clutches.

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Nous avons effectué, au printemps 1983, une étude portant sur la déprédation subie par les couvées d'oeufs du tétras des savanes dans une forêt de pins lodgepole du sud-ouest de l'Alberta. Nous avons observé que le deux-tiers des couvées, aussi bien celles présentes dans les nids naturels que celles déposées dans des nids simulés, furent partiellement ou complètement détruites. Ce résultat est indépendant de la densité des nids simulés. Par contre, les couvées situées dans des endroits caractérisés par un couvert à dominance de conifères, par un couvert arbustif faible ou inexistant, ou par une absence de pistes à moins de 15 m, se sont avérées être les plus susceptibles d'être détruites. L'écureuil roux nous semble être le prédateur le plus fréquemment impliqué dans ces cas d'attaque sur les oeufs.

Many species of grouse (Tetraoninae) annually suffer a level of nest destruction that represents one of the largest sources of loss in productivity of these birds (Johnsgard 1973; Zwickel 1975; Redmond *et al.* 1982). Such losses occur despite anti-predator attributes that include cryptic colouration of plumage and eggs (Johnsgard 1973), nest sites that provide protection from visual predators (Keppie and Herzog 1978; Myrebeget 1976; Picozzi 1975; Redmond *et al.* 1982; Wallestad and Pyrah 1974), high levels of nest attentiveness (McCourt *et al.* 1973; Pulliainen 1971), and an ability to lower heart rate during incubation when approached by a predator (Gabrielsen *et al.* 1977). This loss of eggs has a major impact on reproductive output. Boag *et al.* (1979) suggested that, in Franklin's race of the spruce grouse (*Dendragapus* = [*Canachites*] *canadensis*), productivity was inversely related to population density, invoking predation as the proximate cause of loss in production. Smyth (1983) has since shown that changes in density alone could not explain changes in productivity in this population. Nevertheless, predation was still assumed to be the major proximate cause of loss in production.

In this paper we report the results of a field experiment that tested the influence of nest density, distance of nest from a trail, and dominant vegetation at the nest site on the fate of eggs in a series of artificial and natural nests extant in June 1983.

Methods

The study was conducted in forests dominated by lodgepole pine (*Pinus contorta*) in the foothills of southwestern Alberta. Ninety clutches of eggs were set out in pine forests known to support a population of spruce grouse. Three areas were used; each was about 3 km from a main study area of similar vegetation described by Boag *et al.* (1979). In one area (A), 30 clutches of seven eggs each were set out in a rectangular grid at intervals of ca. 200 m, in a second area (B) an additional 30 nests, also containing seven eggs each, were set out in the same pattern but at ca. 100-m intervals, and in the third area (C) the latter pattern was replicated with only five eggs per nest. Eggs of coturnix quail (*Coturnix coturnix japonica*) were used. Although somewhat smaller than eggs of spruce grouse, their colouration is similar to that of grouse, particularly ptarmigan (*Lagopus* spp.).

Nest sites were chosen to simulate the location of spruce grouse nests (Keppie and Herzog 1978; Redmond *et al.* 1982). A shallow

scrape was made with the lip of a tin can tied to the end of a 2 m long pole. The eggs were then deposited in the scrape from this can and left uncovered. In this way, the observer never trod within about 3 m of the nest.

Each nest was visited at the equivalent of midincubation (day 11) and the termination of incubation (day 22) (McCourt *et al.* 1973; Smyth 1983). Clutches were recorded as either intact, lost (all eggs gone), or missing eggs (number of eggs missing being recorded). On the last day, the following site characteristics were also recorded: distance to the nearest trail (man-made or game), number and species of trees within a circle of radius 2 m from the nest, percent coverage of shrubs (<1 m tall) within the same circle, and presence or absence of logs on the forest floor. At each nest where part or all of the eggs in the clutch were missing, any evidence as to the possible cause of loss was sought. This included egg shell fragments, their distribution in relation to the nest bowl, and any disturbance of the forest litter at or near the nest bowl. Tooth marks were sought on any entire eggs left in the nests as well as on any fragments thereof nearby. Between June 18 and July 9, we spent 35 h observing the reaction of red squirrels when encountering quail eggs that had been placed in groups of five at several locations regularly visited by squirrels outside of our experimental grids.

The fate of clutches from an additional sample of 14 radio-marked female spruce grouse occupying the main study area was also monitored. To avoid human disturbances, nests were not approached while females were incubating, hence clutch size was not known for all birds. At the end of incubation, the same set of measurements as above was recorded.

Results and discussion

Simulated nests

The fate of the clutches set out in artificial nests suggests a relatively constant rate of loss independent of density (Table 1). By the end of the incubation period, only one-third of the clutches remained intact. Of the 11 clutches partially destroyed at the equivalent of midincubation, 10 had lost all eggs by the end of incubation and the remaining partial clutch had lost an additional egg. This suggests that clutches found and partially destroyed were revisited subsequently and eventually completely destroyed. It also suggests that the predator involved was small and did not consume all the eggs at once.

The proximity of nests to trails through the forest was considered because of an assumed increased vulnerability of

TABLE 1. Fate of 90 clutches of Japanese quail eggs set out at two densities in simulated spruce grouse nests under pine-dominated forests of southwestern Alberta

Fate of clutch	Study area					
	A (low density) ^a		B (high density)		C (high density)	
	Day 11 ^b	Day 22 ^c	Day 11	Day 22	Day 11	Day 22
Remained intact	19	12	21	10	18	11
Partially destroyed	3	0	4	7	4	6
Completely destroyed	8	18	5	13	8	13
Totals	30	30	30	30	30	30

^aLow density, nests 200 m apart; high density, nests 100 m apart.

^bDifferences among sites: $\chi^2 = 1.173$, df = 4, not significant ($P > 0.10$).

^cDifferences among sites: $\chi^2 = 5.596$, df = 4, not significant ($P > 0.10$).

clutches in such locations. However, there was no evidence that being within 15 m of a trail rendered an artificial nest more vulnerable (Table 2). In fact, there is a trend in the opposite direction (42% remained intact near trails whereas 30% remained intact far from trails). This may mean that the main egg predators were not using trails for foraging.

We considered the fate of all clutches in relation to the vegetative characteristics at each nest site (Table 3). The results suggest that nests were less vulnerable where deciduous trees (*Populus* spp.) formed the dominant component of the canopy over the nest, and where shrub coverage was more than 10% (Table 3). The presence or absence of logs on the forest floor did not seem to influence the fate of clutches (Table 3). These data suggest a predator associated more with conifers than with deciduous growth.

Evidence gathered at the nest sites where clutches were partially or completely destroyed led us to conclude that rodents were the principle egg predators (Table 4). This evidence consisted of scattered egg shell fragments that were found near the nests and bore parallel scratch marks. These marks, easily visible on the heavily pigmented parts of egg shell fragments and entire eggs in partially destroyed clutches, were concentrated around the ends of each egg suggesting the gnawing of rodents. Furthermore, at many nests, eggs bearing scratches attributed to incisiform teeth had been partially buried nearby in the forest litter, again suggesting the work of rodents. We suspect that many, if not all, clutches for which there was no evidence left at the nest site (the unknown category in Table 4) can be attributed to a rodent egg predator for the following reason. The eggs remaining in many nests with only partial clutches on day 11 bore tooth marks, yet no evidence of the missing eggs was present. In most cases the entire clutch was gone by day 22, and still no evidence of eggs or predator was found.

Both deer mice (*Peromyscus maniculatus*) (Maxson and Oring 1978; Murray *et al.* 1983) and red squirrels (*Tamiasciurus hudsonicus*) (Bump *et al.* 1947; King 1937; Robinson 1980) are known to take bird eggs and were present in the study areas. We think that red squirrels are the most likely species involved in the observed nest predation for several reasons. When provided with a quail egg, a captive deer mouse, having first actively gnawed the small end of the egg without breaking the shell, buried it but did not eat it (V. Lewin, personal communication). The tooth marks left by the mouse were generally finer and concentrated only at the acute tip of the egg. Spruce grouse eggs, which are somewhat larger than quail eggs, were found (see below) to be gnawed at both ends, a feat that would probably be difficult for deer mice. Moreover, the

TABLE 2. The comparative fates of clutches of Japanese quail eggs set out in simulated spruce grouse nests in lodgepole pine forests at varying distances from trails in the forest

Fate of clutch	Distance from trail ^a	
	<15 m	>20 m
Remained intact	18	14
Partially or completely destroyed	25	33
Totals	43	47

^aDifference between the two distances: $\chi^2 = 1.44$, df = 1, not significant ($P > 0.10$).

preponderance of nests destroyed in habitat where the nest site was associated with coniferous canopy and a poorly developed shrub layer is suggestive of red squirrel habitat more than deer mouse (Banfield 1974). In addition, the scattered egg shell fragments found in the field appeared in many cases to have been dropped from the lower branches of an overhanging tree or a nearby log. This is similar to what has been described by Darrow (1938) and attributed to red squirrels.

The reaction of red squirrels when encountering a clutch of eggs was recorded on 79 occasions at the sites set up outside of our experimental grids. Most commonly (43%) no visible reaction to the eggs was noted. However, most of these instances occurred in July when the squirrels appeared to be preoccupied with harvesting spruce cones. The next most common reaction (27%) was to gnaw the small end of the egg. In so doing, the egg was often displaced up to 2 m. The handling time ranged from <5 to 162 s with a mean of 42 s. Such activity invariably left many parallel incisor marks on the shell. In 30% of these cases, the squirrels were successful in puncturing the egg. They would then either leave the egg *in situ* (8%), continue to open the egg by enlarging the hole and apparently eating at least some of the contents (6%), or carry the egg away (16%), hiding it, usually among the needles of a spruce bough where the foliage was thick, but often burying it in the litter on the forest floor. All this evidence coincides well with what we found at sites where eggs were lost from artificial and natural clutches (see below).

In only one case was the evidence suggestive of a mammalian carnivore; the eggs appeared to have had their sides bitten out and the edges of the break pushed in. Because of the size of the bite, a mustelid would appear to be the most likely candidate (Einarsen 1956). An avian predator appeared to have destroyed one clutch; the eggs remained in or near the nest

TABLE 3. Comparative fates of clutches of Japanese quail eggs set out in simulated spruce grouse nests relative to different vegetative characteristics at each nest site

Fate of clutches	Nature of dominant canopy coverage		Level of shrub canopy coverage		Status of logs within 3 m of nest	
	Deciduous (<i>Populus</i> spp.)	Coniferous (<i>Pinus</i> and <i>Picea</i>)	<10%	>10%	Absent	Present
Remained intact	9	23	19	13	13	19
Partially or completely destroyed	5	53	46	12	19	39
Totals	14	76	65	25	32	58
P^a	<0.05		<0.05		>0.10	

^aBased on χ^2 (df = 1) for homogeneity.

TABLE 4. Number of clutches partially or completely destroyed and the possible predator(s) involved based on evidence left at the nest site

Predator	No. of clutches	
	Simulated	Natural
Rodentia (<i>Tamiasciurus hudsonicus</i> , <i>Peromyscus maniculatus</i>)	39	4
Carnivora (<i>Martes pennanti</i> , <i>Mustela erminea</i> , <i>Canis latrans</i>)	1	1
Corvidae (<i>Perisoreus canadensis</i>)	1	0
Unknown	17	4
Totals	58	9

but each had a small hole as though having been pecked (there were no tooth marks). In most cases the contents of the eggs remained within the shell. We suspect gray jays (*Perisoreus canadensis*) to have been involved. Thus, most destruction of clutches, as much as 97% (56 of 58), we attribute to rodents, most likely red squirrels, a very common sciurid of these pine-dominated seral forests.

Natural nests

Evidence from a sample of 16 nesting attempts by spruce grouse, observed in the same season and type of forest but about 3 km distant, fits this same general pattern. Among four clutches for which clutch size was recorded during incubation, and hatching of at least some eggs occurred, only one hatched completely. The others each failed to hatch one egg; in one case the unhatched egg had been removed from the nest bowl and was found with tooth marks, but intact, 1.5 m away. This event had occurred during incubation because the egg contained a partially formed embryo. Three other clutches that hatched, but for which we do not know the clutch size, had a reduced number of chicks, i.e., three or four as opposed to the potential five (Keppie 1975), suggesting the loss of one or two eggs from the clutch before or during incubation. When the shells of eggs from which chicks had hatched were left in the nest bowl, invariably some or all were removed within 24 h, those remaining bore tooth marks. The remaining nine clutches failed completely to hatch their eggs; their clutch size during incubation was not known with certainty, but eggs or egg shells with tooth marks were found near the nests of four of them.

Using the same criteria for classifying the fate of the artificial clutches, only 2 of 16 are known to have remained intact throughout incubation, 3 more may have remained intact (but see above), the remaining 11 were partially or completely destroyed. Thus, a minimum of about two-thirds of spruce grouse clutches were also partially or completely destroyed

during laying and (or) incubation. All but one of these nests (a case of predation attributed to a carnivore) may have been destroyed by rodents.

Since all nests but one, which was under a large log in a clearing, were in conifer-dominated locations, we cannot comment on the relative success of spruce grouse nests in deciduous versus coniferous surroundings. Shrub cover, as with artificial nests, seemed to give some degree of added protection (three of nine clutches were successful at sites where shrub cover was <10%; four of six clutches were successful when shrub cover was >10%). The presence or absence of logs seemed unrelated to egg loss. Only two nests were located within 15 m of a trail; one, within 2 m of a cut line, hatched all eggs, while another 13 m from a game trail, hatched five of its six eggs. Thus, as with artificial nests, proximity to trails did not seem to increase nest vulnerability.

Implications

The results of these experiments suggest that spruce grouse nesting in pine seres of southwestern Alberta are relatively vulnerable to egg predators. However, the data do not support the hypothesis that loss of eggs was density dependent, at least at the densities used in these experiments and likely to be encountered among spruce grouse under field conditions. This may be because the major predator in this study was not an active seeker of eggs but merely an opportunist that took them when encountered, perhaps initially out of curiosity. Under such circumstances the probability of destruction would be largely a function of nest placement relative to the activity centres of these predators. That the clutches in this study were destroyed at a relatively constant rate (one-third after the first 11 days, two-thirds after the first 22 days), and apparently were more vulnerable in one type of habitat than another, suggests such a predator. With such a high level of potential loss, these results have implications of interest in the study of reproductive adaptations of spruce grouse. Spruce grouse are reported to have one of the smallest clutch sizes among the Tetraoninae (Johnsgard 1973; Keppie 1975). These data are based on the number of eggs in incubated clutches (realized clutch size) and not on counts of postovulatory follicles which reflect the number of eggs actually laid (actual clutch size). It has been assumed that these are equal in spruce grouse but, to our knowledge, this assumption remains unconfirmed.

Should it be shown that realized and actual clutch size in spruce grouse are the same, then the reason for the small clutch size needs to be explained. It may be related to the selective pressure on the female to cover the clutch in the shortest time possible. Hence, a clutch of five eggs may represent a compromise between the potential gain through producing extra eggs

and the potential loss through leaving the eggs exposed for the extra time needed to produce them. On the other hand, by living primarily in pine forests over most of their range, spruce grouse may be under nutritional limitations when mobilizing nutrients in the production of eggs (Lack 1968). However, the production of replacement clutches which can and does occur in this species (2 of 14 hens renested in 1983) may argue against such a conclusion.

Should the realized clutch size be less than actual clutch size, the difference may reflect partial clutch loss during laying when the eggs remain uncovered for extended periods of time or even during incubation when the females are foraging. The frequency with which either an egg has been found outside the nest bowl, or a decline of one or two eggs in a clutch has been noted over the incubation period (Keppie 1975; this study) suggests that partial clutch loss in spruce grouse may be common. Such loss may represent the interference of red squirrels.

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