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# Nesting season, nest age, and disturbance, but not habitat characteristics, affect nest survival of Chinese grouse

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## Abstract

Nest survival is a vital component of breeding success, and affects population dynamics, as the loss of nests is the main cause of reproductive failure in birds. To identify key factors for the conservation of Chinese grouse *Tetrastes sewerzowi*, we tested the effects of nest concealment, nest age, nesting season, and habitat edge on nest daily survival rate (DSR) of Chinese grouse using 54 nests found at Lianhuashan Nature Reserve, Gansu, China, 2009–2012. Moreover, we controlled for the effect of research activity by testing the effect of nest checks on DSR. Overall, mammal predation caused 93% of nest failures. DSR was  $0.986 \pm 0.0038$  in the constant model and the probability of a nest with a full clutch of 6 eggs surviving the entire 40-day nesting period was  $0.526 \pm 0.090$ . DSR decreased with nest age and nesting season (from 19 May to 3 July). Mammals instead of avian predators being responsible for most nest failures suggest that nest sites might be selected to avoid visual avian predators, but not olfactory mammalian predators, and the decreasing trend of DSR with nest age and nesting season could attribute to an additive exposure effect. Moreover, nest checks conducted by investigators significantly lowered nest DSR, especially during the late period of nesting season and for older nests. Mammalian predators might locate the nest site by following the investigator's odor. Based on our results, we suggest that the late incubation stage is a particularly vulnerable period for nest survival of Chinese grouse and those researchers should adjust their activities around nests to balance the need of acquiring accurate data and decreasing nest predation risk.

**Key words:** nest age, nest check, nesting season, nest survival, program MARK, *Tetrastes sewerzowi*.

Nest survival is a vital component of breeding success, and affects population dynamics, as the loss of nests is the main cause of reproductive failure in birds (Martin 1993). Factors influencing nest survival of birds can be classified into 3 groups: 1) factors relating to breeding adults, such as nest constancy (Brussee et al. 2016), body condition (Öst and Steele 2010), age and breeding experience (Linz et al. 2008), nest defense behaviors (Remeš 2005; Brussee et al. 2016); 2) factors relating to nest predators, such as

composition of predator communities, predator abundance (Burr et al. 2017), activity patterns of predators (Wegge and Storaas 1990; Bêty et al. 2001); 3) other factors about the environmental conditions, such as nest habitat features (Chalfoun et al. 2002; Stephens et al. 2003; Borgmann and Conway 2015; Fuller et al. 2017), weather conditions (Webb et al. 2012), time-varying factors like nesting season (Grant et al. 2005) and nest age (Smith and Wilson 2010), and the intensity of human disturbance (Sandercock et al. 2015;

Uherkoch et al. 2015). These factors can influence nest survival independently, combinedly, or interactively. For example, experienced breeders can nest at more concealed sites to reduce the chance of being discovered by predators (Öst and Steele 2010), inclement weather conditions may affect nest survival directly or indirectly through changing the behaviors of incubating adults and/or predators (Smith and Wilson 2010). Identifying species-specific key variables that influence nest survival is vital for conservation and management for bird conservation (Kolada et al. 2009; Anteau et al. 2012), especially for threatened species.

Nest habitat selection has long been considered to be an adaptive behavior conducted by parents to increase nest survival (Martin et al. 2000; Traylor et al. 2004; Newlon and Saab 2011). A common hypothesis invoked to explain patterns in nest habitat selection is the nest concealment hypothesis, which predicts that birds should select more concealed nests and those sites should provide higher reproductive success (Martin and Roper 1988; Borgmann and Conway 2015). The prediction of nest concealment hypothesis have been verified in a number of species (*Tympanuchus phasianellus*, Manzer and Hannon 2005; *Bartramia longicauda*, Sandercock et al. 2015; *Meleagris gallopavo silvestris*, Fuller et al. 2017). However, in other studies, researchers have failed to find a positive relationship between nest concealment and nest survival (Davis 2005; Remeš 2005). Borgmann and Conway (2015) reviewed the empirical data on open cup nesting songbirds and found 74% ( $n = 106$ ) of studies failed to support the nest concealment hypothesis. Latif et al. (2012) proposed that the lack of congruence between theory-based expectation and empirical data may arise when birds already occupy “adaptive peaks.” If all breeding birds already nest at low-predation risk sites, then researchers will not find a relationship between nest microhabitat features and nest survival, despite predation risk may ultimately shape nest habitat selection. In such a circumstance, some other factors might come into play. For instance, if the better concealed nests were built to avoid to be discovered by visual predators (avian predators), the increase of the number of olfactory mammalian predators would incur an elevated proportion of nest failures caused by them (Conover et al. 2010). Nevertheless, determining whether nests with better concealment have higher a survival rate is still a basic requirement for conservation of many birds.

Another important feature of nest habitat that potentially influence nest survival is habitat fragmentation. Habitat fragmentation could be categorized at 3 spatial scales: landscape scale (amount of habitat, edge, and variation in patch size across a defined spatial scale, e.g., 10 km), patch scale (the size and shape of the habitat patch where nests were located), and edge scale (distance from a nest to a habitat edge) (Stephens et al. 2003). Some studies have reported elevated nest predation rates in fragmented landscapes (Robinson et al. 1995), small habitat remnants (Small and Hunter 1988), and habitat edges (Kurki and Lindén 1995; Burger et al. 2004). Researchers have developed many hypotheses to explain the elevated nest predation rates in fragmented habitats. Some of the most common hypotheses are that predators are more abundant and/or more active in fragmented landscapes, small habitat patches, and edges, incurring a reduced nest survival in fragmented habitats than in continuous habitats (Marini et al. 1995). Despite some evidence of elevated nest failure in fragmented habitats have been found in some studies (Paton 1994). Chalfoun et al. (2002) reviewed the literatures and found inconsistent results and nest predation rates were more likely to show a positive response to fragmentation when it was measured at the landscape scale than at the finer scales. Furthermore, there is little information on the effects of habitat

fragmentation on nesting success of most bird species (Stephens et al. 2003), impeding us to make proper habitat managements to increase nest survival of a variety of birds.

Factors influencing nest survival may also change across nesting season (Kurki et al. 1997; Wilson et al. 2007; Grant et al. 2005). These factors include nest density, nest concealment, the abundance and behavior of predators, and weather conditions. Nest survival may increase in a linear fashion over the season coincident with increases in vegetation cover for nest concealment (Sullivan and Dinsmore 1990). Alternatively, nest survival may also decrease linearly if predators develop a search image for nests and increase their hunting effort as nesting season progress due to an elevated nutritional demands for reproduction (Gilg et al. 2006). Nest survival may also be higher in early and late nesting season but lower in mid-season when nest density is usually higher and predators may cue in to nests at this stage (Niemuth and Boyce 1995). Similarly, variables that change with nest age may also affect nest survival. For example, incubating females may leave their nests fewer times as nest age increased, leaving fewer cues about nest locations to nest predators (Dinsmore et al. 2002), therefore, older nests may have greater survival probabilities than nests in early stages (Martin 2002). The effects of nesting season and nest age can be confounded if they are synchronized (Smith and Wilson 2010). Determining time-specific patterns in nest survival may improve our understanding of predator-prey interactions, evolution of avian life histories, and aspects of population dynamics that are critical to bird conservation (Grant et al. 2005).

In order to estimate nest survival, investigators need to check the nest status or contents repeatedly in egg-laying and incubation periods. However, researchers have long been concerned about the potentially negative effects of their activities (e.g., nest checks) on nest survival (Grier 1969; Götmark 1992; Armstrong 1996). Investigator activities near/on nests may incur physiological and behavioral responses of incubating birds (Sandvik and Barrett 2001; Beaulieu et al. 2010), which might result in the incubating birds to reduce nest attendance, leave the eggs unprotected to predators, even desert the eggs (Blackmer et al. 2004; Carey 2011), giving rise to a reduced nest survival rate. Concomitantly, researchers may leave scent and physical trails (trampling on vegetation by foot traffic) when they collecting data near nests (Jacobson et al. 2011). Nest predators may be attracted or deterred to these trails (O’Grady et al. 1996; Jacobson et al. 2011), incurring a reduced or increased probability of nest predation. Therefore, the effects of investigator activity on nest survival depend on the sensitivity of prey and predators to investigators, which may vary across species, time, study sites, even different populations of the same species (Götmark 1992; Ibáñez-Álamo et al. 2012). The investigator effect has the potential to create biased results (Uherkoch et al. 2015) that, in turn, could compromise our understanding of a species ecological and behavioral attributes (Serventy and Curry 1984; Carey 2011). However, most studies did not account for the investigator effects when they estimated nest survival.

The Chinese grouse *Tetrastes sewerzowi*, endemic to China, is distributed in alpine conifer forests at elevations between 2,400 and 4,300 m along the eastern edge of the Tibetan Plateau (Sun 2000). As a monogamous bird (Sun et al. 2003), males occupy territories with abundant willows (*Salix* spp.) and other food resources (Zhao et al. 2017), and females pair with males and nest in males’ territories (Sun et al. 2007). Males guard females during the pre-laying and egg-laying periods, when females are actively feeding (Lou et al. 2017), however, males do not accompany females during incubation

**Table 1.** Variables used in analyzing the DSR of Chinese grouse nests and predicted effects at Lianhuashan Nature Reserve, Gansu, China, 2009–2012

Variable	Description	Prediction
Year	2009, 2010, 2011, and 2012	DSR different between years
Shrub cover	Mid-story concealment of a nest	DSR higher when a nest has greater shrub cover
Grass cover	Lower-story concealment of a nest	DSR higher when a nest has greater grass cover
Nest age	Nest age during monitoring periods	DSR higher as nest ages, because DSR higher in older nests, because hens will provide less cues and more concentrate on nests in the process.
Nesting season	Date that at least 1 nest under surveillance (May 19 to July 3)	DSR higher in later incubation periods, because vegetation growth will provide more concealment to nests in late season.
Distance to edge	Straight distance to forest edge	DSR lower for nests near edge
Nest check	Nest checked by an investigator	DSR lower on the day of nest check

(Sun 2004). Due to the relatively short summer season at high elevations, females do not renest if their nests fail during incubation (Sun et al. 2003). The population trend of Chinese grouse is decreasing (Birdlife International 2017), and low-breeding performance has been found to be an important limiting factor for population viability and restoration (Lu and Sun 2011). Nest survival is an important part of breeding performance of Chinese grouse. Determining factors influencing nest survival of Chinese grouse is beneficial to its population restoration and conservation.

Studies that integrate various factors that potentially influence nest survival could provide us important information on nest survival and be helpful to conservation management. Most existing studies examined the effects of some habitat factors (e.g., nest concealment), but omitted the effect of time, which might account for changes among incubation periods (Jacobson et al. 2011; Borgmann and Conway 2015). Here, we examined various habitat and time-varying factors that are potentially important to nest survival of Chinese grouse. More importantly, we examined whether nest checks conducted by investigators was detrimental to nest survival. Specifically, we recorded factors related to nest concealment, distance to forest edge, human disturbance, nesting season, and nest age. Our purposes were 1) describing nest survival of Chinese grouse and 2) identifying the key factors influencing nest daily survival rate (DSR), based on model selection method. Moreover, we 3) estimated the effects of nest checks on DSR by incorporating it into the best supported models. We predicted that DSR would increase with nest concealment, but decrease with distance to forest edge. We also predicted that nest checks would be detrimental to nest survival of Chinese grouse (see Table 1 for predictions for each variable).

## Materials and Methods

### Study area

We studied Chinese grouse at Shahetan Station, 2,600 m–3,570 m above sea level, in the core area of the Lianhuashan Nature Reserve in Gansu Province, China (34°40′67″N, 103°30′84″E). The annual precipitation is 650 mm and the mean annual minimum and maximum temperatures are –27.1°C and 34°C, respectively, at an elevation of 2,100 m (Sun et al. 2006). The study area is fragmented by historical logging and agricultural activities (Zheng and Wang 1998). Sun et al. (2006) found that, among the 1,762 forest patches determined from the satellite image within the 12,000 ha study area at Lianhuashan, 1,362 were <10 ha and only 31 were >100 ha. The forests are now mainly dominated by uncut and selectively cut mature conifer forests and conifer-deciduous mixed forests, with

deciduous forests and shrubs at the forest edges and on sunny slopes. The most common tree species in the study area are spruces (36%, *Picea asperata*, *P. purpurea*, and *P. wilsonii*), firs (23%, *Abies fargesii*, *A. faxoniana*, and *A. sutchuenensis*), willows (23%), and birches (14%, *Betula utilis*). Potential nest predators of Chinese grouse include Asian badger *Meles leucurus*, dhole *Cuon alpinus*, raccoon dog *Nyctereutes procyonoides*, stone marten *Martes foina*, Siberian weasel *M. sibirica*, sand badger *Arctonyx collaris*, Pallas' cat *Felis manul*, leopard cat *F. bengalensis*, Chinese mountain cat *F. bieti*, and Eurasian lynx *Lynx lynx*. Raptors like the northern goshawk *Accipiter gentilis*, besra *A. virgatus*, Eurasian sparrowhawk *A. nisus*, peregrine falcon *Falco peregrinus*, common kestrel *F. tinnunculus*, saker falcon *F. cherrug*, long-legged buzzard *Buteo rufinus*, Sichuan wood owl *Strix davidi*, boreal owl *Aegolius funereus*, and eagle owl *Bubo bubo* might also prey on incubating hens, and thus cause nest failures. A more detailed description of the study area can be found in Klaus et al. (2001), Sun et al. (2003), and Zhao et al. (2018).

### Field surveys

During 2009–2012, 68 nests were found by locating radio-tagged females ( $n = 14$ ), completely searching males' territories ( $n = 30$ ), or receiving reports from local villagers ( $n = 24$ ) who occasionally found nests while collecting mushrooms in the forest (Zhao et al. 2015). However, of the 68 nests, the fates of 9 nests were determined on the location day (5 successful and 4 failed), habitat data of 2 nests were not collected (2 successful), and 3 nests failed because of the deployment of nest data loggers (1 nest deserted by the hen, 2 nests were found to be predated by predators the day after the deployment). All of these nests were excluded from further analysis. Thus, we successfully monitored and collected survival and associated data on 54 nests in the breeding seasons of 2009–2012.

We measured the lengths, breadths, and weights of the eggs on the day the nest was located. We checked each nest every 2–5 days from the day of location until the final fate of the nest was determined. To check the status of a nest, we approached the nest until we could see the hen or the eggs in the nest. The distance from the nest during our nest checks varied from 1 to 6 m, depending on the nearby vegetation and topography. We did not touch the hen or the eggs during a nest check. We also caught 26 incubating hens during the last week of incubation to fit radio-transmitter collars to facilitate data collection on brood movement and habitat use after hatching (for detailed capture procedure, see Zhao et al. (2015) and Zhao et al. (2018)). All hens continued incubation after collars were fitted, and no obvious detrimental effects were observed. We did not evaluate the effects of egg measurement on DSR, which was relatively

high in early nest periods, when most eggs were measured. Therefore, we only considered the effects of nest checks in the following analysis.

A nest was considered successful when at least 1 egg hatched, otherwise unsuccessful (Zhao et al. 2015). An egg with shells detached to 2 halves from the middle was considered to be successfully hatched. When a nest was predated, we classified the nest predator categories by inspecting the nest contents. We considered a nest to have been predated by mammals if all eggs disappeared before hatching or egg shells were crushed; or by birds if eggs were not broken at the middle, but had obvious punched marks. Otherwise, the cause of failure was defined as unknown. The identification of nest predators based on nest remains has been criticized, because predation by many predators can result in the same damage pattern (e.g., scratch marks or punctuation marks on eggs and nest material disturbance, Larivière 1999). However, we believed this technique was effective in this study, as we attributed the predator identities to 2 main animal categories (mammalian or avian), instead of species.

The 3 habitat variables we included in model building were percent shrub cover, percent grass cover, and the distance to the forest edge (m). Shrub cover and grass cover would represent nest concealment, whereas distance to forest edge represents edge effects. We considered these 3 variables to be meaningful in determining nest survival of Chinese grouse, based on the literature (Kurki and Lindén 1995; Sun et al. 2007; Rhim 2012), where nest site selection or nest survival of 3 forest grouse species (Chinese grouse, hazel grouse *T. bonasia*, and black grouse *Tetrao tetrix*) were found to be related to these 3 habitat variables. We used the line-intercept method (Canfield 1941) to measure percent shrub cover, which measured the overlap of all shrubs between 0.5 and 5 m in height along two 20 m rope transects perpendicularly centered on the nest. We measured percent grass cover every 5 m along these 20 m transects using 20 cm × 20 cm Daubenmire frames (Daubenmire 1959), and used the mean value of all frames as an index of surrounding grass cover. Lastly, we calculated the straight line distance between each nest and the nearest forest edge using a digital map in ArcGIS 10.2. We measured habitat variables after all nests' fates had been determined in early July.

### Statistical analysis

We calculated the nest daily survival rate (DSR) of Chinese grouse and estimated the influences of explanatory variables using the nest survival module in Program MARK (White and Burnham 1999). Compared with the traditional apparent nest survival method (i.e., number of successful nests divided by the total number of nests found) and Mayfield's method (number of failed nests divided by the cumulative number of days that the sampled nests were monitored), which assumed a constant DSR (Mayfield 1961; Mayfield 1975), Program MARK allow researchers to build models that incorporate temporal variation of DSR and is more appropriate for our analysis (Dinsmore et al. 2002; Rotella et al. 2004; Rotella 2007).

To evaluate nest DSR, nest age must be determined accurately (Stanley 2004). We determined nest age by considering that eggs were laid every other day with a mean incubation period of 28 days for successful nests (Sun et al. 2003). For the unsuccessful nests that had been found during incubation, we first calculated the initial egg weight using the formula  $W = 0.543 \times L \times B^2$  (Zhao et al., unpublished data),  $W$  represents initial egg weight,  $L$  is egg length,  $B$  is egg breadth, and 0.543 is the species-specific weight coefficient (Hoyt 1979) calculated from fresh eggs. Then we calculated nest age at location day as  $Age = 2.04 + 5.424 (W - W_i)$  (calculated from 22

successfully hatched nests found during 2009–2012, Zhao et al., unpublished data), where  $W_i$  was egg weight on the day of location. Using this method, we could estimate nest age of unsuccessful nests accurately (−2 to 4 days of real age, Zhao et al., unpublished data). We standardized nesting season among years by using the earliest date we began recording data on nest survival during any year from 2009 to 2012 as the first day of the nesting season (Moynahan et al. 2007; Rotella 2007), and the latest hatching or failure date in any year as the last day of season. Thus, we defined a 46-day nesting season beginning 19 May and ending 3 July. This season comprised 45 daily intervals for which DSR was estimated.

We used a multicollinearity test to calculate generalized variation inflation factors (GVIF) between the 6 independent variables in R (R Core Development Team, 2014). If the GVIF value of a variable was larger than 10, there were correlations between this variable and other variables (Fox and Monette 1992; Nicolas et al. 2010). The GVIF values of all the 6 independent variables were <2 (Supplementary Table S1), therefore we considered that none of these variables were correlated with each other and included them all in the following analysis.

We employed an information-theoretic method (Burnham and Anderson 2002) to simultaneously evaluate the relative support of competing models describing DSR and variables of interest (Table 1). We constructed 10 models *a priori* to represent DSR as functions of hypothesized combinations of biotic and abiotic sources of variation: year, nest age, nesting season, distance to edge, shrub cover, and grass cover. We used the logit link functions in all our candidate models. All of our model development and selection were based on Akaike's information criterion corrected for small samples ( $AIC_C$ , Akaike 1973; Burnham and Anderson 2002; Johnson and Omland 2004). The most parsimonious model with the smallest  $AIC_C$  value was considered to be the best model. Model weight ( $w_i$ ) was defined as the probability that the model was the best model and we used it to assess the relative support for each model (Burnham and Anderson 2002). We examined the effects of nest checks by incorporating it (e.g., a nest was checked on a given day was coded as “1”; otherwise as “0”) into the 3 best-supported models ( $\Delta AIC_C < 2$ , Burnham and Anderson 2002). If the effect of nest checks was significant, we should find that the  $AIC_C$  values would decrease at least 2 units when we added nest checks into the best models (Arnold 2010). We also tested whether the effects of nest checks were different among different nesting seasons and nest age by including their interaction terms.

We considered the effects of variables in a model to be meaningful when the 95% confidence intervals of  $\beta$  coefficients did not overlap zero (Arnold 2010). All results were presented as means  $\pm$  standard error.

### Results

In total, 54 nests (980 exposure days) were used in our nest survival analysis (Supplementary Table S2), of which 14 failed during incubation, 13 by mammalian predation (93%), and 1 for an unknown reason. Eggs of 8 nests disappeared totally with no eggshells or egg contents left. Partial predation occurred in 7 nests (13%), 5 by mammals, 1 by a bird, and 1 by a human, with an average egg loss of  $3.7 \pm 0.9$  (range 1–7) eggs per nest. Females in 6 of the 7 partially predated nests continued to incubate after partial predation; 1 female deserted her nest after 3 of the 6 eggs disappeared. In the nests where incubation continued, predation occurred during the second half of the incubation period, whereas partial predation in the



**Table 2.** Models incorporating time and habitat variables influencing nest survival of Chinese grouse at the Lianhuashan Nature Reserve, Gansu, China, during 2009–2012

Model	<i>K</i>	$\Delta AIC_C$	$w_i$	Deviance
S(Nesting season)	2	0.000	0.459	122.280
S(Nest age)	2	0.969	0.283	123.250
S(Nest age + Nesting season)	4	1.885	0.179	122.153
S(.)	1	5.531	0.029	129.820
S(Grass cover)	2	6.710	0.016	128.719
S(Shrub cover)	2	7.230	0.012	129.510
S(Distance to edge)	2	7.518	0.011	129.799
S(Shrub cover + Grass cover)	3	8.706	0.006	128.974
S(Grass cover + Shrub cover + Distance to edge)	4	9.754	0.004	128.805
S(Year)	4	10.553	0.002	128.006

Models are ranked from the most supported ( $\Delta AIC_C = 0$ ) to the least supported; *K* is the number of parameters. The Akaike's weight ( $w_i$ ) is the weight of the evidence for model *i*, given the data. Minimum  $AIC_C = 126.293$ .

deserted nest occurred after 10–12 days of incubation (i.e., in first half of the incubation phase).

DSR in the constant model was  $0.986 \pm 0.0038$  and the probability of a nest with a full clutch of 6 eggs surviving the entire 40-day nesting period (12 days for egg laying and 28 days for incubation) was  $0.526 \pm 0.090$ . Among the 10 *a priori* models, the 3 best models including nesting season, nest age, and their combination received 92.2% of support (sum of  $w_i$ , Table 2). Timing of incubation in the nesting season ( $\beta_{\text{Nesting season}} = -0.099 \pm 0.039$ , 95% CI =  $-0.177$  to  $-0.023$ ) and nest age ( $\beta_{\text{Nest age}} = -0.095 \pm 0.041$ , 95% CI =  $-0.175$  to  $-0.016$ ) both influenced DSR significantly (Table 2). Nest concealment ( $\beta_{\text{Grass cover}} = -1.199 \pm 1.618$ , 95% CI =  $-4.370$  to  $1.971$ ;  $\beta_{\text{Shrub cover}} = -0.227 \pm 1.789$ , 95% CI =  $-3.735$  to  $3.280$ ), distance to edge ( $\beta_{\text{Distance to edge}} = 0.00028 \pm 0.002$ , 95% CI =  $-0.003$  to  $0.004$ ), and year ( $\beta_{2010} = -1.057 \pm 1.074$ , 95% CI =  $-3.161$  to  $1.048$ ;  $\beta_{2011} = -0.602 \pm 1.099$ , 95% CI =  $-2.758$  to  $1.554$ ;  $\beta_{2012} = -1.478 \pm 1.420$ , 95% CI =  $-2.930$  to  $2.635$ ) did not influence nest survival.

The  $AIC_C$  values of the 3 best models decreased about 6 units when we added nest checks into these models (Table 3). Nest checks significantly lowered DSR of Chinese grouse ( $\beta_{\text{Nest check}} = -1.153 \pm 0.387$ , 95% CI =  $-2.086$  to  $-0.236$ , Figure 1). The effect of nest checks varied as nesting season progressed ( $\beta_{\text{Nest check} \times \text{nesting season}} = -0.058 \pm 0.016$ , 95% CI =  $-0.113$  to  $-0.005$ ), but did not change with nest age ( $\beta_{\text{Nest check} \times \text{nest age}} = -0.048 \pm 0.015$ , 95% CI =  $-0.102$  to  $0.005$ ).

## Discussion

For the first time, we estimated nest survival of Chinese grouse and tested the effects of a variety of factors that potentially affected nest survival. Our results indicated that about half nests of Chinese grouse endured the entire egg-laying and incubation periods and were successful (at least 1 chick hatched). Nest predation by mammalian animals was the main cause of nest failure of Chinese grouse, which accounted for 93% of total loss. DSR was not influenced by nest concealment, distance to forest edge, or year. Instead, DSR showed a pattern that varied over time, with decreasing survival probabilities as nests aged and the nesting season progressed. Moreover, nest checks conducted by investigators had a negative effect on DSR.

Based on a maximum likelihood analysis, our results showed the probability was 0.52 for a nest containing 6 eggs surviving through the egg-laying and incubation periods (ca. 40 days). This is lower than the apparent nest survival rate, which is 0.74 in this study (40/54) and 0.63 (34/54) in a previous study conducted at the same study site (Sun et al. 2003). Apparent nest survival is always higher than real nest survival because it does not account for the bias resulted from that successful nests are more likely to be discovered by investigators than failed nests (Shaffer and Burger 2004; Rotella et al. 2004). More studies on nest survival of different populations of Chinese grouse at other sites are needed in future.

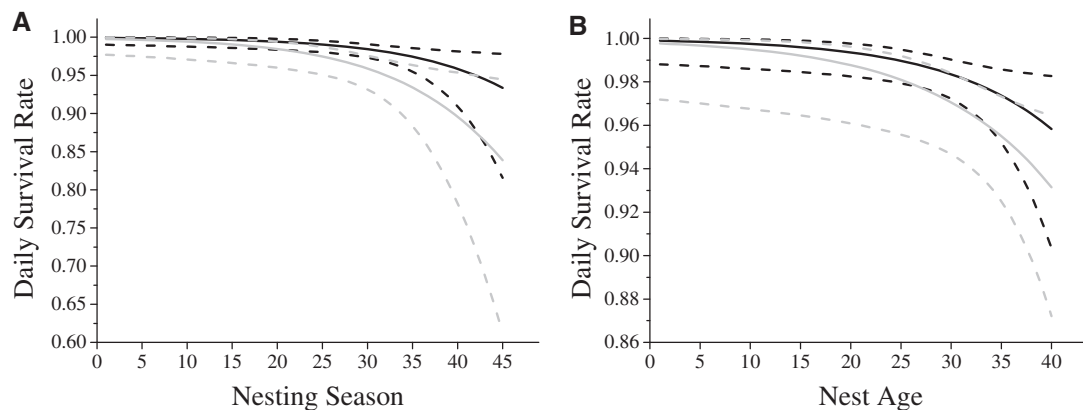
Predation is the most common cause of nest failure of Chinese grouse. This is in accordance with results on the overwhelming majority of birds species studied to date (Martin 1993; Lee and Lima 2016). All of the 13 nest predations were due to loss of eggs conducted by mammalian predators. Predation on incubation females were not observed during our study periods. Data from 41 females fitted with radio-transmitters also recorded no deaths caused by predators during incubation (Zhao et al. 2018). Our results were different from a previous study conducted at the same site by Sun et al. (2003), which found the most important causes of nest failures were death of incubating females and egg collection by local villagers. Sun et al. (2003) recorded that 25% of nest failures (5/20) were caused by predation on incubating females and 35% (7/20) of nest failures were due to egg collection by local villagers who collected mushroom and Chinese medicines during the breeding seasons. Sun et al.'s (2003) study was conducted during 1995–2000, when the forest ground was covered by dense arrow bamboo *Sinarundinaria nitida*. However, the bamboo was flowered and removed by local villagers in the first decade of the 21st century. Without the bamboo layer, incubating females might spot the approaching predators earlier and flee before the attacks (Yusuke et al. 2011; Fuller et al. 2017). This was supported by the fact that the mean understory cover was only 0.24 in this study (Supplementary Table S2), much lower than the mean value of 0.41 ( $n = 59$ ) in Sun et al. (2007). No nest failures were caused by local villagers compared with that 35% nest failures (7/20) were attributed to the egg collection by local villagers in Sun et al. (2003). This could be explained from 2 aspects. Fewer villagers now rely on collecting mushrooms or Chinese medicines for a living in recent years because of its lower profits compared with going out and working. In another aspect, local villagers may have better environmental and wildlife protection awareness, leaving the eggs and females untouched when they found a nest. In short, our study revealed different causes of nest failures compared with the previous study (Sun et al. 2003).

We found that Chinese grouse nests with greater concealments did not have higher survival probabilities. This violates the prediction of the nest concealment hypothesis (Martin and Roper 1988; Borgmann and Conway 2015), which assumed birds should select nest sites with greater cover and thus have higher survival probabilities. In other grouse species, greater cover led to higher nest survival was found in white-tailed ptarmigan *Lagopus leucura* (Wiebe and Martin 1998), hazel grouse (Rhim 2012), and sharp-tailed grouse *T. phasianellus* (Burr et al. 2017); in contrast, studies of spruce grouse *Dendragapus canadensis* (Deon 1997), ruffed grouse *T. umbellus* (Larson et al. 2003), and rock ptarmigan *L. mutus* (Cotter and Gratto 1995) found nest cover did not influence nest survival. Latif et al. (2012) proposed that if birds already nest at the low-predation sites, then nest survival would no longer correlate with nest habitat characteristics, even though predation ultimately shaped microhabitat selection (adaptive peak hypothesis). An earlier study also found

**Table 3.** Results of the best models after incorporating nest checks to describe nest survival of Chinese grouse at the Lianhuashan Nature Reserve, Gansu, China

Model	$K$	AIC <sub>C</sub>	$\Delta$ AIC <sub>C</sub>	$w_i$	Deviance
S(Nest check + Nesting season)	3	120.091	0.000	0.434	114.066
S(Nest check + Nest age)	3	121.837	1.746	0.181	115.812
S(Nest check $\times$ Nesting season)	4	122.091	2.001	0.160	114.050
S(Nest check + Nesting season + Nest age)	4	122.106	2.016	0.159	114.065
S(Nest check $\times$ Nest age)	4	123.853	3.763	0.066	115.812

$K$  is the number of parameters. The Akaike's weight ( $w_i$ ) is the weight of the evidence for model  $i$ .

**Figure 1.** Predicted DSR of Chinese grouse nests in relation to nesting season, nest age, and nest checks at Lianhuashan Nature Reserve, Gansu, China, 2009–2012. Black solid line: predicted DSR; Black dashed line: 95% confidence interval of the predicted DSR; Gray solid line: predicted DSR with nest checks, Gray dashed line: 95% confidence interval of the predicted DSR with nest checks. (A) DSR to nesting season; (B) DSR to nest age.

that, despite Chinese grouse selecting nest sites with greater shrub cover than random sites within males' territories (Sun et al. 2007), this variable was not different between successful and failed nests. If Chinese grouse's selection of nest microhabitat is in accordance with the "adaptive peak hypothesis," then predators would find a nest by chance and we would not find a positive relationship between nest concealment and nest survival. Another possibility was that nest habitat might be adaptive in some other ways that were not incorporated in our analysis, for example, animals inherently select habitat at multiple spatial scales (Johnson 1980; Stanley et al. 2015; Zhao et al. 2017). If larger scale (e.g., landscape) habitat features were more important (Stanley et al. 2015), that might have hindered us from finding a relationship between DSR and microhabitat variables.

Contrary to our prediction, DSR decreased as the nesting season progressed and nest age increased, inconsistent with most other studies, which found that DSR increased during incubation (Wilson et al. 2007; Smith and Wilson 2010; Brussee et al. 2016). Nevertheless, similar results have been observed in several passerine species, such as lark bunting *Calamospiza melanocorys* (Jehle et al. 2004), clay-colored sparrows *Spizella pallida*, and vesper sparrows *Poocetes gramineus* (Grant et al. 2005), in which the decreasing DSR was caused by increased off-nest activities of incubating individuals and thus provided cues for predators during the late incubation period. This also occurs in some galliform species, such as greater sage-grouse *Centrocercus urophasianus* and Columbian sharp-tailed grouse *T. p. columbianus*, in which it was suggested that nests provided more cues of their presence to predators as they aged (Rus et al. 2015). Incubating female Chinese grouse have been found to increase their off-nest bouts as nest aged (Zhao et al. unpublished data). So we might explain our results based on the

increased activities or cues left by incubating females in the late incubation period. However, young leaves, grasses, and forbs sprouted as nests aged and the nesting season progressed, which might increase the concealment of nests in the late incubation period. Conover et al. (2010) and Coates and Delehanty (2010) showed that nest habitat characteristics of greater sage-grouse were selected to avoid visual predators, such as avian species, but not olfactory predators, such as mammalian species. Most predations on nests of Chinese grouse were caused by mammalian species after the growth of grass and shrubs increased the nest concealment in the late period of incubation. Thus nest concealment of Chinese grouse may also be selected to avoid avian predators instead of mammalian predators.

Another, not mutually exclusive possibility is that decreased survival through incubation might reflect an additive exposure to risk (Grant et al. 2005). The longer a nest is active, the more likely it will lose eggs to predation. Cumulating losses of individual eggs will result in a higher rate of nest loss later in incubation (Grant et al. 2005), which was also supported in our study. Although the partial nest predation rate might be underestimated, because we only counted eggs when females were not at the nest during nest checks, we still observed 7 nests (13%) that had endured partial egg loss. More importantly, 6 of the 7 recorded instances of partial predation happened during the second half of the incubation period and females continued to incubation after partial predation occurred. This demonstrated that the occurrence of partial predation might attribute to an additive effect and incubating females were more tolerance to disruptive predator interference in the late incubation period.

Distance to forest edge did not influence nest survival of Chinese grouse. This is inconsistent with our original expectation that a positive relationship between nest survival probabilities and distance to edge should exist. Patterns of increased nest predation resulting

from more abundant nest predators in fragmented habitats than in continuous habitats have been found in many studies (Storaas and Wegge 1987; Marini et al. 1995), including black grouse, a similar ground nesting species in conifer forest (Kurki and Lindén 1995). The incongruence results between these studies and ours might result from that most nests found in this study were in the forest interiors ( $315.2 \text{ m} \pm 20.7 \text{ m}$ , Supplementary Table S2). Paton (1994) reviewed the literature and concluded that the edge effect (reduced nest survival near edges) usually occur within 50 m of an edge and increased depredation rates extend farther than 50 m from an edge are less convincing. Moreover, we could not exclude the possibility that fragmentation indeed decreased nest survival of Chinese grouse at larger spatial scales. A review on fragmentation effects on nest survival conducted by Stephens et al. (2003) showed that studies that measured fragmentation at landscape scales were more likely to detect effects of fragmentation on nest success than those measured at patch and edge scales. Given the highly fragmented habitat features at Lianhuashan Nature Reserve (Sun et al. 2006; Zheng and Wang 1998) and that habitat fragmentation is a main threat to Chinese grouse across its distribution range (Sun 2000), it is highly desirable to examine the effects of fragmentation on breeding success of Chinese grouse across different spatial scales.

Our study documented a negative influence of nest checks on DSR, due to increased nest predation. Decreased DSR caused by investigator disturbance has also been found in many species, such as Lewis's woodpecker *Melanerpes lewis* (Newlon and Saab 2011), short-tailed shearwaters *Puffinus tenuirostris* (Carey 2011), and greater sage-grouse (Gibson et al. 2015). Contradictory results have also been found in some other studies (Weidinger 2008), including on the lark sparrow *Chondestes grammacus* (Jacobson et al. 2011), rock ptarmigan *Lagopus montanus* (Cotter and Gratto 1995), and common blackbird *Turdus merula* (Ibáñez-Álamo and Soler 2010). This inconsistency might be due to different predator communities (Ibáñez-Álamo et al. 2012), availability of alternative prey (Bêty et al. 2001), nest distribution patterns (Picman 1988), and other species-specific factors. In our study, mammalian predators were the main cause of nest failures, which might have been attracted by investigators and followed their odors to locate nest sites. The negative effect of nest checks was more pronounced as the nesting season progressed (Figure 1). Researchers should balance their activities between obtaining accurate hatching data and reducing nest predation risk caused by nest checks. For example, monitoring nests using infrared video surveillance might be a surrogate for nest checking, if it does not have a detrimental effect; investigators could also alleviate the potential detrimental effects of nest check by increasing the distance to a nest with the aid of a binocular while checking nests. Moreover, a previous study found that no detrimental effects of catching incubating females on nest survival ( $n = 26$ , Zhao et al. 2018). Based on our results, we suggest that catching females on nests may be more detrimental than nest checks because more time has to be spent near nest and investigators have to touch females during the capture process. Therefore, we recommend to catch females before breeding season and catch females on nest by experienced field workers when there is no other choice to reduce disturbance that may potentially affect nest survival.

In summary, our results highlight that the late incubation period is a more vulnerable period than early incubation period for Chinese grouse nests. Moreover, we demonstrated that the current nest check procedure conducted by investigators had negative effects on nest survival, especially during the late period in incubation. Some other research activities, such as egg measurement, which require

direct contact with the nests or eggs, should also have a detrimental effect, especially for nests found in the more vulnerable late incubation period. We recommend that researchers should adjust their activities around nests to balance the need of acquiring accurate data and decreasing nest predation risk. Mammalian predators accounted for most of nest failures. However, we still know little about the community compositions of mammalian predators. Future studies should pay more attention to identifying the mammalian predators' identities, predator abundance, and predators' activity patterns throughout the nesting season to provide more detailed information about what management actions should be taken to increase nest survival. In addition, more studies are still needed to improve our understanding of how factors not accounted for in this study affect nest survival of Chinese grouse, such as more detailed estimation on the effects of fragmentation and habitat variables at larger scales and weather conditions.

## Supplementary Material

Supplementary material can be found at <https://academic.oup.com/cz>.

## Authors' Contributions

J-M.Z., Y-H.S., and Y.F. conceived the idea and designed the study. J-M.Z. collected the data. J-M.Z., C.Y., Y.Q.L., Y.F., M.S., and Y-H.S. wrote the article, and all authors approved the final version of the article.

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## References

- Akaike H, 1973. Information theory and an extension of the maximum likelihood principle. *Paper Presented at Second International Symposium on Information Theory*. Budapest, Hungary: Akademiai Kiado.
- Anteau MJ, Shaffer TL, Sherfy MH, Sovada MA, Stucker JH et al., 2012. Nest survival of piping plovers at a dynamic reservoir indicates an ecological trap for a threatened population. *Oecologia* 170:1167–1179.
- Armstrong T, 1996. Effects of research activities on nest predation in arctic-nesting geese. *J Wildlife Manage* 60:265–269.
- Arnold TW, 2010. Uninformative parameters and model selection using Akaike's information criterion. *J Wildlife Manage* 74:1175–1178.
- Beaulieu M, Thierry A-M, Handrich Y, Massemin S, Le Maho Y et al., 2010. Adverse effects of instrumentation in incubating Adélie penguins *Pygoscelis adeliae*. *Polar Biol* 33:485–492.
- Bêty J, Gauthier G, Giroux JF, Korpimäki E, 2001. Are goose nesting success and lemming cycles linked? Interplay between nest density and predators. *Oikos* 93:388–400.
- BirdLife International, 2017. *Bonasa sewerzowi*. The IUCN Red List of Threatened Species. Version 2016. [Downloaded on 17 May 2019]. Available from: <https://www.iucnredlist.org/species/22679497/119421341>.

- Blackmer AL, Ackerman JT, Nevitt GA, 2004. Effects of investigator disturbance on hatching success and nest-site fidelity in a long-lived seabird, leach's storm-petrel. *Biol Conserv* 116:141–148.
- Borgmann KL, Conway CJ, 2015. The nest-concealment hypothesis: new insights from a comparative analysis. *Wilson J Ornithol* 127:646–660.
- Brussee BE, Coates PS, Hothem RL, Howe KB, Casazza ML et al., 2016. Nest survival is influenced by parental behaviour and heterospecifics in a mixed-species colony. *Ibis* 158:315–326.
- Burger AE, Masselink MM, Tillmanns AR, Szabo R, Farnholtz M et al., 2004. Effects of habitat fragmentation and forest edges on predators of marbled murrelets and other forest birds on southwest Vancouver Island. Paper presented at Species at Risk 2004 Pathways to Recovery Conference. March 2–6, 2004. Victoria, BC.
- Burnham KP, Anderson DR, 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Berlin: Springer Verlag.
- Burr PC, Robinson AC, Larsen RT, Newman RA, Ellis-Felege SN, 2017. Sharp-tailed grouse nest survival and nest predator habitat use in North Dakota's Bakken oil field. *PLoS ONE* 12:e0170177.
- Canfield R, 1941. Application of the line interception method in sampling range vegetation. *J Forest* 39:388–394.
- Carey MJ, 2011. Investigator disturbance reduces reproductive success in short-tailed shearwaters *Puffinus tenuirostris*. *Ibis* 153:63–372.
- Chalfoun AD, Thompson FR, Ratnaswamy MJ, 2002. Nest predators and fragmentation: a review and meta-analysis. *Conserv Biol* 16:306–318.
- Coates PS, Delehanty DJ, 2010. Nest predation of greater sage-grouse in relation to microhabitat factors and predators. *J Wildlife Manage* 74:240–248.
- Conover MR, Borgo JS, Dritz RE, Dinkins JB, Dahlgren DK, 2010. Greater sage-grouse select nest sites to avoid visual predators but not olfactory predators. *Condor* 112:331–336.
- Cotter RC, Gratto CJ, 1995. Effects of nest and brood visits and radio transmitters on rock ptarmigan. *J Wildlife Manage* 59:93–98.
- Daubenmire R, 1959. A canopy-coverage method of vegetational analysis. *Northwest Sci* 33:43–64.
- Davis SK, 2005. Nest-site selection patterns and the influence of vegetation on nest survival of mixed-grass prairie passerines. *Condor* 107:605–616.
- Deon RG, 1997. Vegetative concealment, proximity to trails and predator activity as relative factors affecting nest success and egg loss in spruce grouse *Dendragapus canadensis*. *Can Field-Nat* 111:399–402.
- Dinsmore SJ, White GC, Knopf FL, 2002. Advanced techniques for modeling avian nest survival. *Ecology* 83:3476–3488.
- Fox J, Monette G, 1992. Generalized collinearity diagnostics. *Publ Am Stat Assoc* 87:178–183.
- Fuller AK, Spohr SM, Harrison DJ, Servello FA, 2017. Nest survival of wild turkeys *Meleagris gallopavo silvestris* in a mixed-use landscape: influences at nest-site and patch scales. *Wildlife Biol* 19:138–146.
- Götmark F, 1992. The effects of investigator disturbance on nesting birds. *Curr Ornithol* 9:63–104.
- Gibson D, Blomberg EJ, Atamian MT, Sedinger JS, 2015. Observer effects strongly influence estimates of daily nest survival probability but do not substantially increase rates of nest failure in greater sage-grouse. *Auk* 132:397–407.
- Gilg O, Sittler B, Sabard B, Hurstel A, Sané R et al., 2006. Functional and numerical responses of four lemming predators in high arctic Greenland. *Oikos* 113:193–216.
- Grant TA, Shaffer TL, Madden EM, Pietz PJ, Johnson D, 2005. Time-specific variation in passerine nest survival: new insights into old questions. *Auk* 122:661–672.
- Grier JW, 1969. Bald eagle behavior and productivity responses to climbing to nests. *J Wildlife Manage* 33:961–966.
- Hoyt DF, 1979. Practical methods of estimating volume and fresh weight of bird eggs. *Auk* 96:73–77.
- Ibáñez-Álamo JD, Sanllorente O, Soler M, 2012. The impact of researcher disturbance on nest predation rates: a meta-analysis. *Ibis* 154:5–14.
- Ibáñez-Álamo JD, Soler M, 2010. Investigator activities reduce nest predation in blackbirds *Turdus merula*. *J Avian Biol* 41:208–212.
- Jacobson MD, Tsakiris ET, Long AM, Jensen WE, 2011. No evidence for observer effects on lark sparrow nest survival. *J Field Ornithol* 82:184–192.
- Jehle G, Amy YA, Savidge JA, Skagen SK, 2004. Nest survival estimation: a review of alternatives to the Mayfield estimator. *Condor* 106:472–484.
- Johnson D, 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- Johnson J, Omland K, 2004. Model selection in ecology and evolution. *Trends Ecol Evol* 19:101–108.
- Klaus S, Selsam P, Sun Y, Fang Y, 2001. Analyse von satellitenbildern zum schutz bedrohter arten - Fallbeispiel chinahaselhuhn *Bonasa sewerzowi*. *Natur Und Landschaft* 33:281–285.
- Kolada E, Casazza M, Sedinger J, 2009. Ecological factors influencing nest survival of greater sage-grouse in mono county, California. *J Wildlife Manage* 73:1341–1347.
- Kurki S, Helle P, Lindén H, Nikula A, 1997. Breeding success of black grouse and capercaillie in relation to mammalian predator densities on two spatial scales. *Oikos* 79:301–310.
- Kurki S, Lindén H, 1995. Forest fragmentation due to agriculture affects the reproductive success of the ground-nesting black grouse *Tetrao tetrix*. *Ecography* 18:109–113.
- Larivière S, 1999. Reasons why predators cannot be inferred from nest remains. *Condor* 101:718–721.
- Larson MA, Clark ME, Winterstein SR, 2003. Survival and habitat of ruffed grouse nests in northern Michigan. *Wilson Bull* 115:140–147.
- Latif QS, Heath SK, Rotenberry JT, 2012. How avian nest site selection responds to predation risk: testing an 'adaptive peak hypothesis'. *J Anim Ecol* 81:127–138.
- Lee JK, Lima SL, 2016. Nest building under the risk of predation: safe nests are not always the best option. *J Avian Biol* 47:768–778.
- Linz GM, Sawin RS, Lutman MW, 2008. The influence of breeding experience on nest success in red-winged blackbird. *West N Am Naturalist* 74:123–129.
- Lou Y, Shi M, Fang Y, Swenson JE, Nan L et al., 2017. Male vigilance and presence are important for foraging by female Chinese grouse in the pre-incubation period. *Wildlife Biology* 1:wlb.00257.
- Lu N, Sun YH, 2011. Population viability analysis and conservation of Chinese grouse *Bonasa sewerzowi* in Lianhuashan Nature Reserve, north-west china. *Bird Conserv Int* 21:49–58.
- Manzer DL, Hannon SJ, 2005. Relating grouse nest success and corvid density to habitat: a multi-scale approach. *J Wildlife Manage* 69:110–123.
- Marini MA, Robinson SK, Heske EJ, 1995. Edge effects on nest predation in the Shawnee National Forest, southern Illinois. *Biol Conserv* 74:203–213.
- Martin TE, 1993. Nest predation among vegetation layers and habitat types: revising the dogmas. *Am Nat* 141:897–913.
- Martin TE, 2002. A new view of avian life-history evolution tested on an incubation paradox. *P Roy Soc. B-Biol Sci* 269:309–316.
- Martin TE, Roper J, 1988. Nest predation and nest-site selection of a western population of the hermit thrush. *Condor* 90:51–57.
- Martin TE, Scott J, Menge C, 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. *P Roy Soc B-Biol Sci* 267:2287–2293.
- Mayfield H, 1961. Nesting success calculated from exposure. *Wilson Bull* 73:255–261.
- Mayfield H, 1975. Suggestions for calculating nest success. *Wilson Bull* 87:456–466.
- Moynahan BJ, Lindberg MS, Rotella JJ, Thomas JW, 2007. Factors affecting nest survival of greater sage-grouse in Northcentral Montana. *J Wildlife Manage* 71:1773–1783.
- Newlon KR, Saab VA, 2011. Nest-site selection and nest survival of Lewis's woodpecker in aspen riparian woodlands. *Condor* 113:183–193.
- Nicolas T, Marc D, Jean-Paul J, Marc P, Pierre D, 2010. Multivariate analysis of a fine-scale breeding bird atlas using a geographical information system and partial canonical correspondence analysis: environmental and spatial effects. *J Biogeogr* 31:1841–1856.
- Niemuth ND, Boyce MS, 1995. Spatial and temporal patterns of predation of simulated sage grouse nests at high and low nest densities: an experimental study. *Can J Zool* 73:819–825.
- O'Grady DR, Hill DP, Barclay RM, 1996. Nest visitation by humans does not increase predation on chestnut-collared longspur eggs and young. *J Field Ornithol* 67:275–280.



- Öst M, Steele BB, 2010. Age-specific nest-site preference and success in eiders. *Oecologia* 162:59–69.
- Paton P, 1994. The effect of edge on avian nest success: how strong is the evidence? *Conserv Biol* 8:17–26.
- Picman J, 1988. Experimental study of predation on eggs of ground-nesting birds: effects of habitat and nest distribution. *Condor* 90:124–131.
- R Core Development Team, 2014. R: A Language and Environment for Statistical Computing. Vienna: R Foundation for Statistical Computing.
- Remeš V, 2005. Nest concealment and parental behaviour interact in affecting nest survival in the blackcap *Sylvia atricapilla*: an experimental evaluation of the parental compensation hypothesis. *Behav Ecol Sociobiol* 58:326–332.
- Rhim S, 2012. Ecological factors influencing nest survival of hazel grouse *Bonasa bonasia* in a temperate forest, South Korea. *Forest Ecol Manag* 282: 23–27.
- Robinson SK, Frank R, Thompson IIF, Donovan TM, Whitehead DR et al., 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267:1987–1990.
- Rotella J, 2007. Modeling nest-survival data: recent improvements and future directions. *Stud Avian Biol* 34:145–148.
- Rotella JJ, Dinsmore SJ, Shaffer TL, 2004. Modeling nest-survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. *Anim Biodiv Conserv* 27:187–205.
- Rus A, Stonehouse K, Shipley L, 2015. Nest survival of greater sage-grouse and Columbian sharp-tailed grouse in Lincoln County, Washington. The Wildlife Society Annual Conference (Washington Chapter), April 14–17, 2015. Grand Mound, Washington, DC.
- Sandercock BK, Alfaro-Barrios M, Casey AE, Johnson TN, Mong TW et al., 2015. Effects of grazing and prescribed fire on resource selection and nest survival of upland sandpipers in an experimental landscape. *Landscape Ecol* 30:325–337.
- Sandvik H, Barrett RT, 2001. Effect of investigator disturbance on the breeding success of the black-legged kittiwake. *J Field Ornithol* 72:30–42.
- Serventy D, Curry P, 1984. Observations on colony size, breeding success, recruitment and inter-colony dispersal in a Tasmanian colony of short-tailed shearwaters *Puffinus tenuirostris* over a 30-year period. *Emu* 84:71–79.
- Shaffer TL, Burger A, 2004. A unified approach to analyzing nest success. *Auk* 121:526–540.
- Small MF, Hunter ML, 1988. Forest fragmentation and avian nest predation in forested landscapes. *Oecologia* 76:62–64.
- Smith PA, Wilson S, 2010. Intra-seasonal patterns in shorebird nest survival are related to nest age and defence behaviour. *Oecologia* 163:613–624.
- Stanley TR, 2004. Estimating stage-specific daily survival probabilities of nests when nest age is unknown. *Auk* 121:134–147.
- Stanley TR, Aldridge CL, Saher DJ, Childers TM, 2015. Daily nest survival rates of Gunnison sage-grouse *Centrocercus minimus*: assessing local- and landscape-scale drivers. *Wilson J Ornithol* 127:59–71.
- Stephens SE, Koons DN, Rotella JJ, Wiley DW, 2003. Effects of habitat fragmentation on avian nesting success: a review of the evidence at multiple spatial scales. *Conserv Biol* 115:101–110.
- Storaas T, Wegge P, 1987. Nesting habitats and nest predation in sympatric populations of capercaillie and black grouse. *J Wildlife Manage* 51: 167–172.
- Sullivan BD, Dinsmore JJ, 1990. Factors affecting egg predation by American crows. *J Wildlife Manage* 54:433–437.
- Sun YH, 2000. Distribution and status of the Chinese grouse *Bonasa sewerzowi*. *Wildlife Biol* 6:271–275.
- Sun YH, 2004. Distribution, reproductive strategy and population biology of the Chinese grouse *Bonasa sewerzowi* [PhD thesis]. Beijing Normal University, Beijing, China.
- Sun YH, Fang Y, Jia CX, Klaus S, Swenson JE et al., 2007. Nest site selection of Chinese grouse *Bonasa sewerzowi* at Lianhuashan, Gansu, China. *Wildlife Biol* 13:68–72.
- Sun YH, Klaus S, Fang Y, Selsam P, Jia C, 2006. Habitat isolation and fragmentation of the Chinese grouse *Bonasa sewerzowi* at Lianhuashan mountains, Gansu, China. *Acta Zool Sin* 52:202–204.
- Sun YH, Swenson JE, Fang Y, Klaus S, Scherzinger W, 2003. Population ecology of the Chinese grouse *Bonasa sewerzowi* in a fragmented landscape. *Biol Conserv* 110:177–184.
- Traylor JJ, Alisauskas RT, Kehoe FP, 2004. Nesting ecology of white-winged scoters *Melanitta fusca deglandi* at Redberry Lake, Saskatchewan. *Auk* 121: 950–962.
- Uherkoch BD, Schmutz JA, Wright KG, 2015. Nest visits and capture events affect breeding success of yellow-billed and Pacific loons. *Condor* 117: 121–129.
- Webb SL, Olson CV, Dzialak MR, Harju SM, Winstead JB et al., 2012. Landscape features and weather influence nest survival of a ground-nesting bird of conservation concern, the greater sage-grouse, in human-altered environments. *Ecol Process* 1:1–15.
- Wegge P, Storaas T, 1990. Nest loss in capercaillie and black grouse in relation to the small rodent cycle in Southeast Norway. *Oecologia* 82:527–530.
- Weidinger K, 2008. Nest monitoring does not increase nest predation in open-nesting songbirds: inference from continuous nest-survival data. *Auk* 125:859–868.
- White GC, Burnham KP, 1999. Program mark: survival estimation from populations of marked animals. *Bird Study* 46: S120–S139.
- Wiebe KL, Martin K, 1998. Costs and benefits of nest cover for ptarmigan: changes within and between years. *Anim Behav* 56:1137–1144.
- Wilson S, Martin K, Hannon SJ, 2007. Nest survival patterns in willow ptarmigan: influence of time, nesting stage, and female characteristics. *Condor* 109:377–388.
- Yusuke S, Yuichi T, Hiroshi N, 2011. Nest site selection and nesting biology of rock ptarmigan *Lagopus muta japonicus* in Japan. *Bird Study* 58: 200–207.
- Zhao JM, Fang Y, Lou YQ, Sun YH, 2015. Brood habitat selection of Chinese grouse *Tetrastes sewerzowi* at Lianhuashan, Gansu, China. *Wilson J Ornithol* 127:310–318.
- Zhao JM, Fang Y, Lou YQ, Swenson JE, Sun YH, 2018. Brood rearing has an immediate survival cost for female Chinese grouse *Tetrastes sewerzowi*. *J Ornithol* 159:1019–1029.
- Zhao JM, Fang Y, Ma YH, Sun YH, 2017. The importance of willow to the Chinese grouse: evidence from analysis on their breeding territories at Lianhuashan, China. *Avian Res* 8:32.
- Zheng G, Wang Q, 1998. *China Red Data Book of Endangered Animals: Aves*. Beijing: Science Press.