Hunting and Nesting Phenology Influence Gobbling of Wild Turkeys

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ABSTRACT Wild turkeys (Meleagris gallopavo) use a polygynous mating system whereby males engage in multiple courtship behaviors, including vocalizations (gobbling) to attract females and compete with other males for breeding opportunities. Males must balance the risk of courtship behaviors with the reproductive potential of each courtship behavior. Male turkeys are primarily hunted during the reproductive period, so the associated risk of courtship behaviors is increased. Many state agencies attempt to set hunting season frameworks that maximize hunter satisfaction by allowing hunting when gobbling activity is greatest and most females are theoretically incubating nests, but the relationship between gobbling activity and nesting phenology is unclear. We used autonomous recording units and global positioning system transmitters to monitor gobbling activity by male turkeys and reproductive behaviors of female turkeys in the Piedmont region of Georgia, USA. We used 13,177 gobbles, behavioral data from 82 females during the reproductive season, and daily estimates of harvest of males by hunters to examine relationships between daily gobbling activity, cumulative removal of males, and reproductive behaviors (laying, incubating) of females during 2017–2018. We observed a weak negative relationship between daily gobbling activity and gobbling activity the following day. As the reproductive season progressed, gobbling activity decreased. As the proportion of females engaged in laying or incubating behaviors increased, expected daily gobbling activity increased. Conversely, we observed that hunting and removal of males had a negative effect on daily gobbling activity, and this effect was disproportionately greater than the positive effect of female reproductive behaviors. Our findings suggest that hunting and removal of males are important determinants of gobbling activity, and that corresponding reductions in gobbling activity may have mediating effects on the mating system of wild turkeys. © 2019 The Wildlife Society.

KEYWORDS eastern wild turkey, gobbling, hunting, Meleagris gallopavo silvestris, nesting phenology, reproduction.


Signals used in mate attraction should communicate reproductive potential and increase mating opportunities (Emlen and Oring 1977, Pomiankowski and Iwasa 1993, Gintis et al. 2001, Andersson and Simmons 2006, Edward 2015). Signals are designed to express fitness benefits and establish dominance among males (Orians 1969), and females select mates based on signals (Emlen and Oring 1977, Alonso et al. 2012). Therefore, males are expected to adjust signaling in response to female behaviors (Orians 1969, Cox and Le Boeuf 1977). Previous authors have noted 2 primary ways in which female behaviors influence signaling of males.
First, as females become reproductively active or fertile, males increase rates of competition and signaling for breeding opportunities (Birkhead et al. 1987, Montgomerie and Thornhill 1989). Second, as numbers of available females decrease with onset of incubation, operational sex ratios skew greatly towards males, and male competition for remaining available females should increase (Weir et al. 2011). As male competition increases, frequencies of courtship displays and signaling should likewise increase until reaching a threshold when signaling is no longer profitable (Emlen and Oving 1977).

Signaling can be energetically costly and negatively influence survival of males by increasing predation risk (Berglund 1993, Berg et al. 2005, Stewart et al. 2005, Zanette et al. 2006), and predation risk can alter reproductive behaviors and strategies (Forsgren and Magnhagen 1993, Candolin 1998). Risk-reward theory predicts that signaling must provide a greater reward than the associated costs to make the signal beneficial, with the reward being an opportunity to mate (Orians 1969, Olson and Owens 1998, Gintis et al. 2001, Hooper and Miller 2008). Signaling to attract a mate, however, can pose risk by attracting predators (Magnhagen 1991). For an individual to engage in signaling, there must be the perception of a greater chance of attracting mates than predators, or the individual should cease or alter the behavior. Thus, risk-reward tradeoffs often lead to signaling events being temporarily and spatially correlated to periods of increased potential for mate acquisition (Luther 2009). When predation risk remains low, signaling is predicted to be high, but when risk increases signaling should decrease (Gintis et al. 2001, Hooper and Miller 2008).

Wild turkeys (Meleagris gallopavo) use a polygynous mating system, and males exhibit phenotypic characteristics influenced by sexual selection such as fleshy head ornaments, beards, and large body size (Amadon 1959; Buchholz 1995, 1997; Krakauer 2008). Males use elaborate courtship displays and vocalizations (gobbling) to attract females, maintain dominance hierarchies, and compete with other males for breeding opportunities (Bevill 1973, Healy 1992). Previous researchers suggested that rates of gobbling may increase during peaks in nest incubation (Bevill 1973, Hoffman 1990, Miller et al. 1997, Norman et al. 2001, Lehman et al. 2005), whereas contemporary researchers challenged these earlier works (Chamberlain et al. 2018). Gobbling chronology is used by agencies to establish regulatory frameworks, which dictate the timing and intensity of male harvest (Little et al. 2000, Swanson et al. 2005, Isabelle and Reitz 2015). Furthermore, because male wild turkeys are primarily hunted during their reproductive season, the increased risk associated with hunting may negatively influence gobbling (Kienzler et al. 1995, Norman et al. 2001, Wightman et al. 2019). Hence, research is needed to evaluate how female reproductive behaviors coupled with potential influences of hunting and removal of males could influence gobbling activity. We hypothesized that female reproductive behaviors and hunting could influence daily gobbling; therefore, our objectives were to evaluate potential relationships between daily gobbling activity, hunting and removal of males, and female reproductive behaviors. We predicted that daily gobbling activity would be positively associated with female reproductive behaviors but negatively associated with hunting and removal of males.

**STUDY AREA**

We conducted research on B. F. Grant and Cedar Creek Wildlife Management Areas (WMA; Fig. 1) and surrounding privately owned areas in the Piedmont region of Georgia, USA during 2017–2018. The Piedmont region was characterized by gently rolling hills and narrow valleys. The B. F. Grant WMA was located in Putnam County, Georgia, approximately 13 km northwest of Eatonton, Georgia. This 4,613-ha area was owned by the Warnell School of Forestry and Natural Resources at the University of Georgia, and was managed cooperatively with the Georgia Department of Natural Resources, Wildlife Resources Division (GADNR). It was bisected by Big Indian Creek and the western boundary was formed by Little River. The property was comprised of managed forest and agricultural land for livestock. Agricultural lands were mostly grazed mixed fescue (Festuca spp.) fields and hay fields planted in rye grass. Forested areas consisted of loblolly pine (Pinus taeda) forests, mixed hardwood and pine (Pinus spp.) forests, and hardwood lowlands containing white oak (Quercus alba), sweet gum (Liquidambar styraciflua), yellow poplar (Liriodendron tulipifera), hickory (Carya spp.), and other oak species (Quercus spp.). The understory was dominated by sweet gum, eastern redbud (Cercis canadensis),

![Figure 1. Locations of B. F. Grant and Cedar Creek Wildlife Management Areas in north-central Georgia, USA.](image-url)
muscadine (Vitis rotundifolia), flowering dogwoods (Cornus florida), and briars (Rubus spp.). Forest management was primarily through patch cuts, thinning, and prescribed fire.

Cedar Creek WMA was located in Jasper, Jones, and Putnam counties, Georgia, approximately 16 km southwest of Eatonton, Georgia. This 16,187-ha area was owned by the United States Forest Service (USFS) and managed in partnership between the USFS and GADNR. Cedar Creek WMA was bisected by Big Cedar Creek and Murder Creek, and contained portions of Glady, Cedar, and Badger creeks. The site was composed of managed loblolly pine forests, mixed hardwood and pine forests, hardwood valleys containing mostly white oak, sweet gum, yellow poplar, hickory, other oak species, and small openings for wildlife. The understory composition was similar to that on B. F. Grant WMA. Forests of Cedar Creek WMA were primarily managed through thinning and periodic (3- or 4-year return interval) dormant-season fire (Jan–Mar). The land cover composition of B. F. Grant and Cedar Creek WMAs was 39.5% hardwood forests, 32.1% pine forests, 5.4% mixed forests, 19.8% open areas, 0.1% water, and 3.1% developed areas. Areas surrounding the properties were predominately mixtures of pine forest and agricultural fields for livestock. Climate on our study sites was characterized by hot, dry summers (Jun–Sep) and cool, wet winters (Nov–Feb). During the study, mean temperature was 17.9 °C (range = 3–32 °C; https://usclimatedata.com; accessed 15 Oct 2019). Average elevation across our study areas was 520 m (https://weatherspark.com; accessed 15 Oct 2019).

Both sites had annual spring turkey hunting seasons. The season on B. F. Grant WMA consisted of 3 hunting segments, which included an adult-child hunt from 25 March to 2 April 2017 and 24 March to 1 April 2018, an 80-person quota hunt from 3 April to 9 April 2017 and 2 April to 8 April 2018, and a general (open to the public) hunt from 10 April to 15 May 2017 and 9 April to 15 May 2018. On Cedar Creek WMA, the season was a general hunt from 25 March to 15 May 2017 and 24 March to 15 May 2018. The annual bag limit for both sites was 3 males/hunter. Hunters were required by GADNR to check-in before hunting on either site but were not required to check-in daily. The number of hunters that used our study sites was 1,080 in 2017 and 964 during 2018.

METHODS
We captured turkeys using rocket nets (Delahunt et al. 2010) during January–March 2017 and 2018. We sexed captured birds following Pelham and Dickson (1992). We banded all captured birds with uniquely numbered aluminum rivet-style leg bands. We radio-marked all females with backpack-style global positioning system (GPS) units (Lotek Wireless, Newmarket, ON, Canada; Guthrie et al. 2011). We programmed GPS units to record locations hourly from 0500 through 2000 and 1 roost location at 2359 for the life of the units (Cohen et al. 2018). All capture, handling, and marking procedures were approved by the Institutional Animal Care and Use Committee at the University of Georgia (protocol number A2016 04-001-R1).

We monitored radio-tagged turkeys >1 time/week from time of capture until the end of the reproductive season (late Jul) using 3-element handheld antennas and receivers (R2000, R4000; Advanced Telemetry Systems, Isanti, MN, USA). We downloaded GPS locations remotely each week until evaluation of GPS locations showed the female visiting the same location daily (laying a clutch) or locations concentrated around a central location and did not significantly deviate for several days (incubating nest), at which point we began downloading locations ≥1 time weekly (Yeldell et al. 2017, Chamberlain et al. 2018, Wood et al. 2018). Throughout the course of the reproductive season, we classified females into reproductive phases, which included prenesting (1 Mar to onset of laying), laying, incubation, and brooding (Wood et al. 2018). For purposes of our study, we were only interested in whether females were laying or incubating nests (i.e., reproductively active). We determined laying dates based off the first estimated visit to the nest site from the GPS data (Yeldell et al. 2017, Chamberlain et al. 2017, Wood et al. 2018). When we could not determine the date of first visit because of GPS failure, we used clutch size to determine lay date by backdating from the first day of incubation. If we did not find eggs or found an insufficient number of eggshells, we assumed laying began 12 days prior to incubation based on average clutch size (Yeldell et al. 2017). We determined a female to be incubating when GPS locations did not deviate from a central location for several days (Yeldell et al. 2017). When a female began incubating, we monitored her daily until she left the nest site. Upon the female leaving the nest, we located the nest site to determine if the nest was successful (hatched ≥1 egg) or failed (nest abandoned, egg fragments, lack of eggs, or female mortality; Wood et al. 2018). After nest failure, we continued to monitor females for additional nest attempts.

We deployed 24 autonomous recording units (ARUs; Song Meter, SM4 Digital Field Recorders, Wildlife Acoustics, Concord, MA, USA) to collect ambient acoustic recordings from 1 March through 30 June. We constructed a 2-km grid of the study area and placed ARUs within each grid cell in areas predicted to have turkeys present based on field observations and previous research, which included hardwood stands, edges of fields or openings, managed pine stands, and areas near water or other riparian zones (Colbert 2013, Wightman et al. 2019). We also separated ARUs >2 km apart to prevent overlap in sampling. We placed microphones at a height of approximately 10 m in pine trees to reduce interference associated with understory and midstory vegetation (Colbert et al. 2015). We set ARUs to collect data from 0500 hours to 1100 hours, which encompasses >85% of daily gobbling activity (Wightman et al. 2019).

We searched audio files for gobbles using the call recognition software (CRS) Raven Pro versions 1.4 and 1.5
Normal values are a measure of convergence derived by 

\[
\text{Log N} = \log(N_0) + r_t
\]

where \( r_{\text{expected}} \) was the expected rate of change in daily gobbling activity, \( \beta_{\text{daily gobbling}} \) was the mean growth rate of gobbling, \( \beta_1 \) was the coefficient for the effect of gobbling a day prior, \( \beta_{\text{reproduction}} \) was the coefficient for proportion of females in reproduction in matrix \( X_{\text{reproduction}} \) and \( \beta_{\text{hunting}} \) was the coefficient for hunting in matrix \( X_{\text{hunting}} \). We modeled the observation process as follows:

\[
y_t \sim \text{Normal}(\log(N_t), \tau_{\text{aberration}}),
\]

where \( y_t \) was the logged observed number of gobbles each day (\( t \)). We calculated 95% credible intervals (CrI) for each parameter estimate. We used a vague normal prior with a mean of 0 and precision of 0.001 for each estimated parameter.

We used Markov chain Monte Carlo (MCMC) to estimate the posterior distributions of the model parameters. We generated 3 MCMC chains using a thinning rate of 15,000 iterations/chain, and 5,000 burn-in values. We inspected trace plots of the MCMC chains as an indicator of convergence. Furthermore, we used the Gelman-Rubin statistic, \( \bar{R} \), to check chain convergence (Gelman et al. 2004); \( \bar{R} \) values are a measure of convergence derived by comparing variance between multiple chains to the variance within each chain. All estimated parameters in our model had \( \bar{R} \) values \( \leq 1.1 \), which indicated model convergence.

**RESULTS**

Using the 24 ARUs, we collected 5,629 days of audio recordings from 1 March through 30 June 2017 and 2018. We processed 3,203,607 detections and positively identified 13,177 gobbles (Table 1). We observed an average of 275 gobbles/ARU/year and noted that 72% of gobbling activity occurred within 1 hour of sunrise (Fig. 2). We observed most gobbles (63%) during March and noted that gobbling declined markedly from April (31%) through May (4%) both years.

We captured 82 female wild turkeys during 2017 (\( n = 42 \)) and 2018 (\( n = 40 \)). During 2017, 42 females (38 adults, 4 juveniles) incubated 58 nests. We noted laying behaviors from 7 March through 30 June of 2017. Mean date of initiation of laying behaviors was 14 April, and the median date of initiation of laying behaviors was 2 April during 2017. Earliest onset of incubation in 2017 was 20 March and incubation behaviors continued through 30 June. Mean date of initiation of incubation was 27 April, whereas the median date of initiation of nest incubation was 15 April. During 2018, 40 females (36 adults, 4 juveniles) incubated...
54 nests. We noted laying behaviors from 1 March to 30 June of 2018. Mean date of initiation of laying behaviors was 8 April, and median date of initiation of laying behaviors was 31 March during 2018. Earliest onset of incubation in 2018 was 15 March and incubation behaviors continued through 30 June. During 2018, the mean date of nest incubation was 22 April and the median date of initiation of nest incubation was 14 April in 2018.

The GADNR reported the harvest of 113 males during 2017 (n = 51) and 2018 (n = 62), or on average 1 male/368 ha annually. Daily gobbling activity declined markedly after the onset of hunting and removal of males (Fig. 3).

The results from the state-space model indicated daily gobbling activity was negatively influenced by gobbling the previous day (β = -0.62, 95% CrI = -0.89, -0.35) and daily gobbling activity generally declined throughout the reproductive season (Table 2). The state-space model accurately predicted gobbling activity compared to our observed gobbling activity (Fig. 3). Our results supported our hypothesis that female reproductive behaviors and hunting collectively influence daily gobbling. We observed a positive effect of female reproductive behaviors on predicted gobbling activity (β = 1.15, 95% CrI = 0.52, 1.81; Fig. 4). Conversely, we observed that hunting negatively influenced daily gobbling activity (β = -1.31, 95% CrI = -1.54, -0.58; Fig. 5). We expect daily gobbling activity to decrease by a factor 3.7 (odds ratio calculated by 1/exp [-1.31]) for every 4.4 male turkeys removed/10 km².

### DISCUSSION

Our findings support the hypothesis that female reproductive behaviors and hunting influence daily gobbling activity. We noted a negative relationship between predicted gobbling activity relative to gobbling the previous day. Daily gobbling activity was positively related to the proportion of female turkeys exhibiting reproductive behaviors (laying, incubating nests). Conversely, daily gobbling activity was negatively related to hunting, and gobbling activity declined precipitously with onset of hunting and harvest of males. We offer that this finding is a consequence not only of the removal of vocal males from the landscape, but also elevated predation risk (hunting activity) prompting males to reduce vocalizations and adopt alternative strategies (e.g., roost at different sites each night to locate receptive females) to secure reproductive opportunities (Wakefield et al. 2020). Collectively, our findings suggest that hunting is an important mediating effect on daily gobbling activity in the turkey population we studied.

Wild turkeys have pulsatile testosterone levels that result in day-to-day fluctuations in breeding behaviors (Bacon et al. 1991), and vocalizations associated with breeding activity are influenced by changes in testosterone levels that increase in

### Table 1

<table>
<thead>
<tr>
<th>Site</th>
<th>Year</th>
<th>Detections</th>
<th>Gobbles</th>
<th>Gobbles (%)</th>
<th>False positives (%)</th>
<th>Gobbles/unit</th>
</tr>
</thead>
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<tr>
<td>CC</td>
<td>2017</td>
<td>874,052</td>
<td>4,103</td>
<td>0.47</td>
<td>99.53</td>
<td>256.44</td>
</tr>
<tr>
<td>CC</td>
<td>2018</td>
<td>1,145,534</td>
<td>3,868</td>
<td>0.34</td>
<td>99.66</td>
<td>241.75</td>
</tr>
<tr>
<td>BFG</td>
<td>2017</td>
<td>603,826</td>
<td>3,396</td>
<td>0.56</td>
<td>99.44</td>
<td>424.50</td>
</tr>
<tr>
<td>BFG</td>
<td>2018</td>
<td>580,195</td>
<td>1,810</td>
<td>0.31</td>
<td>99.69</td>
<td>226.25</td>
</tr>
</tbody>
</table>

Figure 2. Proportion of gobbles by male wild turkeys recorded by 30-minute intervals from 0500 to sunrise, and 330 minutes after sunrise on B. F. Grant and Cedar Creek Wildlife Management Areas, Georgia, USA, 2017–2018.
spring (Lisano and Kennamer 1977, Wada 1981, Johnsen 1998, Fusani 2008). Testosterone levels in many species, including within the order Galliformes, oscillate temporally, which results in predictable fluctuations in calling activity throughout the breeding season (Wada 1981, Møller et al. 2005). Many behaviors in avian species synchronize (Evans and Patterson 1971) including calling and breeding behaviors (Stokes and Williams 1968, Fusani 2008), so we would expect synchronized calling and breeding behaviors to be a result of synchronized fluctuations in testosterone. Previous authors have noted similar fluctuations in daily gobbling activity in wild turkeys (Chamberlain et al. 2018, Wightman et al. 2019); hence, we were not surprised to observe a negative relationship between predicted daily gobbling activity relative to gobbling activity the previous day. An alternative, and not mutually exclusive, explanation is that vocal males are moving and roosting away from stationary ARUs on consecutive nights because male wild turkeys exhibit low fidelity to roost sites on consecutive nights during the reproductive season (Byrne et al. 2015, Wakefield et al. 2020). However, it is logical to assume that if some males moved away from ARUs to roost on consecutive nights, others would move towards them.

Previous studies have demonstrated positive correlations between onset of nest initiation (laying) and gobbling

![Figure 3](image-url) Predicted daily gobbling activity by male wild turkeys from results of a state-space model (black line) with 95% credible intervals (shaded grey) compared to observed daily gobbling activity (dotted line) on B. F. Grant and Cedar Creek Wildlife Management Areas, Georgia, USA, 2017–2018. Onset of hunting is denoted with the dashed vertical line.

![Figure 4](image-url) The predicted rate of change \( r = \log (\text{gobbles}_{t+1}/\text{gobbles}_t) \) with 95% credible intervals in daily gobbling activity of male wild turkeys relative to the proportion of global positioning system-marked female wild turkeys in reproduction (laying or incubating a nest) on B. F. Grant and Cedar Creek Wildlife Management Areas, Georgia, USA, 2017–2018.

![Figure 5](image-url) The predicted rate of change \( r = \log (\text{gobbles}_{t+1}/\text{gobbles}_t) \) with 95% credible intervals in daily gobbling activity of male wild turkeys as a function of hunting and cumulative removal of males on B. F. Grant and Cedar Creek Wildlife Management Areas, Georgia, USA, 2017–2018.

Table 2. Parameters and associated means and uncertainty (SD and credible intervals) from a state-space model for the relationship between daily gobbling activity (daily gobbling), female reproductive behaviors (reproduction), and hunting, and variance of observed and predicted (process) gobbling by male wild turkeys on Cedar Creek and B. F. Grant Wildlife Management Areas, Georgia, USA, 2017–2018.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>M</th>
<th>SD</th>
<th>2.5%</th>
<th>50%</th>
<th>97.5%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Observation variance</td>
<td>0.435</td>
<td>0.257</td>
<td>0.062</td>
<td>0.429</td>
<td>0.958</td>
</tr>
<tr>
<td>Process variance</td>
<td>0.831</td>
<td>0.285</td>
<td>0.344</td>
<td>0.815</td>
<td>1.394</td>
</tr>
<tr>
<td>Intercept</td>
<td>2.002</td>
<td>0.451</td>
<td>1.087</td>
<td>2.010</td>
<td>2.889</td>
</tr>
<tr>
<td>Daily gobbling</td>
<td>−0.621</td>
<td>0.135</td>
<td>−0.886</td>
<td>−0.623</td>
<td>−0.345</td>
</tr>
<tr>
<td>Hunting</td>
<td>−1.062</td>
<td>0.243</td>
<td>−1.540</td>
<td>−1.064</td>
<td>−0.581</td>
</tr>
<tr>
<td>Reproduction</td>
<td>1.151</td>
<td>0.329</td>
<td>0.520</td>
<td>1.145</td>
<td>1.808</td>
</tr>
</tbody>
</table>

Wakefield et al. • Hunting and Nesting Effects on Gobbling
activity (Kienzler et al. 1995, Miller et al. 1997, Chamberlain et al. 2018), similar correlations between peaks in gobbling activity and nest incubation (Hoffman 1990, Norman et al. 2001), and lags between the onset of laying and peaks in gobbling activity (Chamberlain et al. 2018). Because periods of laying and incubation were not mutually exclusive in our study population (females laying while others incubating), we modeled relationships between daily gobbling activity and the proportion of females exhibiting laying or incubation behaviors. We offer that the observed positive relationship between daily gobbling activity and proportion of females exhibiting laying or incubation behaviors relates to the receptivity and availability of females on the landscape as the breeding season progresses. Male wild turkeys become receptive to breeding before females (Williams and Austin 1988, King and Millar 1995), so males begin signaling well before securing breeding opportunities. Specifically, our findings suggest that males initiate gobbling ≥30 days before initial onset of incubation, and about 45 days before median incubation dates.

As females become receptive to copulation, signaling increases as males attempt to attract females and secure mating opportunities (Cox and Le Boeuf 1977, Emlen and Oring 1977, Montgomery and Thornhill 1989). Fertile periods in birds typically cease with the fertilization of the last egg in the oviduct (Birkhead et al. 1987), which would fall within the laying sequence. Furthermore, although sperm storage facilitates sperm competition and allows birds to lay fertile eggs weeks after copulation (Birkhead and Moller 1992, Khillare et al. 2018), males can increase fitness by copulating with females prior to egg laying. Hence, male competition and signaling escalates presumably as males seek mating opportunities with females entering into the laying sequence because copulating with these receptive females increases the likelihood the male will be represented in the clutch (Emlen and Oring 1977, Birkhead et al. 1987, Brillard and Bakst 1990). As numbers of receptive females decline with onset of incubation, competition amongst males and frequency of courtship displays (i.e., vocalizations) should increase (Weir et al. 2011, Chamberlain et al. 2018). We note that operational sex ratios could become altered as females begin incubating nests, but these ratios also could be skewed through harvest of males while laying and onset of incubation are occurring, as noted herein.

Predation risk can negatively affect signaling and courtship displays (Lima 2009). Courtship behaviors like gobbling can increase predation risk because predators (i.e., hunters) may also be attracted to calls (Burk 1982, Berglund 1993). Hedrick (2000) noted that males of various species may alter courtship displays in response to elevated predation risk. The risk allocation hypothesis suggests that during periods of increased predation risk animals should allocate more efforts to antipredator behavior (Lima and Bednekoff 1999), and hunting can function as an intense, temporally variable form of elevated predation risk (Crosmary et al. 2012, Bonnot et al. 2013). Because male wild turkeys are hunted primarily during their breeding season, hunting artificially increases predation pressures on the male segment of the population (Humberg et al. 2009), which can influence male behavior. Indeed, hunting suppresses gobbling activity (Kienzler et al. 1995, Lehman et al. 2005, Wightman et al. 2019) and influences male spatial behaviors (Gross et al. 2015).

Male wild turkeys are the only gamebird in the conterminous United States hunted specifically during peaks in reproductive activities (Chamberlain et al. 2018, Isabelle et al. 2018), and hunting is generally timed to expose hunters to periods when gobbling activity is greatest (Miller et al. 1997, Lehman et al. 2005). Gobbling not only attracts females but also serves to maintain established male dominance hierarchies (Healy 1992, Kienzler et al. 1995, Wightman et al. 2019). We offer that hunting potentially removes a segment of vocal males from the landscape while also prompting remaining males to reduce gobbling (Lehman et al. 2005, Chamberlain et al. 2018), and in our study, cease gobbling well before the end of the reproductive season. Vocal males are theoretically more dominant individuals (Neumann et al. 2010, Bolt 2013), and removing them from the breeding population prior to peaks in onset of nest incubation could negatively influence fitness potential within the population (Ginsberg and Milner-Gulland 1994, Milner et al. 2007). Likewise, our observation that remaining males in the population cease gobbling early in the reproductive season suggests that remaining males may adopt alternative reproductive strategies to secure breeding opportunities (Burk 1982, Zuk and Kolluru 1998, Hedrick 2000).

Predation risk, whether real or perceived, is increasingly posited as a mechanism that produces cascading effects of predator presence and activity on prey populations (Laundré et al. 2010). Likewise, persistent influences of predation risk on individual behaviors may scale up to influence population dynamics (Creel et al. 2007, Matassa and Trussell 2011). As predation risk increases and expanses of landscapes become riskier, factors such as resource availability may become less important in structuring prey populations than risk of predation (Laundré et al. 2014). Our findings contribute to a growing literature suggesting that human disturbance, hunting, and harvest can create changes in prey behavior that oppose adaptive responses to sexual selection (Ciuti et al. 2012), which has potential to outpace selective forces with regards to phenotypic, genetic, and life-history traits (Hutchings and Baum 2005, Darimont et al. 2009). Human harvest of male wild turkeys may be selective for desirable behavioral traits (i.e., aggressive and vocal males) because increased calling activity by males is widely known to most influence hunter satisfaction (Little et al. 2000, Casalena et al. 2011). We postulate the notable negative influence of hunting on calling behavior of males could be an important influence on the mating system of wild turkeys (Allendorf and Hard 2009).

**MANAGEMENT IMPLICATIONS**

Wild turkeys are one of the few birds hunted during their breeding season, making it prudent to explore effects of
hunting on behaviors and fitness. Managers are faced with balancing hunter satisfaction, which is predominately influenced by turkey gobbling and abundance, along with maintaining sustainable populations available for recreational use. Our results are relevant to managers of publicly hunted areas charged with balancing hunting activity, hunter satisfaction, and turkey harvest. We observed that reproductive activities of female turkeys had a positive influence on daily gobbling activity of males. Conversely, we observed marked declines in daily gobbling activity after onset of hunting, and noted that hunting and harvest of males had a disproportionately greater negative effect on daily gobbling activity than the positive effect of female reproductive behaviors. Our findings suggest that hunting and harvest of males are important determinants of gobbling activity that could contribute to future declines in hunter satisfaction. We recommend that managers maintain hunting below a threshold that will cause daily gobbling activity to decline. Our findings suggest that a proxy of about 4 males removed per 10 km$^2$ would be such a threshold, and we encourage future work to test this threshold across other geographies. Furthermore, future research should experimentally manage harvest to decouple gobbling (and reproductive) and hunting activity, in hopes of reducing confounding effects of concomitant declines in gobbling and increased hunting activity.

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