

INVESTIGATOR DISTURBANCE AND CLUTCH PREDATION IN WILLOW PTARMIGAN: METHODS FOR EVALUATING IMPACT

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Abstract.—The possible effect of investigator disturbance on clutch predation in two populations of Willow Ptarmigan (*Lagopus lagopus*) was investigated using three different techniques. No significant difference was found in (1) the proportion of hens that succeeded in producing broods for hens whose nests were found vs. those that were not located, (2) proportion of broodless hens on an intensively studied area vs. an area that was not studied, (3) the proximity of nest flags for successful vs. depredated nests. A new technique was developed to compare rates of visits and types of nest checks between successful and depredated nests. This method controlled for period under observation and stage of breeding. Methods for minimizing investigator disturbance are discussed.

MÉTODOS PARA EVALUAR EL IMPACTO DEL DISTURBIO CAUSADO POR EL INVESTIGADOR EN LA DEPREDACIÓN DE CAMADAS DE INDIVIDUOS DE *LAGOPUS LAGOPUS*

Sinopsis.—Utilizando tres técnicas diferentes se estudió, en dos poblaciones de *Lagopus lagopus*, el posible efecto del disturbio causado por el investigador en la depredación de camadas. No se encontró diferencia significativa en (1) la proporción de hembras exitosas en producir polluelos (al compararse aquellas cuyos nidos fueron localizados vs. aquellas cuyos nidos no fueron localizados), (2) proporción de hembras sin camadas en un área de estudio intensiva vs. áreas que no fueron estudiadas, y (3) la proximidad de banderolas a de nidos (entre nidos exitosos vs. nidos depredados). Una nueva técnica fue desarrollada para comparar el efecto de la tasa de visitas y tipos de examen a nidos entre nidos exitosos y depredados. Este método puede ser regulado para períodos de observación y etapas reproductivas. Se discuten métodos para minimizar el disturbio causado por los investigadores.

Patterns and levels of clutch predation are important in avian studies of life history traits (e.g., Perrins 1977, Slagsvold 1982) and population regulation (e.g., Bergerud et al. 1985). The techniques used to monitor nesting birds, however, may alter the natural rate of clutch predation; hence the results may not be independent of how they were obtained (Lenington 1979). This problem is not uncommon; in a recent review, Götmark (1992) found that 39 of 78 studies that considered investigator disturbance reported a significant ($P < 0.05$) effect on clutch predation or overall nesting success.

The direction and magnitude of potential disturbance by human activities will differ from study to study depending upon the ecology of the

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study species, the degree of observer disturbance, the type of predators, the habitat structure and whether natural or artificial nest sites are used by breeding birds. Thus, researchers should be aware of and test for the possibility that their activities have influenced natural rates of predation.

Ground-nesting birds often suffer high levels of clutch predation (Ricklefs 1969), particularly those using crypsis to avoid detection. Visiting or marking nests, handling eggs and/or flushing the hen may increase (Picozzi 1975), decrease (MacIvor et al. 1990) or not influence (Evans and Wolfe 1967, Galbraith 1987, Keppie and Herzog 1978, Klimstra and Roseberry 1975, Livezey 1980) rates of clutch predation.

In this paper we examine the effect of our research activities on clutch predation in two northern Canadian populations of Willow Ptarmigan (*Lagopus lagopus*), a dispersed, cryptic ground-nesting grouse. We used three approaches. First, we tested directly for potential investigator disturbance by comparing the proportion of hens with broods when nests were found and subjected to normal visit schedules and when clutches were not located. Second, in 2 yr of high clutch predation, we compared proportion of hens found with broods in an area not previously surveyed to that observed on our intensively studied area where most nests were located. Third, we compared the number of visits to nests and the distance at which marker flags were placed from nests that were depredated and those that were successful in hatching chicks. For this third approach, we develop a new method for evaluating investigator disturbance that removes inherent biases in nest-visit data. Depredated clutches, on average, have fewer total days of observation at earlier stages of nesting than successful clutches, and thus, depredated clutches have fewer total visits to the nest, but a higher rate of visits. In this method, we compare number of visits to depredated and successful clutches that were found at equivalent stages of breeding and for similar periods of observation.

In testing for observer effects we follow the Popperian tradition of erecting null hypotheses (of no effect) and attempting to falsify them (Popper 1968). Failure to reject a null hypothesis, however, does not mean that it is true: such results are not robust unless statistical power analysis is used to determine the probability of accepting the alternate hypotheses (Cohen 1988; Muller and Benignus 1992; Peterman 1989, 1990). Hence we determine the power of our tests to detect a range of effect sizes. As incorrectly concluding that our activities have no effect has potentially serious consequences, we increase the power of our tests by setting the probability of rejecting a null hypothesis to $\alpha = 0.10$ (Cohen 1988, Peterman 1989).

METHODS

Study sites.—The study was conducted at two sites in northern Canada: the Chilkat Pass (CP) in northwestern British Columbia (59°50'N, 136°30'W) from 1985 to 1988 and La Perouse Bay (LPB) in northern Manitoba (58°24'N, 94°24'W) from 1981 to 1984. CP is located in sub-alpine tundra and LPB in subarctic tundra. Both areas are dominated

by willow (*Salix* spp.) and dwarf birch (*Betula glandulosa*) with an understorey of grasses and sedge, but LPB is more open with more standing water (Hannon et al. 1988).

Clutch predation in the study sites varies from 20 to 70% (Martin et al. 1989). The major clutch predator at CP is the red fox (*Vulpes vulpes*), with few aerial clutch predators (O'Reilly and Hannon 1989). At LPB the major clutch predators are avian: Herring Gull (*Larus argentatus*), Parasitic Jaeger (*Stercorarius parasiticus*) and Common Raven (*Corvus corax*), but red fox and ermine (*Mustela erminea*) also occur (Martin 1985).

At LPB, nests were found by locating the roost of the male and searching around it with the aid of a pointing dog. At CP most hens were radio-tagged prior to laying (Schieck 1988) and most clutches were found using telemetry. When a nest was discovered at either site, its position was marked with a 20–30 cm piece of yellow flagging tape 4–40 m from the nest site. The distance and direction to the nest were printed on the flag with a black marker.

Nests located when hens were still laying were visited about every second day. During incubation we observed hens from a distance of greater than 10 m from the nest about five times, and flushed them about three times. Due to variation in the stage clutches were found, weather conditions and time or geographic constraints, all nests did not receive exactly the same number of visits.

We defined any movement of a hen from her nest due to our activities as a flush, although in many cases hens did not fly but remained on the ground close to the nest. A successful nest is one where at least one chick hatched and left the nest.

Success of clutches located or not located.—We used two different methods to test the null hypothesis that clutches visited during laying and incubation have the same probability of predation as clutches that were not located.

In CP in 1986, on a study plot where resident hens had been color-banded and censused but most nests were not found, hens were located using pointing dogs during the brood-rearing period to determine whether they had produced chicks. A hen was considered to have lost her first nest if she was encountered without chicks and had a regrowing brood patch, or if she was observed on a renest or with chicks from a renest clutch. Regular visits to the territory and synchronous onset of clutch initiation for first nests allow us to assign first and renest clutches accurately. The null hypothesis predicts that the ratio of successful to depredated clutches should be the same regardless of whether we located them or not. We calculated the probability of this hypothesis being correct using a log-likelihood contingency analysis (Sokal and Rohlf 1981).

In 1985 and 1987, clutch predation was high at CP (65% and 69% of first clutches, respectively). In these years we searched for Willow Ptarmigan broods on a 1.4 km² area of comparable habitat about 10 km from our study area to determine whether high clutch predation was widespread

or restricted to our study area. On 21 Jul. 1985 and 18 Jul. 1987, four or five observers accompanied by three pointing dogs systematically searched the area for 4 h and counted number of hens with and without broods. On our intensively studied area, we made similar searches on 18 Jul. (8 h) and 19 Jul. (5 h) 1985 and 19 Jul. (6 h) and 21 Jul. (2.5 h) 1987. Weather conditions were comparable on all census days. The null hypothesis was that proportion of broodless hens should be the same on the two areas.

Number of visits to successful and depredated nests.—If nest visits have no effect on clutch fate, then depredated and successful clutches should have received the same number of visits. As visits to depredated nests cease after the clutch is lost, however, they will routinely have received fewer visits in total than successful nests. In addition, clutch predation differs annually and with nesting attempt (first or reneat; Martin et al. 1989), and may depend upon the stage of laying or incubation. Our visit schedule varied depending upon whether the clutch was located during laying or incubation. Hence direct comparisons of depredated and successful nests for the total number of visits or the visit rate would give misleading results. We thus compared the number of visits to each depredated nest with the number of visits to a group of successful nests from the same year and nesting attempt and that were found at approximately the same stage of nesting (± 1 d), over the same number of days of observation. Stage when the clutch was located was calculated by subtracting the date located from the date of onset of incubation, hence nests found during incubation have positive values and those found during laying have negative values. When clutches were found during laying but depredated before the onset of incubation (thus lacking a clutch size), stage of discovery and stage of loss were estimated by assuming that the hen would have laid the average clutch size for that nesting attempt, at that site, at the average laying rate of 1 egg/day, and would have started incubation after laying the penultimate egg (Hannon et al. 1988, Martin et al. 1989). For example, a first nesting attempt that was either found or depredated on the day the 5th egg was laid was assigned a stage of discovery or stage of loss of day -3 at CP or day -6 at LPB respectively (mean clutch size for first nests was eight eggs at CP and 11 eggs at LPB [Martin et al. 1989]).

The number of days a nest was under observation was calculated by subtracting the date that the clutch was found from the date of hatch for successful nests or the date of failure for depredated nests. Only depredated nests where the date of loss was known within ± 2 d were included in the analysis.

The number of visits to the group of comparable successful nests for a given depredated nest forms a distribution. In order to avoid making assumptions about the shape of the distribution, we calculated the percentile of this distribution on which the number of visits to the depredated nest fell. The minimum number of successful nests required to make this

calculation was two; above this minimum the percentile obtained was independent of group size. For example, nest A was depredated on day 10 of incubation and had been observed for 15 d (i.e., was discovered at day -5). There were five successful nests (i.e., from the same nesting attempt and year) that were found between days -6 and -4. These nests were visited 2, 5, 6, 8 and 10 times, respectively, during the first 15 d that the clutch was under observation. If nest A had received only one or two visits, it would be assigned a percentile of 0 (i.e., it had as many or fewer visits than all comparable successful nests). If nest A was visited 10 or more times, it was assigned a percentile of 100, and if it was visited seven times a percentile of 62.5 (calculated by interpolating linearly between six visits [50th percentile] and eight visits [75th percentile]).

The null hypothesis predicts that, on average, the number of visits to clutches that were depredated should fall in the middle of the distribution of visits to comparable successful nests. If the null hypothesis is correct, then the average percentile for depredated nests should be 50. This prediction was evaluated statistically using a Wilcoxon's signed-ranks test (Sokal and Rohlf 1981).

The analysis was conducted three times for each site to test for three levels or types of disturbance. In the first instance all visits to the nest were used, regardless of the distance from which the nest was observed or whether the female was sitting on the nest. Secondly, the data were restricted to instances where the female was found on the nest. Lastly, only visits where the female was flushed from the nest were included.

Proximity of marker flags to nests.—We compared the distance that nest marker flags were placed from the nest for successful and depredated nests for each site separately, under the null hypothesis that distance of the nest marker had no effect on probability of predation. We controlled for possible differences in flag placement between years and interactions of predation rate and flag placement between years and within a season by using a two factor analysis of covariance (ANCOVA, Sokal and Rohlf 1981), with year and fate (depredated or successful) as fixed factors and date clutch found as a covariate. Flag distance data were not collected in CP in 1987; hence there are three levels of the factor year in the CP analysis.

Although all main effects and interactions were entered in the model, the only variance ratio (F) tests that address the null hypothesis are those that contain the fate factor. The interaction terms containing fate are important because any effect may only be apparent in certain years or times of the season or both. Type III sums of squares were used in determining F values. This means that the mean proximity of marker flags to nests was given equal weight for depredated and successful nests regardless of sample size.

Power analysis.—The power of a statistical test is the probability that it will yield statistically significant results (Cohen 1988). For the parametric tests performed, we calculated power using the tables provided in

Cohen (1988). For the non-parametric Wilcoxon's signed-ranks test, power tables are not available, thus we estimated power using a bootstrap analysis (Manly 1991, Noreen 1989) with 10,000 repetitions.

Statistical power depends upon the type of test and the validity of the assumptions it makes, and is proportional to the chosen probability of making a type I error (α), the sample size, the sample variance and the degree that the results depart from those predicted by the null hypothesis (the effect size). Thus we calculated the power of our tests using the sample size and variance from the data, over a range of possible effect sizes (Muller and Benignus 1992, Peterman 1989). For the parametric tests, we used the definitions of "small," "medium" and "large" effect sizes given by Cohen (1988). These may be thought of as an index of the proportion of overlap between the observed distribution of results and that predicted by the null hypothesis. For the comparison of the number of visits to successful and depredated clutches, we altered the effect size by adding or subtracting visits from the depredated nests and estimating the resulting power using the bootstrap analysis. The number of visits added to or subtracted from each nest was set by an effect size variable (change in visit rate) that dictated the probability of an extra visit to a nest per day under observation. For example, if the change in visit rate was -0.1 , then for each day a nest was under observation we subtracted a visit with a probability of 0.1 , producing on average one less visit every 10 d. As this process is probabilistic, we repeated the simulation 50 times for each change in visit rate.

RESULTS

Success of clutches that were located or not located.—In 1986 at CP, we observed that 27 hens had broods from first clutches from a total of 35 females residing on an area where we did not search for nests. Total brood loss at CP is negligible (3% [Martin et al. 1989]), and thus we estimate that eight hens (23%) had their first clutches depredated. In the same year on another site, we located and visited the nests of 69 hens, of which 13 (19%) clutches were depredated. Thus, clutch predation did not differ in relation to whether we located or did not locate nests ($\chi^2 = 0.17$, $df = 1$, $P = 0.64$). The power of the test was low (significance criterion $\alpha = 0.10$, $df = 1$, effect size $w = 0.03$, sample size $n = 104$, power < 0.27); however the power of the same test to detect "medium" and "large" effect sizes was good ("small" effect $w = 0.1$, power = 0.27 ; "medium" effect $w = 0.3$, power = 0.93 ; "large" effect $w = 0.5$, power > 0.99 ; α , df and n as above).

We pooled data for our brood searches in 1985 and 1987 at CP. We found five of nine females with broods off the study area and 13 of 19 hens with broods on CP ($G = 0.43$, $df = 1$, $P = 0.55$; $\alpha = 0.10$, $df = 1$, effect size $w = 0.12$, $n = 28$, power = 0.18). These data must be interpreted with caution due to the low power to detect even a "medium" effect (i.e., $w = 0.3$, power = 0.49). They suggest that reproductive failure was

widespread in the region during 1985 and 1987, but no higher on the CP study area than elsewhere.

Number of visits to successful and depredated nests.—Nests at LPB were under observation for 1–32 d, during which time they received 1–26 visits, with a mean of 0.62 ± 0.22 (SD) visits a day ($n = 180$ nests). At CP, nests received 1–26 visits over 1–30 d, with a mean of 0.52 ± 0.28 visits a day ($n = 338$ nests).

The number of visits to depredated and successful nests, when compared over the same year, nesting attempt, days under observation and similar stages of nesting, did not differ significantly for either site or any subset of the data examined, but the power of the tests at the observed effect sizes was low (Table 1).

Figure 1 shows the effect on power of changing the number of visits to depredated nests. All three subsets of the data produced similar responses, so only the analyses for all visits are shown. The figure demonstrates two things: the observed differences in visit rates between depredated and successful nests are negligible; the tests would likely have detected small deviations from equal visit rates had they occurred.

As the lowest power is associated with an effect size of zero (Cohen 1988), the point at which power is at a minimum in the figure must correspond to the point at which successful and depredated nests receive an equal number of visits. In the figure, minimum power occurs with a small negative change in visit rate, indicating that our data contain a small positive effect. The magnitude of this effect is approximately 0.02 at both LPB and CP, meaning that depredated nests were visited on average one more time for each 50 d under observation than comparable successful nests.

Estimated power increases steeply on either side of the zero effect size. We found good power (>0.80 , [Cohen 1988]) in all 50 simulations after a change in visit rate from the zero effect level (-0.02 at LPB and CP) to ± 0.16 in LPB and ± 0.07 in CP, whereas the median power at these effect sizes was 0.98 and 0.96, respectively.

Proximity of marker flags to nests.—The average distance of the nest to the nest flag was 16.2 ± 7.3 m (SD) at CP and 10.0 ± 5.7 (SD) at LPB ($n = 130$ at CP, $n = 167$ at LPB). No factors that included the fate of a clutch explained a significant proportion of the variance in the proximity of marker flags; however at LPB the interactions between fate and year, and between fate, year and date at LPB were close to the critical α of 0.10 (Table 2). Power to detect a “small” main effect or interaction was poor, but a “medium” or “large” effect would likely have been detected (Table 2).

DISCUSSION

Martin et al. (1989) showed that clutch predation was the single factor that accounted for the greatest loss in potential annual production of Willow Ptarmigan at both LPB and CP. In this paper we have been

TABLE 1. Results of Wilcoxon's signed-ranks test of the null hypothesis that depredated nests were visited the same amount as successful nests for two populations of Willow Ptarmigan.

	d	P	Power
Chilkat Pass ($n^1 = 114$)			
All visits	-1.36	0.17	0.39
Female on	-0.93	0.35	0.24
Flush	-0.80	0.42	0.18
La Perouse Bay ($n^1 = 52$)			
All visits	-0.49	0.62	0.14
Female on	-0.16	0.87	0.11
Flush	-0.32	0.75	0.12

¹ Number of depredated nests in the comparison.

unable to demonstrate that our activities of locating, marking and visiting nests had a significant influence on predation rate.

Although our statistical tests had poor power at the observed effect sizes, we have demonstrated that the parametric tests would have had a good power to detect "small" to "medium" effects, as defined by Cohen (1988), and that the comparison of visits to successful and depredated nests would have detected small deviations from equal visit rates. We conclude that either our research activities had no effect on clutch predation rates, or that there is an effect, but that it was small. Hence in the following paragraphs we discuss how our methods may have minimized disturbance effects.

Mammals, mainly foxes, are the major nest predators at CP (O'Reilly and Hannon 1989). Many investigators discuss the possibility that mammals may discover nests by following trails left by humans (Götmark 1992). In his review of effects of investigator activities on avian nesting success, however, Götmark (1992) found no studies that demonstrated increased nest predation by mammals as a result of investigator disturbance. In our study and probably others, investigators traversed the study area many times engaged in activities other than nest visits making it unprofitable for scent predators to follow human trails. Foxes are trapped in the Chilkat Pass area and may thus avoid human scent (see also MacIvor *et al.* 1990).

Götmark (1992) did find some evidence for several species that nests visited by researchers were at greater risk of being depredated by avian predators. Avian predators may locate nests using the activity of the hen, disturbance of vegetation around the nest (Dwernychuck and Boag 1972), following investigators (Strang 1980) or searching around nest markers (Picozzi 1975, Reynolds 1985). Thus, we would expect that the risk that nest visits might increase failure would be greater at LPB where there were more avian predators than CP. We found no effect at LPB, however, suggesting that our activities were not obvious enough to attract avian predators. In addition, flags were placed on the study area in the course

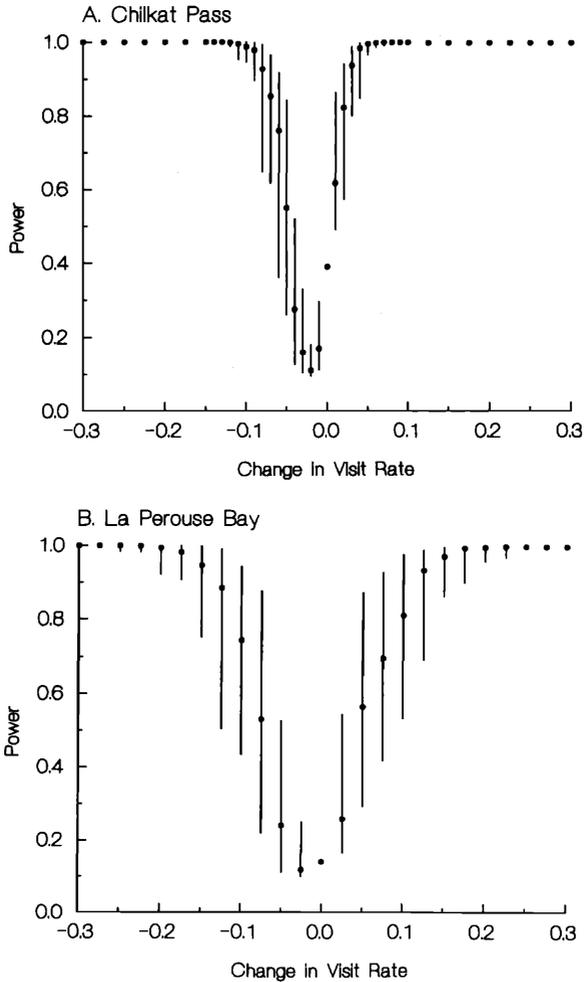


FIGURE 1. Power to detect differences in the number of visits to depredated and successful nests for two populations of Willow Ptarmigan (A. CP; B. LPB). Hypothetical effect sizes were simulated by increasing or decreasing the observed number of visits to depredated nests. Effect size is the change in visit rate (probability of adding or subtracting a visit to each depredated nest for each day it was under observation). The dot denotes the 50th percentile and the vertical line extends between the 5th and 95th percentiles of the distribution of 50 simulations at each of a range of effect sizes.

of other research activities, reducing the profitability for predators of searching around flags for nests.

The potential for clutch predation caused by our activities may have been minimized because of the precautions we took when visiting and marking nests. Flags were placed in random directions from the nest and

TABLE 2. Results of two factor ANCOVA of the null hypothesis that the proximity of marker flags to nests was unrelated to nest success in two populations of Willow Ptarmigan. Main effects are fate (successful or depredated) and year, and the covariate is date nest located.

Source of variation	df	F	P	Power for given effect size		
				"Small"	"Medium"	"Large"
Chilkat Pass						
Fate	1	0.12	0.73	0.30	0.86	>0.99
Fate•Year	2	0.58	0.56	0.23	0.72	0.97
Fate•Date	1	0.12	0.73	0.30	0.86	>0.99
Fate•Year•Date	2	0.61	0.55	0.23	0.72	0.97
<i>n</i> = 126; residual mean square = 44.01; residual df = 114.						
La Perouse Bay						
Fate	1	1.31	0.25	0.35	0.93	>0.99
Fate•Year	3	1.81	0.14	0.23	0.72	0.97
Fate•Date	1	1.31	0.25	0.35	0.93	>0.99
Fate•Year•Date	3	1.91	0.13	0.23	0.72	0.97
<i>n</i> = 167; residual mean square = 23.57; residual df = 152.						

at variable distances. Whenever we flushed a hen we first checked the area for the presence of predators and removed conspicuous head gear. We avoided disturbing vegetation around the nest, did not kneel or place our equipment near the nest and kept our visits as short as possible. We varied the direction of our approach to the nest and when an egg count was not required we checked the hen on the nest from a distance using binoculars.

Studies on the effects of research activities on the reproductive success of breeding birds have intrinsic scientific value as it is always desirable to acquire knowledge about disturbance and to attempt to correct for any biases. Both scientific and ethical concerns are heightened when the study species is threatened or endangered or when the study has a conservation focus. The subject of investigator disturbance is often not addressed because it requires extra effort which must be diverted away from the main focus of research. Our method of comparing the number of visits to each depredated nest with the distribution of visits made to a comparable group of successful nests is widely applicable to a variety of field studies since it requires only routinely collected nest visit data and an estimate of when the nest was depredated. We are currently utilizing this approach to examine investigator disturbance in a number of systems.

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NORTH AMERICAN LOON FUND

The North American Loon Fund (NALF) announces the availability of 1994 grants in support of management research, and educational projects directly related to the conservation of the family Gaviidae.

Proposals in the range of \$500 to \$3000 are most likely to be considered for funding. Further guidelines for prospective applicants are available upon request from the NALF Grants Committee. Deadline for submission of proposals is December 15, 1993. Funding awards will be announced by March 30, 1994.

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