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# Does researcher activity impact nest survival of sharp-tailed grouse?

Megan C. Milligan and Lance B. McNew

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Nest survival is a key vital rate of game birds and frequently studied to guide population management. Common scientific protocols are invasive and often involve flushing females from their nests to assess nest contents and status. Biased inference of population dynamics, and thus improper management recommendations, may result if nest survival estimates are affected by researcher activities. We evaluated whether standard nest monitoring protocols for game birds biased estimates of nest survival for sharp-tailed grouse *Tympanuchus phasianellus*, a common ground-nesting bird in northern grassland ecosystems in the US. We hypothesized that flushing females from nests would negatively affect estimates of daily nest survival and result in biased inferences about population growth regardless of potentially mediating environmental conditions. Our results indicated that cumulative precipitation received during the nesting period had the largest effect on nest survival. Flushing sharp-tailed grouse from nests resulted in reduced nest survival during dry periods, although differences over the entire nesting period were not statistically significant. Downward-biased estimates of nest survival for females that were flushed did not significantly bias estimates of population growth rates. With minimal data loss, we successfully monitored nests of radio-marked females without flushing and recommend that researchers carefully consider potential biases related to research techniques when determining nest monitoring protocols.

Keywords: flushing, observer effects, population monitoring, prairie grouse

The estimation of population vital rates to inform population and habitat management is a primary objective of wildlife science (Bradbury et al. 2001). However, biases in vital rates resulting from research activity can complicate comparisons across studies and result in erroneous conclusions about important population processes, including population growth (Rotella et al. 2000, Gibson et al. 2015). For example, small observer effects on daily survival rates can result in significantly biased estimates when those rates are extrapolated across long exposure periods (Rotella et al. 2000). Understanding potential observer effects is important because it allows for both the development of research that minimizes detrimental effects of observers and the appropriate accounting of observer effects (Caldwell et al. 2013). Furthermore, if observer effects are properly accounted for, research can still yield unbiased vital rate estimates for use in population assessments, thus resulting in final inferences that are useful for management.

In studies of avian nesting ecology, researchers typically visit the nest site at least once to document nest contents

and status, which often results in incubating females being flushed from their nests (Klett et al. 1986, McNew et al. 2012, Peterson et al. 2015). Nest visits also allow researchers to candle or float eggs to estimate nest age or incubation stage, which can be important for constructing breeding phenologies and assessing the influence of temporal variation on nest survival (Dinsmore et al. 2002, McNew et al. 2009). Flushing females from nests, however, may bias estimates of nest survival in a variety of ways. First, flushing or otherwise disturbing a female on the nest can increase rates of abandonment for some species (Pierce and Simons 1986, Boellstorff et al. 1988, Gibson et al. 2015). Second, visits to the nest could provide olfactory or visual cues allowing predators and brood parasites to find the nest (Picozzi 1975, Westmoreland and Best 1985, Whelan et al. 1994, Hein and Hein 1996, Caldwell et al. 2013). Alternatively, human presence may deter some predators from approaching nests (MacIvor et al. 1990, O'Grady et al. 1996) and potentially upward-bias estimates of nest survival (Westemeier et al. 1998, Burr et al. 2017). Finally, disturbing the female could increase the total exposure period of the nest due to altered incubation patterns (Pierce and Simons 1986, Sandvik and Barrett 2001).

Given the potential difficulties with detecting important effects of nest visits on survival due to inadequate statistical power (Rotella et al. 2000), it is important to evaluate both

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internal and external factors that may mediate the potential bias induced by researchers. For example, effects may be species- or habitat-specific and may depend on the observation methods used, although one study found that while flushing had the strongest effect, all forms of nest observation increased the risk of nest failure for island scrub-jays *Aphelocoma insularis* (Caldwell et al. 2013). Furthermore, researcher activity may differentially affect individual birds depending on intrinsic qualities associated with either the bird or the nest attempt. For example, younger female greater sage-grouse *Centrocercus urophasianus* and those with lower quality nest sites were more likely to abandon nests following flushing (Gibson et al. 2015). External variables, such as habitat type, annual weather conditions or the local predator community may also influence the behavior of individuals following nest disturbance (Caldwell et al. 2013). To understand and potentially mitigate the effects of research activity on populations, it is necessary to evaluate potential mediating factors that could influence both the effects of observers and our ability to detect effects.

We investigated whether common study protocols that include flushing females from nests influenced estimates of nest survival for sharp-tailed grouse *Tympanuchus phasianellus* in the northern mixed-grass prairie. Prairie grouse *Tympanuchus* spp., including sharp-tailed grouse, are widely recognized as indicator species for grassland habitats and are frequently studied to guide management decisions (Hillman and Jackson 1973, Poiani et al. 2001, Roersma 2001). Accepted protocols for studying prairie grouse involve flushing females off the nest at least once (Pitman et al. 2005, Goddard and Dawson 2009, McNew et al. 2012). While previous research has found significant negative effects of flushing greater sage-grouse from nests on either abandonment rates or daily nest survival (Connelly et al. 2011, Gibson et al. 2015), effects may differ for prairie grouse. For example, Westemeier et al. (1998) did not observe negative effects of flushing on the nest survival of greater prairie-chickens *T. cupido* in Illinois, although mediating factors were not considered. Furthermore, while numerous studies have evaluated potential effects of observers on the nest survival of a variety of species (Westmoreland and Best 1985, Caldwell et al. 2013, Gibson et al. 2015), few have extrapolated those potentially biased field estimates to examine the effects on population-level inferences.

In order to better understand the biases of research activities, we evaluated the effects of potentially biased field estimates on population-level inferences for sharp-tailed grouse in eastern Montana during 2017–2018. Our objectives were to 1) estimate whether flushing females from nests affected estimates of daily and overall nest survival, 2) evaluate factors mediating the effect of flushing on nest survival and 3) assess whether researcher-induced biases in nest survival might impact inferences regarding predicted population growth rates. We hypothesized that flushing females from nests would have a negative effect on daily nest survival and that the biased estimates of nest survival would influence inferences related to overall nest survival and population growth.

## Study area

Our study was conducted in southern Richland and McKenzie Counties in eastern Montana and western

North Dakota, respectively, during 2017–2018. The study area was centrally located within the distribution of sharp-tailed grouse in an area with historically stable populations (Hamerstrom and Hamerstrom 1961, Yde 1977). The study area was primarily managed for cattle production and composed of Great Plains mixed-grass prairie interspersed with Great Plains badlands and wooded draws and ravines (LANDFIRE 2013). The vegetation was a mixture of mid and short grasses, with western wheatgrass *Pascopyrum smithii*, little bluestem *Schizachyrium scoparium*, needle-and-thread *Hesperostipa comata*, Kentucky bluegrass *Poa pratensis*, blue grama *Bouteloua gracilis* and crested wheatgrass *Agropyron cristatum* being the dominant graminoids.

## Methods

We captured grouse during March–May at nine leks using walk-in funnel traps. Females were fitted with VHF radio-transmitters (model A4050; Advanced Telemetry Systems, Isanti, MN, USA). Radio-marked females were located by triangulation or homing  $\geq$  three times/week during the nesting period (April–July). When females localized in an area (i.e. located in the same location for  $\geq$  two consecutive visits), we assumed that the female was attending a nest. We randomly selected half of the females and used portable radio receivers and handheld Yagi antennas to locate and flush birds so we could count the eggs and record the nest location with a handheld GPS unit. Nests were only approached on days with no precipitation and observers wore rubber boots and walked in overlapping circles to avoid leaving a direct scent trail to nests. Nests were visited again to confirm nest fate after the female was located away from the nest for  $\geq$  two days during incubation or  $\geq$  one day after expected hatch date. The remaining half of our radio-marked sample of females was never flushed and nest attempts were monitored via radio-telemetry from a distance of  $> 25$  m. A female was assumed to be incubating if she was located in the same location for two consecutive visits and nest sites were only visited after the female was located away from the nest for  $\geq$  two days during incubation or  $\geq$  one day after the expected hatch date. Expected hatch dates were calculated using average incubation periods (Connelly et al. 1998) from when the female started incubating (i.e. located on the nest on consecutive visits). All nests were marked using natural landmarks at a distance of  $\geq 25$  m.

Once a female departed the nest, we classified nest fate as successful ( $\geq$  one chick produced) or failed, and further classified cause of failure based on eggshell remains, predator sign or female behavior (Elbroch 2003). Nests were considered failed if the eggs were destroyed by flooding, trampling by livestock or construction equipment. Nests were considered depredated if the entire clutch disappeared before the expected date of hatching, or if eggshell and nest remains indicated that the eggs were destroyed by a nest predator. Nests were considered abandoned if eggs were cold and unattended for  $> 5$  days.

Results from a concurrent nest survival analysis indicated that visual obstruction (VOR) was the most important habitat predictor of daily nest survival at our study area and was positively related to nest survival

(Milligan et al. 2020a). Therefore, we included a measurement of VOR as an indicator of habitat quality to evaluate whether the effects of flushing differed based on the quality of a nest site. We recorded visual obstruction readings (VOR) at the nest bowl and at four points 6 m from the nest in each cardinal direction within three days of hatching or expected hatch date in the case of failure (Gibson et al. 2016). At each point, VOR was measured in each cardinal direction from a distance of 2 m and a height of 0.5 m using a Robel pole (Robel et al. 1970) and the averaged VOR measurements represented our measure of nest quality.

The two study years differed drastically in the amount of precipitation received, so we obtained daily precipitation data from the National Oceanic and Atmospheric Association (NOAA) station in Sidney, MT, to capture annual variation and assess interactions between environmental conditions and observer effects. We calculated cumulative precipitation for each nest during the 30-day period preceding the nest's fate date (date the nest failed or hatched) to represent the amount of precipitation received during the nesting period for each individual nest attempt. Total precipitation from April to June was 52.6 mm in 2017 and 242.4 mm in 2018.

## Statistical analyses

We evaluated the effects of flushing and environmental conditions on daily nest survival (DSR) of sharp-tailed grouse over a 77-day nesting period during 28 April–12 July using the nest survival model in Program MARK called from the RMARK package in program R (White and Burnham 1999, Dinsmore et al. 2002, Laake 2013). Before fitting models, we examined correlations for each pair of explanatory variables ( $r \geq 0.6$ ) and included only uncorrelated variables in our candidate models. We considered day 1 for each nest to be the day a nest was found rather than a calendar date so as to evaluate different time periods over which an effect of flushing could persist. Thus, the capture history for each nest started on day one and we used a dummy variable (coded 0/1) to represent whether a nest was flushed. We then created variables to represent the persistence of an effect over varying time periods (1, 3, 5, 7, 10, 14-days) up to the entire nesting period. These models allowed us to evaluate both a short-term disruption of flushing and a potential difference in nest survival across the entire nesting period for the two groups. Flushing a female could alter incubation patterns, thus either increasing the total exposure period during which a nest could fail or influencing incubation behaviors that might signal predators (Pierce and Simons 1986, Sandvik and Barrett 2001), and influencing survival rates throughout the entire nesting period as modeled in the scenario where the effect persists over the entire nesting period. Alternatively, visiting the nest to flush a female could leave either visual or olfactory cues allowing predators to find the nest (Picozzi 1975, Westmoreland and Best 1985, Whelan et al. 1994, Hein and Hein 1996, Caldwell et al. 2013) and thus having a time-varying effect where nest survival is decreased directly following flushing but only persists over a limited number of days as modeled in the other scenarios. We also evaluated additive and interaction models with each flushing variable and other factors that could mediate the effect of flushing. Covariates considered included female age (Pyle 1997),

female condition, precipitation, year and nest quality as measured by average VOR within 6 m of the nest bowl. Female body condition was calculated by regressing body mass adjusted for capture date against the length of the wing chord using the reduced major axis method (Green 2001). Models were compared using Akaike's information criterion for finite samples ( $AIC_c$ ) and model selection was based on minimization of  $AIC_c$  and  $AIC_c$  weights ( $w_i$ ). Variables were considered significant if model-averaged 85% confidence intervals did not overlap zero (Arnold 2010).

Overall nest survival (NSURV) for precocial species is the probability that a nest will survive the entire nesting period, defined as the mean laying plus incubation interval for grouse at our study area and calculated by multiplying daily survival rates across that interval. We estimated the variance of overall nest survival with the delta approximation method (Seber 1982). The average duration of the egg-laying and incubation periods (37 d) was determined from observations of our sample of successful nests and from previous work (Connelly et al. 1998).

To evaluate how biases in estimates of nest survival associated with flushing might influence estimates of population growth rates, we built age-structured deterministic pre-breeding birth-pulse matrix models using estimated vital rates from our study population (Leslie 1945). The age structure included second-year and after second-year females. Fecundity ( $F$ ), or the number of female fledglings produced per female, was calculated using the following equation for prairie-grouse (Hagen et al. 2009, McNew et al. 2012):

$$F = \left[ (\text{NEST} \times \text{CS}_1 \times \text{NSURV}) + \left[ (1 - \text{NSURV}) \times \text{RENEST} \times \text{CS}_2 \times \text{NSURV} \right] \right] \times \text{CPE} \times \text{BSURV} \times \text{FPC} \times 0.5$$

Nesting rate (NEST) was calculated as the percentage of females that attempted a nest. The probability of re-nesting (RENEST) was calculated as the number of observed re-nesting attempts divided by the number of unsuccessful first nests minus the number of females that had first nests but were unavailable to re-nest. A female was considered unavailable if she was killed during the first nest attempt or was not relocated after the failure of a first nest attempt. Clutch sizes ( $\text{CS}_1$  and  $\text{CS}_2$ ) and chicks per egg laid (CPE) were estimated directly from field data collected at nests. Initial brood size was determined by the number of chicks that were known to hatch based on nest observations. Brood success (BSURV) was calculated as the proportion of broods that successfully fledged  $\geq 1$  chick at 14-days post-hatch. Fledging success (FPC) was calculated as the proportion of chicks that survived until fledging among successful broods. All parameters except juvenile survival were calculated using estimated vital rates from our study population (Table 1). Information is lacking on juvenile survival for sharp-tailed grouse, so we used published rates from the literature for other prairie grouse species and set juvenile survival, from 14-days post-hatch to the following spring, to  $0.46 \pm 0.01$  based on averaged rates from two studies of greater and lesser prairie-chickens *T. pallidicinctus* (Pitman et al. 2006,



Table 1. Estimated demographic rates ( $\pm$  SE) for female sharp-tailed grouse during the 2017–2018 breeding seasons used to build deterministic matrix models. Juvenile survival was estimated based on rates reported in the literature for related prairie grouse species (Pitman et al. 2006, McNew et al. 2012).

Demographic rate	Estimate $\pm$ SE
Nesting rate (NEST)	1
Clutch size – first nest (CS <sub>1</sub> )	11.06 $\pm$ 0.57
Clutch size – renests (CS <sub>2</sub> )	9.57 $\pm$ 0.60
Renesting rate (RENEST)	0.61 $\pm$ 0.10
Chicks per egg laid (CPE)	0.91 $\pm$ 0.02
Brood success (BSURV)	0.69 $\pm$ 0.05
Fledglings per chick hatched (FPC)	0.62 $\pm$ 0.06
Juvenile survival (14-days post hatch to following spring)	0.46 $\pm$ 0.01
Annual adult survival	0.40 $\pm$ 0.04

McNew et al. 2012). We used estimates for NSURV from the top model (described below) to calculate fecundity for females that were and were not flushed from nests. We used bootstrapping procedures to calculate 95% confidence intervals for fecundity estimates by randomly drawing from the underlying distributions of input parameters (McNew et al. 2012). Using these estimates of fecundity, estimates of juvenile survival from the literature and estimates of annual survival from our study population (Table 1), we built deterministic matrix models where the top elements were the products of juvenile survival and fecundity for second-year and after second-year females, respectively, and the bottom elements were the annual survival of second-year and after second-year females, respectively. Previous research found no difference in either nest survival or annual adult survival between second-year and after second-year females (Milligan et al. 2020a, b), so those rates were held constant across age groups. We then calculated the determinant to estimate finite population growth rates ( $\lambda$ ) for females that were and were not flushed from nests.

We also compared nest initiation dates and clutch sizes between the two treatment groups to evaluate whether other nesting parameters were influenced by our monitoring methods. Information on initiation dates and clutch sizes can be used to construct breeding phenologies and calculate fecundity, respectively, and could be biased if a nest is not visited until after its fate date. We used a two-tailed t-test ( $p < 0.05$ ) to compare both the Julian date of nest initiation and clutch size between groups.

## Results

We located 113 first nests laid by 102 individual females during 2017–2018, including nests from 11 individuals that were monitored in both years. Of 59 nests that were not flushed, 41% failed, while 52% of the 54 nests that were flushed failed, with the majority of failures due to predation (Fig. 1). In 2017, a dry year, 31 nests were flushed, of which 61% failed, compared to 48% of the 29 nests that were not flushed. In 2018, 23 nests were flushed, of which 39% failed, compared to 33% of the 30 nests that were not flushed. The effect of precipitation on daily nest survival accounted for 87% of the relative support of the data. Models with effects

of flushing received similar support to models without effects of flushing (Table 2). There was some evidence that the effect of flushing persisted over longer time periods, but models with shorter time periods also received some support (Table 2). For comparisons we used the parsimonious ‘precipitation  $\times$  flush (constant)’ model ( $\Delta AIC_c = 0.10$ ) and constrained daily nest survival to be constant after a bird was flushed (Table 2). Daily nest survival increased with cumulative precipitation ( $\beta_{\text{precip}} = 0.01 \pm 0.004$ ) and was lower for females that were flushed from nests during periods of low precipitation ( $\beta_{\text{flush}} = -0.81 \pm 0.41$ ;  $\beta_{\text{precip} \times \text{flush}} = 0.01 \pm 0.006$ ), although when estimates were extrapolated over the entire nesting period, model-averaged confidence intervals of nest survival overlapped for the two groups (Fig. 2). For nests that were never flushed, overall survival was calculated as  $DSR_{\text{unflushed}}^{37}$ . The median date of first flush was on day 12 of the nest attempt and flushing could not impact daily nest survival before a nest was flushed, so overall survival for nests that were flushed was calculated as  $DSR_{\text{unflushed}}^{12} \times DSR_{\text{flushed}}^{25}$ . Estimates of overall nest survival  $\pm$  SE ranged from  $0.21 \pm 0.06$  and  $0.41 \pm 0.10$  for flushed and unflushed nests that received 10 mm of precipitation during the nesting period to  $0.64 \pm 0.12$  and  $0.72 \pm 0.08$  for flushed and unflushed nests that received 140 mm of precipitation during the nesting period (Fig. 2).

The distribution of precipitation received by nests in our study was bimodal, which reflects the fact that the study encompassed both a drought and a wet year (Fig. 3). We used estimates of nest survival across the range of monitored precipitation levels to estimate the finite rate of population growth ( $\lambda$ ) for subpopulations of females that were and were not flushed from nests (Fig. 2). Estimated rates of population growth increased with cumulative precipitation and were proportionally up to 50% higher, depending on precipitation, for our sample of females not flushed from their nests. However, bootstrapped 95% confidence intervals of  $\lambda$  overlapped between the treatment groups (Fig. 2).

Average nest initiation was the same regardless of whether a female was flushed ( $p = 0.94$ ,  $\bar{x} = 9$  May for both flushed and non-flushed birds). We were unable to obtain clutch size information for a subset of unvisited nests ( $n = 15$ ) that were depredated due to the removal or destruction of all eggs, but average clutch sizes for the remaining nests were similar regardless of whether a female was flushed or not ( $p = 0.21$ ;

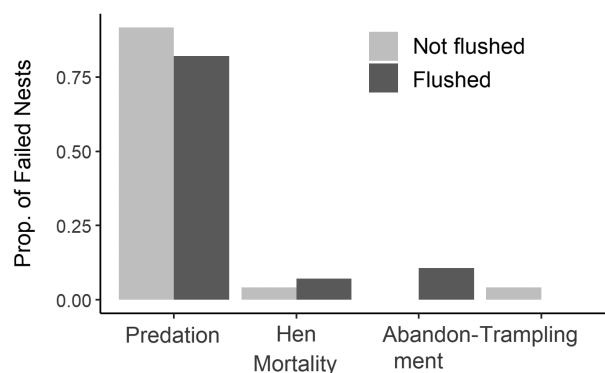


Figure 1. Proportion of nests that failed due to predation, hen mortality, abandonment or trampling by cattle.

Table 2. Support for candidate models evaluating the effects of flushing on sharp-tailed grouse nest survival in 2017–2018. The number of parameters (K), AIC<sub>c</sub> values, ΔAIC<sub>c</sub> values, model weights ( $w_i$ ) and deviance are reported and only models that accounted for any model weight are included. The time period associated with each 'Flush' variable represent the time period over which a potential effect existed.

Model	K	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	AIC <sub>c</sub> $w_i$	Deviance
Precipitation	2	418.70	0.00	0.11	414.69
Flush (constant) × Precipitation	4	418.79	0.10	0.11	410.78
Flush (constant) + Precipitation	3	419.03	0.33	0.09	413.02
Flush (5-days) × Precipitation	4	419.22	0.52	0.09	411.20
Flush (10-days) × Precipitation	4	419.56	0.86	0.07	411.54
Flush (7-days) × Precipitation	4	420.26	1.57	0.05	412.25
Flush (14-days) + Precipitation	3	420.29	1.59	0.05	414.28
Flush (10-days) + Precipitation	3	420.61	1.92	0.04	414.60
Flush (7-days) + Precipitation	3	420.65	1.96	0.04	414.64
Flush (1-day) + Precipitation	3	420.66	1.96	0.04	414.65
Flush (3-days) + Precipitation	3	420.66	1.97	0.04	414.65
Flush (5-days) + Precipitation	3	420.66	1.97	0.04	414.65
Flush (3-days) × Precipitation	4	420.69	2.00	0.04	412.68
Flush (1-day) × Precipitation	4	421.61	2.92	0.03	413.60
Flush (14-days) × Precipitation	4	421.83	3.14	0.02	413.82
Flush (constant) × Female age	4	423.71	5.01	0.01	415.69
Flush (3-days) × Female age	4	423.98	5.28	0.01	415.96
Flush (1-day) × VOR	4	424.44	5.74	0.01	416.42
Flush (1-day) × Female age	4	424.46	5.76	0.01	416.44
VOR	2	424.64	5.95	0.01	420.64
Year	2	424.66	5.96	0.01	420.65
Flush (3-days) × VOR	4	424.72	6.02	0.01	416.70
Flush (constant) + VOR	3	424.79	6.10	0.01	418.78

$\bar{x} = 11.7 \pm 2.74$  for flushed birds;  $\bar{x} = 11.2 \pm 2.01$  for non-flushed birds).

## Discussion

Similar to previous work on greater prairie-chickens (Westemeier et al. 1998), flushing sharp-tailed grouse from their nests did not have statistically significant negative effects on nest survival, although differences may be biologically relevant, particularly for small or declining populations. Depending on the amount of precipitation received, flushing a nest only once reduced its overall probability of survival by 0.05–0.19 (11–92%) in periods of low precipitation (< 70 mm). These downward biases in nest survival when nests were flushed did not translate to incorrect inferences regarding population growth, but the study population was stable with overall high demographic rates.

While previous studies found that the negative effects of flushing greater sage-grouse were primarily due to increased rates of abandonment (Gibson et al. 2015), the majority of our nests failed due to predation. Among the nests in our study that were abandoned ( $n=3$ ), two were flushed early during the egg-laying period and the third was abandoned > 1 week post-flush after the eggs did not develop properly (Milligan unpubl.). This suggests that flushing female sharp-tailed grouse did not increase nest abandonment as long as females are not flushed immediately following the beginning of egg-laying, which is consistent with previous work on prairie grouse (Westemeier et al. 1998).

Previous studies observed varied individual responses of greater sage-grouse to research activity that depended upon the quality of either the nest or the individual female (Gib-

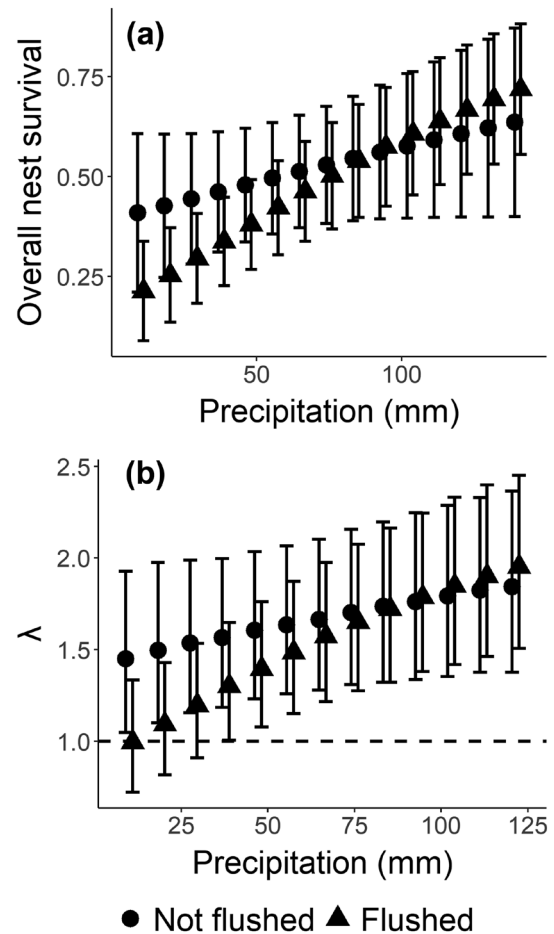


Figure 2. Estimated overall nest survival ( $\pm$  85% confidence intervals; A) and finite population growth rate ( $\lambda \pm$  95% confidence intervals; B) in relation to cumulative precipitation during the nesting period (30-day period prior to nest fate) for birds that were and were not flushed off the nest. The dashed horizontal line in B represents a stable population ( $\lambda = 1$ ) and points are offset for clarity.

son et al. 2015). Our results, however, suggest that the negative effect of flushing sharp-tailed grouse was not mediated by characteristics associated with either the nest or the female, including nest quality as measured by visual obstruction and either female age or condition. Rather, nest survival was primarily influenced by the amount of precipitation received during the 30-days period prior to nest fate. Previous research suggests that wet conditions during incubation can improve

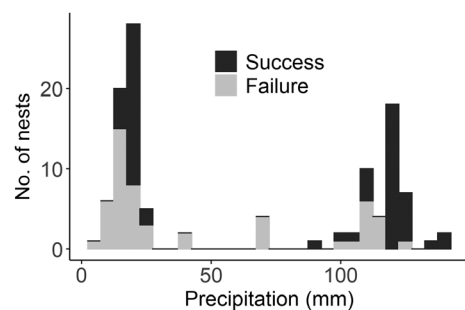


Figure 3. Number of nests by the amount of precipitation (mm) received during the 30-days period prior to the nest's fate (failed or hatched) with successful nests in black and failed nests in light gray.

the ability of mammalian predators to detect nests (moisture-facilitated nest depredation hypothesis; Roberts et al. 1995), but the positive effect of cumulative precipitation in our study is likely linked to vegetation growth. During the growing season when birds are nesting, plant phenology creates temporal variation in vegetation structure and biomass, which is linked to precipitation (Rosenzweig 1968, Gibson et al. 2016). Precipitation directly affects the amount of aboveground biomass (Vermeire et al. 2009), which is closely related to nest survival in prairie grouse (Manzer and Hannon 2005, Pitman et al. 2005, McNew et al. 2015, Milligan et al. 2020a). Precipitation effects on vegetation may be more pronounced in the northern mixed grass prairie which receives less and more variable annual precipitation than other areas occupied by related species (Yang et al. 2008, Cleland et al. 2013). Although our study encompasses only two years and further research should evaluate effects on nest survival across the range of precipitation possible in the northern mixed grass prairie, cumulative precipitation was a much better predictor of daily nest survival than a binary year term, which suggests that precipitation rather than other unmeasured variation between years was driving the differences in nest survival seen in our study.

Although estimates of nest survival were reduced for females that were flushed off the nest, the effect was not significant, and this translated to no significant difference in estimates of population growth. Estimated rates for both groups suggested an increasing or stable population, but this lack of an effect may not hold in small or declining populations where other components of fecundity or adult survival may be lower (McNew et al. 2012). Regardless of the magnitude of the effect, however, quantifying the impacts of research activity on nest survival would allow studies to correct for any potential bias and thus evaluate the effect of management actions on population growth without bias.

Flushing birds off nests is typically justified by the additional information, such as clutch size and nest age, that can be collected only when a nest is visited. Our results suggest that flushing did not significantly affect estimates of nest survival and will not negatively affect inferences regarding population viability. Nevertheless, our results also suggest that little information was lost by not flushing females off the nest. While we were unable to obtain clutch size information for a subset of unvisited nests, average initiation dates and clutch sizes for the remaining nests were similar regardless of whether a female was flushed or not. Furthermore, we were able to calculate nest initiation dates with reasonable accuracy for all nests with clutch size information by backdating from the beginning of incubation based on clutch size. However, this approach would only work if nests are being monitored  $\geq$  three times per week so that the start of incubation can be determined within one day, so the constraints imposed by a monitoring protocol will limit the feasibility of this approach.

## Management implications

Nest monitoring protocols that involve flushing females from nests have the potential to bias estimates of nest survival to a degree that could be biologically relevant. In

our study, however, the negative effects of flushing on overall nest survival were not statistically significant and did not affect inferences regarding population growth of sharp-tailed grouse. Nevertheless, our estimated vital rates were high, and our population was predicted to remain stable or increase under all conditions (95% CIs for  $\lambda$  overlapped 1). Any potential researcher-induced bias would be more pertinent for populations having population growth rates nearer to 1 as an 11–92% downward bias in nest survival may yield interpretations of a declining population ( $\lambda < 1$ ) when a population is truly stationary or increasing.

Researchers should consider both the data required for a particular study and potential biases when considering nest monitoring protocols and test for biases of researcher activity whenever possible. With minimal data loss, we were able to accurately estimate all nesting parameters (e.g. nest initiation rates, clutch sizes, nest survival, hatch rates) required for evaluations of fecundity without flushing radio-marked females from their nests. Nevertheless, flushing may be necessary to accurately estimate nest age or clutch sizes when radio-marked females are monitored less frequently or nest failure during laying is high. Regardless, we recommend researchers modify nest monitoring protocols when possible, potentially only disturbing a subset of individuals as we did here, to empirically evaluate whether researcher activities influence demographic parameters of interest.

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## Author contributions

Both Megan C. Milligan and Lance B. McNew formulated the research questions and designed the study, MCM collected and analyzed data, and wrote the manuscript, which both authors then reviewed and edited.

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