

Behaviour and Nesting Ecology of Appalachian Ruffed Grouse (*Bonasa umbellus*)

BRIAN W. SMITH^{1,3}, ANDREW N. TRI¹, CHRIS A. DOBONY^{1,4}, JOHN W. EDWARDS^{1,5}, and PETRA BOHALL WOOD²

¹Division of Forestry and Natural Resources, West Virginia University, P.O. Box 6125, Morgantown, West Virginia 26506 USA

²United States Geological Survey, West Virginia Cooperative Fish and Wildlife Research Unit, Division of Forestry and Natural Resources, West Virginia University, P.O. Box 6125, Morgantown, West Virginia 26506 USA

³Current address: United States Fish and Wildlife Service, Division of Migratory Birds, Region 6, P.O. Box 25486, Denver Federal Center, Denver, Colorado 80225-0486 USA

⁴Current address: Fort Drum Military Installation, Fish and Wildlife Management Program, 85 First Street West IMNE-DRM-PWE, Fort Drum, New York 13602 USA

⁵Corresponding author: jedwards@wvu.edu

Smith, Brian W., Andrew N. Tri, Chris A. Dobony, John W. Edwards, and Petra Bohall Wood. 2015. Behaviour and nesting ecology of Appalachian Ruffed Grouse (*Bonasa umbellus*). *Canadian Field-Naturalist* 129(3): 245–253.

The substantial decline of Ruffed Grouse (*Bonasa umbellus*) in the southern Appalachian Mountains has been attributed in part to poor recruitment with possible links to nesting ecology. However, despite extensive research, the incubation ecology of Ruffed Grouse remains poorly understood. During 1999–2001 in West Virginia, we used videography of nesting female Ruffed Grouse to (1) quantify incubation constancy (minutes on the nest/minutes recorded) and nest survival during incubation, (2) determine whether incubation constancy predicts hatch success (proportion of eggs hatched per clutch), (3) determine the effect of the onset of laying on incubation constancy and hatch success, and (4) quantify nest visitors and depredation. Females spent about 96% of the recorded time incubating their clutches. Average incubation time per day increased by 1 h between day 1 and day 24 of incubation. Females generally left their nests twice daily, once in the morning between 0700 and 1000 for 31.7 ± 2.4 minutes (standard error) and again in the evening between 1600 and 1800 for 33.6 ± 1.5 minutes. Daily survival of nests ($99.3 \pm 0.4\%$) and nest survival for the incubation period ($84.9 \pm 9.3\%$) were high. Hatch success (the proportion of eggs that hatched among nests where at least one hatched) was high: $94.9 \pm 0.02\%$. We found no relation between incubation constancy and hatch success. We recorded American Black Bear (*Ursus americanus*), Raccoon (*Procyon lotor*), and Long-tailed Weasel (*Mustela frenata*) as nest predators.

Key Words: Ruffed Grouse; *Bonasa umbellus*; infrared cameras; incubation ecology; incubation constancy; nesting behaviour; predation; hatch success; Appalachian Mountains; West Virginia

Introduction

Ruffed Grouse (*Bonasa umbellus*) populations are more abundant in southern Canada and the Great Lakes region where aspen (*Populus* spp.) stands predominate than in areas where aspen is a relatively minor forest component, such as the southern Appalachian Mountains (Norman *et al.* 2004). Moreover, grouse numbers in the southern portion of their range are declining faster than those of their northern counterparts, although the cause of the decline is unknown (Dessecker and McAuley 2001). Tirpak *et al.* (2006) suggest that the low productivity of grouse in the southern Appalachians may be reduced further by lower habitat quality. Relatively little information (Devers *et al.* 2007) exists concerning incubation behaviour of Ruffed Grouse and how that behaviour may influence nest success, depredation, or overall productivity. This information is critical to our understanding of grouse breeding ecology in a region that is different from the vast majority of Ruffed Grouse range and distribution.

Incubation behaviour in birds varies widely based on three main selection pressures: (1) the need to maintain a constant thermal environment suitable for embryo development, (2) the energy demands on the incubator,

and (3) predation risks (Flint and Grand 1999). Many species of birds exhibit female-only incubation (White and Kinney 1974; Ehrlich *et al.* 1988), which influences reproductive effort and, thus, evolution of life-history traits for these species (Lack 1954; Williams 1966; Conway and Martin 2000a). Females must find a balance between maintaining egg temperature for proper embryo development and foraging to meet their energy demands during incubation (Williams 1996; Conway and Martin 2000b).

The frequency and duration of foraging bouts (leaving the clutch to feed) influence the amount of energy needed to rewarm eggs (Vleck 1981; Williams 1996), whereas the hunger level of a female often determines the length of time she incubates eggs before leaving to forage (Kendeigh 1952; White and Kinney 1974; Weathers and Sullivan 1989). In addition, risk of nest predation can influence incubation behaviour as females reduce activity at or near nests to avoid attracting predators (Prescott 1964; Martin 1996; Martin and Ghalambor 1999). Optimizing foraging time may also reduce the number of egg-exposure days by maximizing the rate of embryonic development (Ricklefs 1969; Bosque and Bosque 1995; Conway and Martin 2000b), there-

by decreasing the overall duration of incubation. For these reasons, incubation and associated behaviours may directly influence reproductive success.

Ruffed Grouse is a ground-nesting species with female-only incubation, relatively large clutches (range 9–14 eggs), brief off-nest periods (recesses), and precocial young (Bump *et al.* 1947; Maxson 1989). Incubation takes 23–24 days and females may not re-lay if they lose their first clutch (Haulton 1999; Rusch *et al.* 2000).

Videography has proved to be a valuable tool for determining incubation behaviour and identifying nest predators for a variety of galliforms (Marini and Melo 1998; Rader *et al.* 2007; Coates and Delehanty 2008; Coates *et al.* 2008). We used videography to better understand Ruffed Grouse incubation ecology in the Southern Appalachians. Our objectives were to: (1) quantify incubation constancy (minutes spent on the nest/minutes recorded) and nest survival through incubation, (2) determine whether incubation constancy predicts hatch success (proportion of eggs hatched per clutch), (3) determine the effect of the onset of laying on incubation constancy and hatch success, and (4) quantify nest visitors and depredation. We made the following predictions based on our knowledge and published findings. (1) Incubation constancy would be similar throughout the incubation period. Maxson (1977) found no significant increase or decrease in incubation time for females, except for the last two days during which hatching began. (2) Hatch success would be positively related to incubation constancy because females that left the nest less frequently would maintain more consistent egg temperature. (3) Females that laid clutches earlier would have higher incubation constancy because ambient temperatures are colder in early spring and more energy is required to maintain clutch temperature. (4) *Peromyscus* spp., *Tamias striatus*, *Procyon lotor*, and *Mephitis mephitis* would constitute the majority of nest visitors and/or nest predators (Bump *et al.* 1947; Henry 1969; Dobony *et al.* 2001).

Study Area

We conducted our research in the MeadWestvaco Wildlife and Ecosystem Research Forest (MWERF) near Adolph (38°42'N, 80°3'W) in Randolph County, West Virginia, as part of the Appalachian Cooperative Grouse Research Project. The MWERF, a 3413-ha second-growth forest, was established in 1994 to examine the impacts of modern and intensive forest management on ecological processes in the Appalachian region.

Elevations in the MWERF range from 740–1200 m, and climate is moist and cool with average rainfall and snowfall of 114 cm and 150 cm, respectively (Fenne-man 1938; Strausbaugh and Core 1977). Soils are acidic and typically well drained (Stephenson 1993). Forest cover is Allegheny hardwood–northern hardwood at higher elevations and cove-hardwood and

mixed mesophytic forest at lower elevations (Eyre 1980). The Allegheny hardwood–northern hardwood forest type is dominated primarily by Yellow Birch (*Betula alleghaniensis* Britton), American Beech (*Fagus grandifolia* Ehrhart), Sugar Maple (*Acer saccharinum* L.), Red Maple (*A. rubrum* L.), Black Cherry (*Prunus serotina* Ehrhart), Red Spruce (*Picea rubens* Sargent), White Ash (*Fraxinus americana* L.), and Fraser's Magnolia (*Magnolia fraseri* Walter). Lower elevation species include Yellow-poplar (*Liriodendron tulipifera* L.), Sweet Birch (*B. lenta* L.), Northern Red Oak (*Quercus rubra* L.), and American Basswood (*Tilia americana* L.) (Ford and Rodrigue 2001). Riparian areas of the MWERF are a mixture of Red Spruce, Eastern Hemlock (*Tsuga canadensis* (L.)), and Rosebay Rhododendron (*Rhododendron maximum* L.). The shrub layer throughout the forest consists of Rosebay Rhododendron and Striped Maple (*A. pensylvanicum* L.).

Methods

Trapping

From 1998 to 2000, we trapped female Ruffed Grouse in the MWERF during the fall. We resumed trapping in early spring (March to mid-April) to replace female grouse that had died or whose radio had failed during winter months. We captured grouse using modified lily-pad traps (Gullion 1965) with 10- to 16-m leads that consisted of 46-cm-high poultry wire to guide grouse into the traps. Leads ran between two trap bodies (i.e., one trap at each end).

On capture, all grouse were weighed, aged as adults or juveniles based on primary shape and moult pattern (Kalla and Dimmick 1995), and banded with number 12 butt-end aluminum leg bands (National Band and Tag, Newport, Kentucky, USA). Females were fitted with a necklace-type radio transmitter (Advanced Telemetry Systems, Isanti, Minnesota, USA). Transmitters weighed 10–11 g, had mortality sensors, and were equipped with two-year batteries. All trapping and handling procedures were approved by the West Virginia University Animal Care and Use Committee (protocol 01-0405).

Nest searching and monitoring

We located females three times a week beginning 1 March and ending with the start of incubation during 1999–2001. Using a two-element Yagi antenna and a telemetry receiver (Wildlife Materials, Model TRX-2000S, Carbondale, Illinois, USA), we obtained a minimum of three azimuths from permanently located telemetry stations and determined female locations via triangulation (Mech 1983). We plotted azimuths on topographic maps. To determine onset of egg laying and incubation, we monitored females' activity and movement, both of which tend to decrease once egg laying commences (Maxson 1977, 1978; Johnsgard 1983). We located nests by homing in on telemetry signals (Mech 1983) and visually observing incubating females.

Camera installation

We installed Fuhrman Microcam2 miniature video cameras (Fuhrman Diversified, Inc., Seabrook, Texas, USA) over grouse nests (three in 1999, 11 in 2000, and seven in 2001). We installed cameras immediately after locating each nest, as long as the nest contained five or more eggs; if a nest contained fewer than five eggs, we delayed installing a camera until after the fifth egg was laid. To reduce disturbance at nest sites, we mounted only the camera (enclosed in a camouflaged aluminum housing) approximately 0.5–0.7 m over the nest. Cameras were connected by a 20-m coaxial cable to time-lapse video cassette recorders (VCRs) and deep-cycle 12-volt marine batteries. We ran cables under logs and shrubs to camouflage their presence, and the VCRs were placed in waterproof black cases that were tucked under shrubs and camouflaged with natural items (e.g., sticks and leaves). We wore rubber gloves and boots to reduce our scent when installing the cameras and when changing VCR tapes. We visited the VCRs daily to change recording tapes (standard T-160 videocassettes) and batteries.

Cameras emitted infrared light (950 nm wavelength) that was not visible to vertebrates (Aidley 1971). In darkness, the infrared emitters were capable of illuminating objects up to one metre from the camera. The camera and infrared emitters were enclosed in a 32 mm × 32 mm × 60 mm aluminum housing and attached to an articulating arm. Recording units recorded four black-and-white images per second (one-third the speed of standard VCR) continuously for 24 h (Williams and Wood 2002). After camera installation, no birds were flushed from their nests during visits to change batteries and videocassettes (assessed visually and via video).

During 2001, we removed three of the seven cameras shortly after installation to avoid researcher-induced nest abandonment (i.e., females appeared cautious or agitated by camera presence as evidenced by erect crest and entering the nest and immediately departing). Over the course of the study, cameras were active at 10 nests during the egg-laying period and 18 early in the incubation period.

Video transcription

We transcribed female behaviour captured on videotape beginning at midnight on the day of camera installation; the time lag from camera installation to midnight appeared sufficient to allow females to accept the camera and resume normal behaviour. From the video footage, we determined: (1) duration of egg-laying visits; (2) onset of incubation; (3) amount of time spent incubating and during recess bouts; and (4) identity of nest visitors. We considered that incubation began when the female remained on her nest overnight. We also used video footage to determine exact times and dates for all hatching events, barring battery/camera failure. Video setups (camera, recorder, and battery) were designed to record for 24 h; however, due to

equipment failure (battery failure, camera or videotape malfunction) and nest depredation, the actual amount of footage transcribed varied by tape (range 4–24 h) and nest (range 104–797 h).

We assigned video transcription data to two categories based on when we started monitoring nests: laying period and incubation period. One female's nesting attempts (WV348, captured first when she was an adult) were recorded in both 2000 and 2001, but we considered them independent because attempts occurred in separate years and nests were in different locations within her home range. We excluded from analyses the first day of incubation or first day of videotape for each bird to reduce bias caused by nest disturbance.

Statistical analyses

We completed all statistical tests on camera data using R 3.0.0 (R Foundation for Statistical Computing, Vienna, Austria). We considered differences or effects statistically significant at $\alpha = 0.10$. We calculated incubation constancy (minutes incubating/total minutes recorded per day) to standardize incubation time among birds and tape time because of equipment failure. We pooled years (1999–2001) and age classes (adults and juveniles) because of the small number of nests in our sample. We calculated hatch success as the proportion of eggs that hatched among nests where at least one egg hatched. We assessed daily survival rates of nests (probability of a grouse nest surviving one day) and nest survival (probability of a grouse nest surviving until hatch) using the Nest Survival platform (Dinsmore *et al.* 2002) in Program MARK 7.0 (White and Burnham 1999). Because of our small sample size, we fit no grouping variables or individual covariates. The constant survival model (daily survival rate is constant) in MARK is a maximum likelihood estimate that is an extension of Mayfield's (1961) estimator (Johnson 1979; Dinsmore *et al.* 2002).

We used generalized linear mixed models to assess relations between nesting behaviours and hatch success, and how those behaviours changed throughout the incubation cycle. The random factor in all linear models was each individual bird, because of lack of independence of measurements on the same individual over the course of nesting. To determine whether incubation constancy was a function of how long a female had been incubating the clutch, we constructed a generalized linear mixed model using the "lme4" library with day in the incubation cycle (1–24) as the fixed variable, individual bird as the random explanatory variable, and incubation constancy as the response variable. We also generated linear mixed models to determine (1) how incubation constancy influenced hatch success, (2) how onset of incubation influenced incubation constancy, and (3) how onset of incubation influenced hatch success. We estimated a pseudo r^2 using the Nakagawa and Schielzeth (2013) method for each generalized linear mixed model to determine how much variation in the data was explained.

Results

After removing cameras where birds were disturbed, we videotaped three nests during 1999, 11 nests during 2000, and four nests during 2001. Average date of onset of incubation was 29 April \pm 1.9 days (standard error; range 23 April–9 May). Average clutch size was 10.6 \pm 0.6 eggs/clutch (range 9–13, n = 18 clutches). Daily survival of nests was 99.3 \pm 0.4%. Probability of a nest surviving the duration of incubation (nest survival) was 84.9 \pm 9.3%.

Egg-laying behaviour

We monitored 10 females via video cameras during the egg-laying stage. Overall, females laid 4.5 \pm 0.7 eggs (range 2–7) after camera placement, averaged 10.6 \pm 0.5 eggs per clutch (range 9–13, n = 10 clutches), and averaged 209 \pm 20 minutes on the nest per egg-laying event (range 58–537 minutes). Following egg deposition, all females attempted to cover their nests with leaf litter. They would also place one to several leaves on their back and/or tail while sitting in the nest bowl, and then slowly walk away from the nest, allowing the leaves to slide off their back onto the nest and eggs. None of the nests in our sample was depredated during egg laying.

Incubation behaviour

We monitored 18 females for a total of 311 incubation-days and recorded an average clutch size of 10.9 \pm 0.4 eggs (range 9–12). Four nests were depredated during this period. Hatch success (proportion of eggs hatched per clutch) was 74.6 \pm 10.9% for all females, but improved to 94.9 \pm 0.02% when we excluded de-

predated clutches. On average, incubation constancy was 95.5 \pm 0.4% (average incubation time was 22.7 \pm 0.1 h/day). There was a weak relation (r^2 = 0.22, t_{279} = 5.37, P < 0.001) between incubation constancy and day of the nesting cycle. From day 1 to day 24 of incubation, average incubation time per day increased by 61.3 \pm 12.2 minutes (Figure 1). Females generally left their nest twice daily, once in the morning between 0700 and 1000 for 31.7 \pm 2.4 minutes and again in late afternoon between 1600 and 1800 for 33.6 \pm 1.5 minutes (Figure 1).

We found no relation between incubation constancy and hatch success (t_{309} = 0.50, P = 0.627) or between onset of incubation and incubation constancy (t_{309} = -1.24, P = 0.217). Our results indicated that incubation constancy is not a good predictor of hatch success.

Nest visitors

During the egg-laying period in 2000, we detected four nest visitors (from three different taxa) at three nests (Table 1), but we recorded no depredation attempts. All visitors (i.e., a mouse, *Peromyscus* sp., several salamanders, *Plethodon* spp., and an Eastern Chipmunk, *Tamias striatus*) entered nest bowls while females were absent from their nests, but did not damage or remove any eggs. We observed no other visitors during the egg-laying stage in any year.

During incubation, we detected one nest visitor (a weasel, *Mustela* sp.) during 1999, four nest visitors (four species and two taxa) at four nests during 2000, and six visitors (one species) at two nests in 2001 (Table 1). We visually observed one additional nest visitor, a

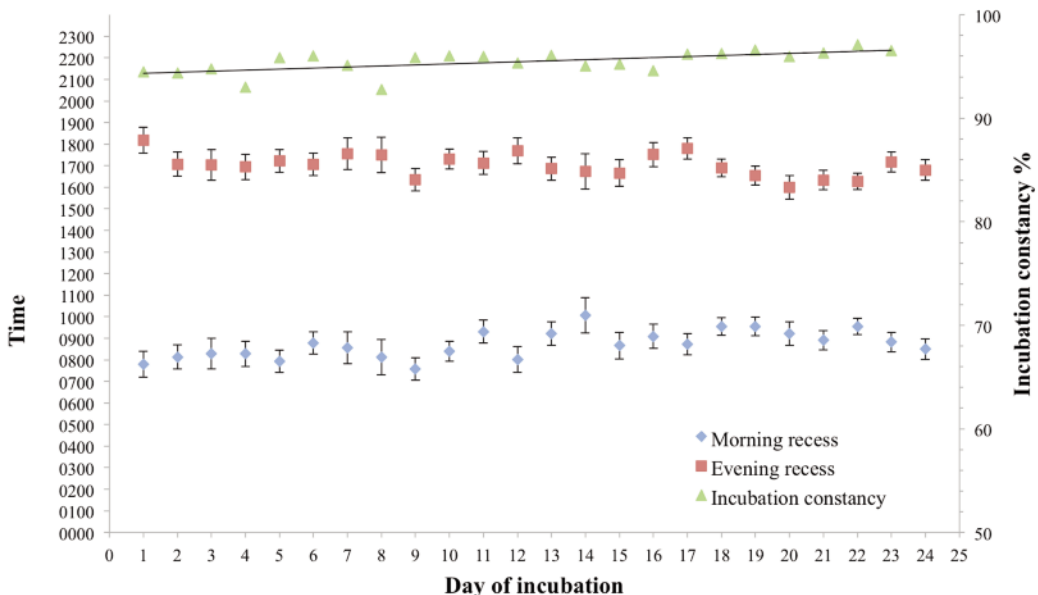


FIGURE 1. Incubation constancy (time on nest as % of recorded time) and recess times (mean \pm standard error) for Ruffed Grouse (*Bonasa umbellus*) in the MeadWestvaco Ecosystem Research Forest in Randolph County, West Virginia, 1999–2001.

TABLE 1. Nest visitors and depredation events recorded during egg laying and incubation at Ruffed Grouse (*Bonasa umbellus*) nests in the MeadWestvaco Ecosystem Research Forest in Randolph County, West Virginia, 1999–2001.

Bird ID	Egg-laying stage			Incubation stage				
	Date, m/d	Visitor	Duration, min:s	Outcome	Date, m/d	Visitor	Duration, min:s	Outcome
<i>1999</i>								
<i>2000</i>								
WV144		<i>Peromyscus</i> sp.	00:02	No eggs harmed	5/2	<i>Mustela</i> sp.	00:47	No eggs harmed
WV144	4/30	<i>Peromyscus</i> sp.	00:30	No eggs harmed	5/2	<i>Plethodon</i> sp.	26:22	No eggs harmed
WV144	5/1	<i>Plethodon</i> sp.	06:57	No eggs harmed	5/7	<i>Ursus americanus</i>	07:51	Female alive, eggs consumed
WV195	4/21	<i>Plethodon</i> sp.	20:50	No eggs harmed	5/6	<i>Procyon lotor</i>	01:34*	Female alive, eggs consumed
					5/16	<i>Mustela frenata</i>	13:36	Female alive, eggs consumed†
<i>2001</i>								
WV362	4/29	<i>Tamias striatus</i>	00:31	No eggs harmed	4/29	<i>Tamias striatus</i>	00:31	No eggs harmed
					5/4	<i>Tamias striatus</i>	00:13	No eggs harmed
					5/8	<i>Tamias striatus</i>	00:05	No eggs harmed
					5/15	<i>Tamias striatus</i>	00:05	No eggs harmed
					5/19	<i>Tamias striatus</i>	00:03	No eggs harmed
					5/14	<i>Tamias striatus</i>	00:03	No eggs harmed

*Raccoon (*Procyon lotor*) returned 52 min. later to search the nest bowl again and check all eggshell fragments for additional contents; it remained in view for 41 s.

†Long-tailed Weasel (*Mustela frenata*) returned to nest the following evening and removed eggs that B. W. S. had replaced (see Smith *et al.* 2003 for details); weasel was in view for 8 min. 54 s.

Raccoon (*Procyon lotor*), in 2000 while changing the battery and videotape in the VCR. The battery had failed overnight and we did not record the nest depredation event. A weasel (*Mustela* sp.) entered the nest of one female during 1999, but did not depredate any eggs. Eastern Chipmunks visited two nests in 2001, but no eggs were removed from either nest despite repeated visits ($n = 5$) at one.

Video cameras recorded depredation events at three nests. A Long-tailed Weasel (*Mustela frenata*), an American Black Bear (*Ursus americanus*), and a Raccoon (*Procyon lotor*) consumed the entire contents of three nests during 2000. We also observed a shrew (*Sorex* sp.) near a nest removing all the shells of hatched eggs from the nest bowl. We are unsure whether the shrew consumed the eggshells or hid them nearby, because we were unable to locate them when we searched the area. Anecdotally, we observed a similar situation at another nest where hatching had recently (< 6 h) occurred; 10 of 11 eggs had hatched, and five shells of the hatched eggs had been pulled under a log about 0.5 m away. This behaviour of shrews (or other small mammals) could influence how researchers assess nest fates or nest predators, as finding no eggs (or nestling remains for songbirds) is usually considered indicative of snake or bird depredation (Hardy 1951; Best and Stauffer 1980; Hernandez *et al.* 1997; Williams and Wood 2002).

Discussion

We recorded incubation constancy of about 96% among successful females, which is similar to that found by Maxson (1977) in Minnesota. High rates of incubation constancy (i.e., > 90%) are common in the order Galliformes (e.g., Williams *et al.* 1971; McCourt *et al.* 1973; Naylor *et al.* 1988; Eaton 1992; Zwickel 1992; Schroeder *et al.* 1999; Coates and Delehanty 2008). We also found a weak, positive relation between incubation constancy and day of the nesting cycle; average incubation time per day increased by about 1 h/day over the period of incubation. Increased constancy in the last few days of incubation has also been noted in Greater Snow Geese (*Chen caerulescens atlanticus*; Reed *et al.* 1995) and Emperor Geese (*Chen canagica*; Thomson and Raveling 1987). Increased incubation constancy may result from increased communication between embryos and females (Reed *et al.* 1995; Rusch *et al.* 2000) or lower tolerance of embryos to sustained and substantial drops in temperature as they develop (MacMullan and Eberhardt 1953; Batt and Cornwell 1972). Cooper and Voss (2013) reported that the rate of heat loss from eggs increased with embryo age in Black-capped Chickadee (*Poecile atricapillus*). Female chickadees responded to the increase in cooling rates by altering their incubation constancy and corresponding recess bouts.

In our study, female Ruffed Grouse initiated egg laying and incubation at dates typical for the region

(Haulton 1999; Devers *et al.* 2007). Clutch size and hatch success reported here were also similar to the range found by Haulton (1999), Tirpak *et al.* (2006), and Devers *et al.* (2007). The female reproductive parameters in our study were representative of Ruffed Grouse in the central and southern Appalachian Mountains.

We found no support for our predictions that hatch success would be positively related to incubation constancy or that early layers would have higher incubation constancy. Female grouse were able to maintain high levels of constancy throughout incubation, which may enhance the likelihood of nest survival.

Diurnal recesses (about 30 minute duration) generally occurred in a bimodal distribution, with females leaving the nest once in the morning and again in late afternoon; no recesses occurred at night. Limiting the number of recesses may reduce the energy cost of incubation by reducing the number of times females must rewarm the clutch (Drent 1970; Gabrielsen and Unander 1987; Williams 1996). Energy demands and the depletion of nutrient reserves in the incubating female may also influence recess patterns. Coates and Delehanty (2008) observed decreased constancy in juvenile Greater Sage-grouse (*Centrocercus urophasianus*) during the later days of incubation and hypothesized that this may have been related to greater diminishing of body reserves compared with adults, which did not display this pattern. We were unable to test for differences in recess patterns between adult and juvenile grouse because of our small sample of juveniles (25%). The grouse we observed remained on their nests for 12–14 h throughout the nocturnal period. The need to forage to replenish their crops likely influenced the maximum duration of incubation (Wiebe and Martin 1997; Coates and Delehanty 2008). Leaving the nest during the day would be more efficient as higher daytime ambient temperatures would decrease the rate of heat loss by eggs during the female's absence.

Long recesses can slow embryo development if egg temperatures drop below a certain threshold (Haftorn 1988); thus, leaving the nest less frequently maximizes the rate of embryonic development, thereby reducing the number of days needed to hatch eggs and during which eggs are exposed to predators (Cody 1966; Ricklefs 1969; Bosque and Bosque 1995). Conway and Martin (2000a) found that nest predation appears to influence passerine incubation by constraining activity at the nest; passerine species that nest in substrates with high nest predation have evolved behaviour to minimize parental activity at the nest (i.e., mainly increased incubation constancy).

We recorded no nest depredation events during egg laying, potentially because activity at and around the nest is much less at this time than during incubation (Maxson 1977), thereby reducing visual or olfactory cues that predators might use to locate nests (Skutch 1949; Conway and Martin 2000a). However, female

activity or olfactory cues at or near nests has the potential to attract both predatory and non-predatory species, possibly affecting nest success. The few depredation incidents we recorded are likely better explained by exposure time, rather than activity around the nest. Visitors during the egg-laying period (i.e., a mouse and several salamanders) did not attempt to remove or consume eggs. In addition, female Ruffed Grouse attempt to conceal their nests on departure from an egg-laying visit (B. W. S. and C. A. D., personal observations), a behaviour similar to that reported in female Wild Turkeys (*Meleagris gallopavo*; Healy 1992). This additional camouflage during the egg-laying period reduces egg visibility and likely reduces predator efficiency. However, once continuous incubation starts, female Ruffed Grouse do not conceal their nests when they depart, which is also similar to behaviour observed in Wild Turkeys (Williams *et al.* 1971).

Nest visitors during the incubation period included both predatory and non-predatory species. Eastern Chipmunks, commonly known to prey on eggs (e.g., Sloan *et al.* 1998), were observed at Ruffed Grouse nests on numerous occasions but never damaged or consumed eggs. Grouse eggs may be too large for chipmunks to open or remove from the nest bowl, but they may visit the nest repeatedly to check for damaged or partly hatched eggs. Mammalian predators destroyed 4 of 18 (22%) nests monitored during our study. This level of depredation was within the range observed throughout the Ruffed Grouse range (16–41%; Bump *et al.* 1947; Johnsgard and Maxson 1989; Rusch 1989; Haulton 1999; Dobony *et al.* 2001; Larson *et al.* 2001). Depredation was also within documented ranges of other grouse species (16–67%; Boag *et al.* 1984; Ritchie *et al.* 1994; Grisham *et al.* 2014). Both raccoons and weasels are common predators on Ruffed Grouse eggs in the Appalachian Mountains (Bump *et al.* 1947; Rusch *et al.* 2000; Dobony *et al.* 2001; Smith *et al.* 2003). American Black Bears are not known as common nest predators of Ruffed Grouse, but were found to depredate nests of Ruffed Grouse in our study. American Black Bears have been noted as predators of songbirds (Williams and Wood 2002) and artificial nests (Sloan *et al.* 1998).

Selection has shaped incubation behaviour in Ruffed Grouse to optimize productivity, maintain energy reserves, and reduce risk of predation. If predators locate nests or incubating females by observing activity around a nest, then females that enter and leave their nest less often will have an advantage in terms of lower risk of predation (Conway and Martin 2000a). Ruffed Grouse nests are usually located against or under an object (Bump *et al.* 1947; Johnsgard and Maxson 1989; Fetting 2002), providing overhead cover and often perimeter cover from one or more directions. Moreover, most nests have a high percentage of vertical cover immediately surrounding nest sites (Thompson *et al.* 1987; Larson *et al.* 2001; Fetting 2002), which may

provide added protection from avian predators (Gullion 1972).

Acknowledgements

This study was conducted as part of the Appalachian Cooperative Grouse Research Project and was supported in part by the West Virginia Division of Natural Resources (Pittman-Robertson Federal Aid in Wildlife Restoration Project W-48-R) and the Division of Forestry and Natural Resources, West Virginia University. We thank the Richard King Mellon Foundation and the Ruffed Grouse Society for additional funding, MeadWestvaco Corporation for logistical support, and the West Virginia Cooperative Fish and Wildlife Research Unit for use of their video surveillance systems. In addition, we thank T. Allen, T. Olexa, R. Smith, and S. Sutton for assistance with fieldwork, Gary Norman for project guidance, Dr. George Seidel for statistical support, and Drs. Jim Belthoff and Barry Grand for reviewing early versions of our manuscript. The use of trade names or products does not constitute endorsement by the United States government.

Literature Cited

- Aidley, D. J.** 1971. *The Physiology of Excitable Cells*. Cambridge University Press, London, UK.
- Batt, B. D. J., and G. W. Cornwell.** 1972. The effects of cold on Mallard embryos. *Journal of Wildlife Management* 36: 745–751.
- Best, L. B., and D. F. Stauffer.** 1980. Factors affecting nesting success in riparian bird communities. *Condor* 82: 149–158.
- Boag, D. A., S. G. Reeb, and M. A. Schroeder.** 1984. Egg loss among spruce grouse inhabiting lodgepole pine forests. *Canadian Journal of Zoology* 62: 1034–1037.
- Bosque, C., and M. T. Bosque.** 1995. Nest predation as a selective factor in the evolution of developmental rates in altricial birds. *American Naturalist* 145: 234–260.
- Bump, G., R. W. Darrow, F. C. Edminster, and W. F. Crissey.** 1947. *The Ruffed Grouse: Life History, Propagation & Management*. New York State Conservation Department, Albany, New York, USA.
- Coates, P. S., and D. J. Delehanty.** 2008. Effects of environmental factors on incubation patterns of greater sage-grouse. *Condor* 110: 627–638.
- Coates, P. S., J. W. Connelly, and D. J. Delehanty.** 2008. Predators of greater sage-grouse nests identified by video monitoring. *Journal of Field Ornithology* 79: 421–428.
- Cody, M. L.** 1966. A general theory of clutch size. *Evolution* 20: 174–184.
- Conway, C. J., and T. E. Martin.** 2000a. Evolution of passerine incubation behavior: influences of food, temperature, and nest predation. *Evolution* 54: 670–685.
- Conway, C. J., and T. E. Martin.** 2000b. Effects of ambient temperature on avian incubation behavior. *Behavioral Ecology* 11: 178–188.
- Cooper, C. B., and M. A. Voss.** 2013. Avian incubation patterns reflect temporal changes in developing clutches. *PLoS ONE* 8(6): e65521.
- Dessecker, D. R., and D. G. McAuley.** 2001. Importance of early successional habitat to ruffed grouse and American woodcock. *Wildlife Society Bulletin* 29: 456–465.
- Devers, P. K., D. F. Stauffer, G. W. Norman, D. E. Steffen, D. M. Whitaker, J. D. Sole, T. J. Allen, S. L. Bittner, D. A. Buehler, J. W. Edwards, D. E. Figert, S. T. Friedhoff, W. W. Giuliano, C. A. Harper, W. K. Igo, R. L. Kirkpatrick, M. H. Seamster, H. A. Spiker Jr, D. A. Swanson, and B. C. Tefft.** 2007. Ruffed grouse population ecology in the Appalachian Region. *Wildlife Monographs* 168: 1–36.
- Dinsmore, S. J., G. C. White, and F. L. Knopf.** 2002. Advanced techniques for modeling avian nest survival. *Ecology* 83: 3476–3488.
- Dobony, C. A., J. W. Edwards, W. M. Ford, and T. J. Allen.** 2001. Nesting success of ruffed grouse in West Virginia. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 55: 456–465.
- Drent, R. H.** 1970. Functional aspects of incubation in the Herring Gull. *Behaviour (Supplement)* 17: 1–132.
- Eaton, S. W.** 1992. Wild Turkey (*Meleagris gallopavo*). No. 22 in *The Birds of North America*. Edited by A. Poole and F. Gill. Academy of Natural Sciences, Philadelphia, Pennsylvania, and American Ornithologists' Union, Washington, DC, USA.
- Ehrlich, P. R., D. S. Dobkin, and D. Wheye.** 1988. *The Birder's Handbook: A Field Guide to the Natural History of North American Birds*. Simon and Schuster, New York, New York, USA.
- Eyre, F. H.** 1980. *Forest Cover Types of the United States and Canada*. Society of American Foresters, Washington, DC, USA.
- Fenneman, N. M.** 1938. *Physiography of the Eastern United States*. McGraw-Hill, New York, New York, USA.
- Fetting, J. L.** 2002. Ruffed Grouse nesting ecology and brood habitat in western North Carolina. M.S. thesis, University of Tennessee, Knoxville, Tennessee, USA.
- Flint, P. L., and J. B. Grand.** 1999. Incubation behavior of Spectacled Eiders on the Yukon-Kuskokwim Delta, Alaska. *Condor* 101: 413–416.
- Ford, W. M., and J. L. Rodrigue.** 2001. Soricid abundance in partial overstory harvests and riparian areas in an industrial forest landscape of the central Appalachians. *Forest Ecology and Management* 152: 159–168.
- Grisham, B. A., P. K. Borsdorf, C. W. Boal, and K. K. Boyd.** 2014. Nesting ecology and nest survival of lesser prairie-chicken on the Southern High Plains of Texas. *Journal of Wildlife Management* 78: 857–866.
- Gabrielsen, G., and S. Unander.** 1987. Energy costs during incubation in Svalbard and Willow Ptarmigan hens. *Polar Research* 5: 59–69.
- Gullion, G. W.** 1965. Improvements in methods for trapping and marking ruffed grouse. *Journal of Wildlife Management* 29: 109–116.
- Gullion, G. W.** 1972. *Improving your Lands for Ruffed Grouse*. Ruffed Grouse Society of North America, Rochester, New York, USA.
- Haftorn, S.** 1988. Incubating female passerines do not let the egg temperature fall below the 'physiological zero temperature' during their absences from the nest. *Ornis Scandinavica* 19: 97–110.
- Hardy, F. C.** 1951. Ruffed Grouse nest predation by blacksnakes. *Wilson Bulletin* 63: 42–43.
- Haulton, G. S.** 1999. Ruffed Grouse natality, chick survival, and brood microhabitat selection in the southern Appalachians. M.Sc. thesis, Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA.
- Healy, W. M.** 1992. Wild turkey biology: Behavior. Pages 46–65 in *The Wild Turkey: Biology and Management*.

- Edited by J. G. Dickson. Stackpole Books, Mechanicsburg, Pennsylvania, USA.*
- Henry, V. G.** 1969. Predation on dummy nests of ground-nesting birds in the southern Appalachians. *Journal of Wildlife Management* 33: 169–172.
- Hernandez, F., D. Robbins, and R. Cantu.** 1997. Evaluating evidence to identify ground-nest predators in west Texas. *Wildlife Society Bulletin* 25: 826–831.
- Johnsgard, P. A.** 1983. *The Grouse of the World*. University of Nebraska Press, Lincoln, Nebraska, USA.
- Johnsgard, P. A., and S. J. Maxson.** 1989. Nesting. Pages 130–137 in *Ruffed Grouse*. Edited by S. Atwater and J. Schnell. Stackpole Books, Harrisburg, Pennsylvania, USA.
- Johnson, D. H.** 1979. Estimating nest success: the Mayfield method and an alternative. *Auk* 96: 651–661.
- Kalla, P. I., and R. W. Dimmick.** 1995. Reliability of established aging and sexing methods in Ruffed Grouse. *Proceedings of the Annual Conference of the Southeast Association of Fish and Wildlife Agencies* 49: 580–593.
- Kendeigh, S. C.** 1952. Parental care, its evolution in birds. *Illinois biological monograph* 22. University of Illinois Press, Urbana, Illinois, USA.
- Lack, D.** 1954. *The Natural Regulation of Animal Numbers*. Oxford University Press, London, UK.
- Larson, M. A., M. E. Clark, and S. R. Winterstein.** 2001. Survival of ruffed grouse chicks in northern Michigan. *Journal of Wildlife Management* 65: 880–886.
- MacMullan, R. A., and L. L. Eberhardt.** 1953. Tolerance of incubating pheasant eggs to exposure. *Journal of Wildlife Management* 17: 322–330.
- Marini, M. A., and C. Melo.** 1998. Predators of quail eggs, and the evidence of the remains: implications for nest predation studies. *Condor* 100: 395–399.
- Martin, T. E.** 1996. Life history evolution in tropical and south temperate birds: what do we really know? *Journal of Avian Biology* 27: 263–272.
- Martin, T. E., and C. K. Ghalambor.** 1999. Males feeding females during incubation. I. Required by microclimate or constrained by nest predation? *American Naturalist* 153: 131–139.
- Maxson, S. J.** 1977. Activity patterns of female Ruffed Grouse during the breeding season. *Wilson Bulletin* 89: 439–454.
- Maxson, S. J.** 1978. Spring home range and habitat use by female Ruffed Grouse. *Journal of Wildlife Management* 42: 61–71.
- Maxson, S. J.** 1989. Patterns of activity and home range of hens. Pages 118–129 in *Ruffed Grouse*. Edited by S. Atwater and J. Schnell. Stackpole Books, Harrisburg, Pennsylvania, USA.
- Mayfield, H. R.** 1961. Nesting success calculated from exposure. *Wilson Bulletin* 73: 255–261.
- McCourt, K. H., D. A. Boag, and D. M. Keppie.** 1973. Female Spruce Grouse activities during laying and incubation. *Auk* 90: 619–623.
- Mech, L. D.** 1983. *Handbook of Animal Radio-tracking*. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Nakagawa, S., and H. Schielzeth.** 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4: 133–142.
- Naylor, B. J., K. J. Szuba, and J. F. Bendell.** 1988. Nest cooling and recess length of incubating Spruce Grouse. *Condor* 90: 489–492.
- Norman, G. W., D. E. Stauffer, J. Sole, T. J. Allen, W. K. Igo, S. Bittner, J. Edwards, R. L. Kirkpatrick, W. M. Giuliano, B. Tefft, C. Harper, D. Buehler, D. Figert, M. Seamster, and D. Swanson.** 2004. Ruffed Grouse ecology and management in the Appalachian region. Final project report of the Appalachian Cooperative Grouse Research Project. Accessed 7 May 2014. <http://www.dgif.virginia.gov/wildlife/grouse/grouse-project.pdf>.
- Prescott, K. W.** 1964. Constancy of incubation for the Scarlet Tanager. *Wilson Bulletin* 76: 37–42.
- Rader, M. J., T. W. Teinert, L. A. Brennan, F. Hernandez, N. J. Silvy, and X. B. Wu.** 2007. Identifying nest predators and nest fates of bobwhites in southern Texas. *Journal of Wildlife Management* 71: 1626–1630.
- Reed, A., R. J. Hughes, and G. Gauthier.** 1995. Incubation behavior and body mass of female Greater Snow Geese. *Condor* 97: 993–1001.
- Ricklefs, R. E.** 1969. An analysis of nesting mortality in birds. *Smithsonian contributions to zoology* 9. Smithsonian Institution Press, Washington, DC, USA.
- Ritchie, M. E., M. L. Wolfe, and R. Danvir.** 1994. Predation of artificial Sage Grouse nests in treated and untreated sagebrush. *Great Basin Naturalist* 54: 122–129.
- Rusch, D. H.** 1989. The grouse cycle. Pages 210–226 in *Ruffed Grouse*. Edited by S. Atwater and J. Schnell. Stackpole Books, Harrisburg, Pennsylvania, USA.
- Rusch, D. H., S. DeStefano, M. C. Reynolds, and D. Lauten.** 2000. Ruffed Grouse (*Bonasa umbellus*). No. 515 in *The Birds of North America*. Edited by A. Poole and F. Gill. Academy of Natural Sciences, Philadelphia, Pennsylvania, and American Ornithologists' Union, Washington, DC, USA.
- Schroeder, M. A., J. R. Young, and C. E. Braun.** 1999. Sage Grouse (*Centrocercus urophasianus*). No. 425 in *The Birds of North America*. Edited by A. Poole and F. Gill. Academy of Natural Sciences, Philadelphia, Pennsylvania, and American Ornithologists' Union, Washington, DC, USA.
- Skutch, A. F.** 1949. Do tropical birds rear as many young as they can nourish? *Ibis* 91: 430–455.
- Sloan, S. S., R. T. Holmes, and T. W. Sherry.** 1998. Depredation rates and predators at artificial bird nests in an unfragmented northern hardwoods forest. *Journal of Wildlife Management* 62: 529–539.
- Smith, B. W., C. A. Dobony, J. W. Edwards, and W. M. Ford.** 2003. Observations of Long-tailed Weasel, *Mustela frenata*, hunting behavior in central West Virginia. *Canadian Field-Naturalist* 117: 313–315.
- Stephenson, S. L.** 1993. An introduction to the upland forest region. Pages 1–9 in *Upland Forests of West Virginia*. Edited by S.L. Stephenson. McClain Printing Co., Parsons, West Virginia, USA.
- Strausbaugh, P. D., and E. L. Core.** 1977. *Flora of West Virginia*. Seneca Books, Inc., Morgantown, West Virginia, USA.
- Thompson III, F. R., D. A. Freiling, and E. K. Fritzell.** 1987. Drumming, nesting, and brood habitats of Ruffed Grouse in an oak-hickory forest. *Journal of Wildlife Management* 51: 568–575.
- Thompson, S. C., and D. G. Raveling.** 1987. Incubation behavior of Emperor Geese compared with other geese: interactions of predation, body size, and energetics. *Auk* 104: 707–716.
- Tirpak, J. M., W. M. Giuliano, C. A. Miller, T. J. Allen, S. Bittner, J. W. Edwards, S. Friedhoff, W. K. Igo, D. F. Stauffer, and G. W. Norman.** 2006. Ruffed Grouse nest success and habitat selection in the central and southern Appalachians. *Journal of Wildlife Management* 70: 138–144.

- Vleck, C. M.** 1981. Hummingbird incubation: female attentiveness and egg temperature. *Oecologia* 51: 199–205.
- Weathers, W. W., and K. A. Sullivan.** 1989. Nest attentiveness and egg temperature in the Yellow-eyed Junco. *Condor* 91: 628–633.
- White, F. N., and J. L. Kinney.** 1974. Avian incubation. *Science* 186: 107–115.
- White, G. C., and K. P. Burnham.** 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 (Supplement): 120–138.
- Wiebe, K. L., and K. Martin.** 1997. Effects of predation, body condition and temperature on incubation rhythms of White-tailed Ptarmigan *Lagopus leucurus*. *Wildlife Biology* 3: 219–227.
- Williams, G. C.** 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *American Naturalist* 100: 687–690.
- Williams, G. E., and P. B. Wood.** 2002. Are traditional methods of determining nest predators and nest fates reliable? An experiment with Wood Thrushes (*Hylocichla mustelina*) using miniature video cameras. *Auk* 119: 1126–1132.
- Williams, J. B.** 1996. Energetics of avian incubation. Pages 375–416 in *Avian Energetics and Nutritional Ecology*. Edited by C. Carey. Chapman and Hall, New York, New York, USA.
- Williams, Jr., L. E., D. H. Austin, T. E. Peoples, and R. W. Phillips.** 1971. Laying data and nesting behavior of Wild Turkeys. Pages 90–106 in *Proceedings of the 25th Annual Conference*. Southeastern Association of Game and Fish Commissioners, Columbia, South Carolina, USA.
- Zwickel, F. C.** 1992. Blue Grouse (*Dendragapus obscurus*). No. 15 in *The Birds of North America*. Edited by A. Poole and F. Gill. Academy of Natural Sciences, Philadelphia, Pennsylvania, and American Ornithologists' Union, Washington, DC, USA.

Received 11 July 2014

Accepted 7 June 2015