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Natality of ruffed grouse *Bonasa umbellus* in central Wisconsin, USA

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Radio-marked female ruffed grouse *Bonasa umbellus* were monitored in central Wisconsin, USA, during 1983-1988 to estimate nesting rates (the percentage of hens that initiate a clutch), clutch size, nest success, and the prevalence and success of renests. All 23 radio-marked females initiated a clutch, 22 completed a first clutch; the remaining hen was killed by a predator during laying. Mean clutch size of first nests was 11.0 ± 0.5 eggs (range = 7-13). Five of nine (56%) hens attempted to renest with a mean clutch size of 7.4 ± 1.3 eggs (range = 6-9). Mean nest success was 46%; 43% for yearlings and 60% for adults. First nests produced the large majority of eggs that hatched (86.1%) compared to renests (13.9%). Productivity was estimated at 5.8 chicks hatched for each hen alive on 20 April, the mean date of the first egg laid.

Key words: clutch size, natality, nest success, renest, ruffed grouse, *Bonasa umbellus*, Wisconsin, USA

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Natality among tetraonids varies greatly, depending on food, predation pressure, nesting cover, age, social interactions, etc. (Keppie 1981, Bergerud 1988, Martin et al. 1989, Jönsson et al. 1991). Little is known about the natality of ruffed grouse, even though it is a well studied species. Although clutch size and nest success have been estimated for ruffed grouse (see Bergerud 1988), there is a paucity of information on two critical components of natality: 1) the percentage of hens that initiate a clutch, and 2) the prevalence and success of renests. Thus, we

present additional information on these components of the bird's natality.

Bump et al. (1947) speculated that up to 25% of ruffed grouse hens did not breed in some years; yet, this was an indirect estimate prior to the use of radio-telemetry. Brander (1967) radio-marked four hens and located nests for the three yearlings but not for the adult. Maxson (1978), using telemetry, recorded 100% of hens (N = 15) nested in contiguous mixed-hardwood forests during a cyclic population high in Minnesota, USA. However,

some hens were captured on the nest during this study, thereby precluding an accurate estimate of the percentage of hens that attempted to nest. Maxson (1977) also provided the first indirect evidence of a renesting attempt by ruffed grouse.

Our objective was simply to increase the limited amount of information on ruffed grouse natality by studying a population in the fragmented forests of central Wisconsin, USA. We estimated nesting rates (the percentage of females initiating a clutch), clutch size, nest success, and the prevalence and success of renesting by monitoring radio-marked yearling and adult female grouse.

Study area and methods

The study was conducted during 1983-88 in Marquette and Waushara counties in central Wisconsin (44°01'N, 89°23'W). The study area was a mosaic of forests (36%), cropland and pasture (48%), commercial forest of Red pine *Pinus resinosa* (8%), and marsh lands (8%) (Small & Rusch 1989).

We trapped hens from July through November, and in April and May using lily-pad traps (Dorney & Mattison 1956). We also recaptured some hens at the nest to replace transmitters. We estimated age by molt progression (Hale et al. 1954) and calamus diameter ratios (Rodgers 1979). We fitted hens weighing >350g with a 16 - 21 g radio-transmitter attached to a poncho (Amstrup 1980), and one anodised aluminum leg band; hens <350g were not fitted with a radio-transmitter. Hens less than 12 months of age were classified as yearlings, all others as

adults. To estimate the date of first egg and hatch date, we assumed laying rates of 1.5 days per egg and an incubation period of 23 days (Bump et al. 1947:288).

Once their nest was found each female was located by triangulation every other day, followed by a visit to the nest on the predicted hatch date to estimate the number of eggs that successfully hatched. If the estimated location of the hen diverged from the nest, we examined the nest to estimate the time and cause of nest failure. If a first clutch was destroyed we continued to monitor the hen to estimate renesting occurrence and success. Due to the relatively small number of first nest attempts (N = 23) observed during the study, we did not perform statistical analyses to examine potential age-specific differences in nesting parameters.

Results

A total of 23 radio-marked hens survived until 20 April, the mean date of the first egg laid. Only one hen was captured in spring, on 27 March, approximately 25 days before she laid her first egg. Twenty-two of the 23 radio-marked hens completed a first clutch during 1983-88; the remaining hen was killed by a predator after laying four eggs. Predators destroyed nine complete first clutches and killed one additional hen. Two completed clutches were accidentally destroyed during recapture attempts and were excluded from the remaining analyses for first nest attempts; one of the hens whose nest was destroyed re-nested. A clutch of 13 eggs did not hatch because of infertility or early embryonic death; the hen incubated these

Table 1. Ruffed grouse nest success, clutch size, and hatch success in Marquette and Waushara counties, Wisconsin, USA, 1983-1988^a.

Age	Nests		Clutch size		Hatch success	
	No attempted	No successful (%)	Mean (sd)	Range	No laid	No hatched ^b (%)
First Nest						
Yearling	17 ^c	8 (47)	11.0 (0.5)	7-13	176	80 (45.5)
Adult	4	2 (50)	10.8 (0.4)	10-11	43	19 (44.2)
Combined	21	10 (48)	11.0 (0.5)	7-13	219	99 (45.2)
Renest						
Yearling	4	1 (25)	7.0 (1.2)	6-8	28	8 (28.6)
Adult	1	1 (100)	9.0 (-)	-	9	8 (88.9)
Combined	5	2 (40)	7.4 (1.3)	6-9	37	16 (43.2)
Total						
Yearling	21	9 (43)	10.3 (4.7)	6-13	204	88 (43.1)
Adult	5	3 (60)	10.4 (0.8)	9-11	52	27 (51.9)
Combined	26	12 (46)	10.3 (3.9)	6-13	256	115 (44.9)

^a Two complete clutches destroyed during trapping are not included.

^b From nests in which at least one egg hatched.

^c Data from a yearling that was killed after laying four eggs was included only in the nest success estimate.

inviability for 52 days. Based on these results, we calculated first nest success at 48%, with a mean first clutch size of 11.0 ± 0.5 eggs (Table 1).

Fifty-six percent of hens which survived after their first nests were destroyed attempted to re-nest, with a re-nest success of 40% and a mean clutch size of 7.4 ± 1.3 eggs (see Table 1). Renesting hens incubated their first clutch for an average of 9.4 days (range = 5 - 18), and began laying their second clutch 4.8 days after nest destruction (12 - 27 May). The difference in first clutch size between hens that re-nested and hens that did not was minimal (10.6 vs. 11.6 eggs). Precise estimates of first nest initiation and destruction were recorded for only five hens; the mean time invested (days of egg laying and incubation) in first nests was similar for the three hens which re-nested compared to the two that did not (22.0 vs. 21.5 days).

Combined nest success was 46%; 43% for yearlings and 60% for adults. Combined hatch success was 44.9% for nests in which at least one egg hatched, and did not differ significantly between yearlings and adults ($z = 1.25$, $P = 0.21$, see Table 1). The mean number of eggs hatched was 9.9 and 8.0 for successful first nests and re-nests, respectively, with overall productivity estimated at 5.8 (115/20) chicks hatched for each hen alive on 20 April. Of 115 eggs hatched from 256 total laid, the large majority were from first nest attempts compared to re-nests (86.1% vs. 13.9%). We did not detect any possible effects of radio-transmitters on breeding hens, yet we did not monitor unmarked hens for a proper comparison.

Discussion

The 100% nesting rate of ruffed grouse observed in our study supports previous results of Brander (1967) and Maxson (1978). Although Bump et al. (1947: 359) speculated that nesting rates could be as low as 75% for ruffed grouse, their inference may have been biased by indirect estimates. The radio-telemetry studies of nesting hens suggest, therefore, that high nesting rates are common for ruffed grouse. These comparable results were recorded at both high and low densities (this study; see Small et al. 1991), and in both fragmented and contiguous forests, implying that nesting may neither be limited by social exclusion (Hannon et al. 1982) nor by nesting habitat. Finally, high nesting rates by ruffed grouse would follow Bergerud's (1988:580) conclusion of forest grouse in general: "... nearly all adult females breed and nest and that most yearlings attempt to do so". However, Hannon & Zwickel (1987) reported that a small percentage of females may not nest in some blue grouse *Dendragapus obscurus* populations.

The 46% nest success rate for ruffed grouse observed in our study is lower than the 61% mean rate summarised

from 13 studies by Bergerud (1988: 593). Our lower nest success rate could be a result of the high proportion of yearlings in the sample, as our trapping effort was directed primarily towards yearlings. Adults ($N = 5$) comprised only 22% of our marked population, a percentage lower than expected from age-specific survival estimates from the same study (Small et al. 1991), and from age ratios reported from other ruffed grouse populations (Rusch & Keith 1971). As yearling female ruffed grouse generally exhibit a lower nest success than adults (61% vs. 71%, Bergerud 1988: 600; 43% vs. 60% our study), the bias towards yearlings in our sample would yield a lower nest success estimate. Finally, the large majority (91%) of nest failures in our study was due to destruction by predators, typical for tetraonids (Bergerud 1988: 593, Storch & Willebrand 1991). Perhaps, the extensive fragmentation within our study area may have increased nest predation, consistent with results from other studies (e.g. Andr  n et al. 1985, Wilcove 1985) which indicate that forest fragmentation increases nest predation.

The proportion of hens that re-nested after their first nest was destroyed in our study was 56% and this is a substantially higher proportion than the 12-22% reported previously for ruffed grouse (Bump et al. 1947: 364, Maxson 1977). In addition, the amount of parental investment in the first clutch did not appear to determine whether a hen would initiate a second clutch. The high percentage of ruffed grouse hens re-nesting in our study is more typical of steppe grouse according to Bergerud (1988: 597), as the percentage of forest grouse hens that usually re-nest is relatively low, e.g., blue grouse 25% (Sopuck & Zwickel 1983), and spruce grouse *Dendragapus canadensis* 10% (Ellison 1974). However, Willebrand (1992) reported a re-nesting frequency of 53% among radio-marked black grouse *Tetrao tetrix*. Thus, we contend that such generalisations be considered tenuous until larger samples of nesting females of both forest and steppe grouse are monitored by radio-telemetry.

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