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# Nocturnal Predation of Females on Nests: An Important Source of Mortality for Golden-cheeked Warblers?

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ABSTRACT.—We monitored 124 female Golden-cheeked Warblers (*Dendroica chrysoparia*) at 133 nests with video cameras from 1997–2002 and 2005–2006 at two study areas in central Texas, USA. Six adult females were depredated by snakes in 781 camera-monitored intervals when females were on the nest at night and exposed to possible nocturnal predation. Daily nest survival was 0.971 (95% CI: 0.959–0.980) and daily adult female predation while nesting was 0.008 (95% CI: 0.003–0.017). We estimated that 14.6% of breeding females were depredated on the nest during the breeding season based on the observed survival rates and assuming females whose first nest was unsuccessful and which survived attempted a second nesting attempt. Females were captured 75% of the times they were on the nest at the time of a nocturnal nest predation by a snake. Predation of nesting females is potentially an important source of mortality for Golden-cheeked Warblers, and warrants further investigation. *Received 7 June 2008. Accepted 30 August 2008.*

Survival of migrant songbirds is generally thought to be high during the breeding season (Sillett and Holmes 2002); however, there is little direct evidence of the frequency or sources of adult mortality during this period. Documenting any predation event on the nest is difficult (Pettingill 1976) and adult mortality is usually inferred from remains left at the nest (Sherry and Holmes 1997, Flaspohler et al. 2001). Often evidence suggests that adults were killed in defense of the nest or circumstantially, and were not the intended victim (Fendley 1980, Quinn 1985, King 1999). Interpretation of evidence at the nest, however, can be an unreliable method to identify nest fate, cause of nest failure, or identity of a predator (Thompson et al. 1999).

Video surveillance has recently been shown to be an effective and reliable method to identify and evaluate the importance of nest predators (Thompson 2007). The main groups of nest predators identified from these studies were sciurids, corvids, raptors, and snakes. Adult mortality was only observed in two studies using video surveillance to monitor songbirds—a thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*) depredated one Chestnut-collared Longspur (*Calcarius ornatus*) female (Pietz and Granfors 2000) and rat snakes (*Elaphe* spp.) depredated three Golden-cheeked Warbler (*Dendroica chrysoparia*) females (Stake et al. 2004). The potential for snake predation of incubating females has long been speculated (Laskey 1946, Mahan 1956), but this phenomenon has rarely been documented (Plummer 1977, Blem 1979, Carter 1992). We believe snakes pose the greatest risk of depredating adult songbirds at the nest because they are the only group known to be significant nocturnal predators, at least in some habitats (Hensley and Smith 1986, Stake and Cimprich 2003, Stake et al. 2004, Reidy et al. 2008), large enough to kill and consume adult songbirds.

We monitored Golden-cheeked Warbler nests with video cameras and report on causes and rates of nest mortality, and identity of nest predators elsewhere (Stake et al. 2004, Reidy et al. 2008). Our objective in this study is to report on the extent of adult mortality at the nest and discuss its potential implications. Golden-cheeked Warblers, a federally endangered species, are endemic breeders in central Texas with strict nesting habitat requirements (Ladd and Gass 1999). The requisite mixed mature Ashe juniper (*Juniperus ashei*) and oak (*Quercus* spp.) woodlands in which they nest are currently being heavily fragmented

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and developed in historically important parts of the breeding range (USDI 1992).

## METHODS

*Study Area.*—We monitored nests of Golden-cheeked Warblers at Fort Hood Military Reservation, Texas, USA (30° 10′ N, 97° 45′ W) from 1997 to 2002 and in 2005, and in Austin, Texas (30° 23′ N, 97° 34′ W) from 2005 to 2006. Fort Hood (Bell and Coryell counties) is a large, active military base in a rural landscape with discrete patches of Golden-cheeked Warbler habitat separated by open valleys leased for cattle grazing. Austin (Travis County) is a large and growing city with historically large amounts of contiguous breeding habitat currently being fragmented by human development.

*Field Methods.*—We mapped territories of banded and unbanded adults from March to May to establish pairing and nesting status of males, and to narrow the nest-searching area. We searched for nests from March to June, typically using adult behavioral cues to locate nests. We placed miniature video cameras with infra-red illumination (Fuhrman Diversified Inc., Seabrook, TX, USA) that allowed continuous monitoring at as many nests as possible during the incubation and nestling stages, prioritizing nests in the incubation stage. Video cameras were attached by a 20-m long cable to a video recorder and battery placed as far from the nest as possible. We monitored nests daily using a monitor that plugged into the video recorder and did not approach the nest while it was active after the camera was installed. We recorded standard monitoring information daily including nest contents and identified nest predators to the lowest possible taxa when we concluded a predation event had occurred. We used banding and territory status, and nest success information to establish the number of females we monitored with video cameras (several females were monitored with video cameras during more than one nesting attempt). Additional monitoring details are available in Stake et al. (2004) and Reidy et al. (2008).

*Data Analyses.*—We estimated daily survival of nests with a logistic exposure model (Shaffer 2004) in SAS 9.1 (SAS Institute 2004). We coded survival as 1 if at least one egg or nestling in the nest survived the interval and as 0 if all nest contents were destroyed. We fit a model with covariates for date, date$^2$, and date$^3$ to account for potentially non-linear effects of date (Grant et al. 2005, Reidy 2007). We ignored other potential temporal covariates such as nest stage or year because there was not much support for them in previous analyses examining factors affecting Golden-cheeked Warbler nest survival (Stake 2003, Peak 2007, Reidy 2007). We estimated daily nest survival with the above model for median nest interval observed in the study (Shaffer and Thompson 2007).

We similarly estimated female daily survival with a logistic exposure model; we coded survival as 1 if the female survived the overnight observation interval and as 0 if she was depredated. We fit a constant survival (intercept only) model because there were too few mortality events to model as a function of covariates. We only included observations from the days females sleep on the nest because that is when they are potentially exposed to predation (nest days 3–21). We estimated female daily predation as 1 − daily survival.

We estimated total loss of adult females during the breeding season due to predation on the nest based on daily nest survival, daily female mortality, and number of nesting attempts. If daily nest survival is assumed constant, the proportion of nests surviving to any given day of the nest cycle can be estimated as $p_k = s^k$, where $p_k$ is the proportion of nests surviving to day k and s is the daily survival estimate. If the daily mortality of females on the nest is defined as m and is also assumed constant for nest days 3–21 (assuming the female begins incubating the penultimate egg of a typical 4-egg clutch, Pulich 1976), the proportion of females lost to predation during the first nest attempt is: $F_1 = \Sigma_{k=3-21} (s^k \times m)$. If we assume females which were successful in their first nesting attempt do not re-nest and that all females whose first attempt failed and which survived re-nest, the proportion of females lost to predation during a second nesting attempt is: $F_2 = (1 - p^{25} - F_1) \times F_1$, where $p^{25}$ is the proportion of females which were successful during their first attempt and $F_1$ is the proportion of females which died on their first attempt. The total proportion of nesting females dying due to predation on the nest, $F_T$, can be estimated as: $F_T = F_1 + F_2$.

TABLE 1. Video camera-monitored nests of Golden-cheeked Warblers at Fort Hood, Texas, USA from 1997 to 2002 and 2005, and in Austin, Texas, USA, in 2005 and 2006. Most years had ≥4 nests with cameras during days 3–21 of the nest cycle and produced at least one snake predation of a female attending the nest.

| Year | Site | Number of nests monitored with cameras (total observation days) | Number of nests monitored during days 3–21 (total observation days) | Number of female mortalities (number of females monitored) |
|---|---|---|---|---|
| 1997 | Fort Hood | 1 (13) | 1 (10) | 0 (1) |
| 1998 | Fort Hood | 2 (36) | 2 (28) | 0 (2) |
| 1999 | Fort Hood | 2 (21) | 2 (16) | 0 (2) |
| 2000 | Fort Hood | 6 (40) | 4 (28) | 1 (6) |
| 2001 | Fort Hood | 30 (292) | 26 (198) | 0 (29) |
| 2002 | Fort Hood | 24 (189) | 15 (125) | 2 (20) |
| 2005 | Fort Hood | 7 (68) | 6 (32) | 0 (7) |
| 2005 | Austin | 18 (174) | 13 (100) | 1 (16) |
| 2006 | Austin | 43 (364) | 31 (244) | 2 (41) |

Females rarely made a third nesting attempt after two failures and we recorded no instances of double brooding (J. L. Reidy, pers. obs.).

## RESULTS

We monitored 133 nests (61 in Austin and 72 on Fort Hood) representing 124 females with video cameras for an effective sample size of 1,197 nest monitoring intervals (Table 1). We recorded 43 nest predations on video; however, 11 of these were considered successful because ≥1 host young fledged despite a nest predation event. Rat snakes were the leading predator at both sites, depredating 21 nests. Texas rat snakes (*Elaphe obsoleta lindheimeri*) and a Great Plains rat snake (*E. guttata emoryi*) depredated 20 and 1 nests, respectively. We recorded females being captured and consumed during six of these nest predations, three at each site. We identified Texas rat snakes as the predator at five adult predation events and a Great Plains rat snake at one.

Daily nest survival was 0.971 (95% CI: 0.959–0.980). We observed six predations of females by snakes over 781 observation days during nest days 3–21, resulting in a daily female predation rate of 0.008 (95% CI: 0.003–0.017). We estimated 0.103 (or 10.3%) of breeding females were depredated during their first nesting attempt. If all surviving females with failed nests re-nested (42% of initial population), we estimated 0.043 (or 4.3%) of breeding females were depredated during their second nesting attempt. Total losses of breeding females to predation amounted to 14.6%. If females spent one less or one more night at the nest (all else being equal), these totals would be 14.0 or 15.2%, respectively.

All predations of females were nocturnal, occurring between 2103 and 2352 hrs CDT from 18 April to 9 May in Austin, and between 0022 and 0448 hrs from 23 April to 17 May at Fort Hood. All nest predations by snakes ($n = 21$) were nocturnal but one, occurring between 2001 and 2352 hrs from 18 April to 19 May in Austin and between 2037 and 0448 hrs from 23 April to 10 June at Fort Hood. One additional nest predation by a snake occurred at 1024 hrs at Fort Hood.

Snakes were not deterred by Golden-cheeked Warblers nesting in the canopy. Nests with depredated females were on average 5.2 m ($n = 6$; range = 4.2 to 6.1 m) above ground and 1.8 m from the main trunk ($n = 6$; range = 0.3 to 4.5 m) on trees with a diameter at breast height averaging 23 cm ($n = 6$; range = 12 to 43 cm). Nests were in Ashe junipers, which are characterized by rough, peeling bark.

Four of the total snake nest predations (19%) were in the incubation stage and 17 (81%) in the nestling stage. Two of four (50%) snake nest predations during the incubation stage resulted in predation of the female. Of the remaining two, the female was present at one and left the nest 3 min prior to the snake appearing at the nest (this was the one diurnal snake predation), and at the other nest, the female abandoned the nest just after sunset, several hrs before the snake predation. A Mourning Dove (*Zenaida macroura*) nest

located just below this nest was depredated the same night suggesting the female may have flushed from and possibly abandoned the nest due to the presence of a predator below her. Four of 17 (23%) snake nest predations during the nestling stage resulted in predation of the female and occurred while the nestlings were young (≤5 days old) and in need of brooding. Eleven (65%) snake nest predations occurred late in the nestling stage when females were no longer brooding. Four of these nest predation events caused at least one nestling to prematurely fledge ('force-fledge') and two nests had already fledged young prior to the snake predation event. Females were present but escaped the remaining two (12%) snake nest predations. Both nests contained 5- or 6-day old nestlings. The female was brooding at one nest and left the nest as the snake appeared in view. This predation event occurred about 30 min after sunset while the female was still alert. She peered below the nest 3 min prior to the snake appearing on camera and flew off the nest as the snake approached. The female at the other nest was sleeping on the rim of the nest and was actually pushed off the nest by the snake as it investigated the nestlings. The snake lurched after the falling female, but when it returned to view at the nest seconds later, it did not appear to have caught the female. This female was not seen returning to the nest. Females were preyed upon during 29% (6/21) of the total snake nest predations, 67% (6/9) of the times they were present during the nest predation, and 75% (6/8) of the nocturnal nest predations for which the female was at the nest.

## DISCUSSION

Snakes consumed females attending the nest during the majority of nest predation events for which females were present, a finding no other study has reported for a songbird. Predation by snakes on female Golden-cheeked Warblers attending the nest likely represents an important source of mortality during the breeding season for this species. Rat snakes are well-known tree climbers (Tennant 1998) and would not be deterred from climbing trees with rough bark (Mullin and Cooper 2002) such as Ashe juniper. A study documenting nest predators of Black-capped Vireos (*Vireo atricapillus*) at Fort Hood also identified Texas rat snakes as the most frequent predator, responsible for 18 of 48 nest predation events (Stake and Cimprich 2003). However, no nest predation by a snake resulted in depredation of an adult. Black-capped Vireos nest in shrubs and the nesting substrate is likely not as stable or sturdy as that of Golden-cheeked Warblers. Adults spending the night at the nest in shrubs would more likely be alerted to an approaching predator.

Little is known about adult survival for Golden-cheeked Warblers, particularly females, and we cautiously speculate about possible implications on population dynamics. Pairing success is commonly used as an indicator of habitat quality with presence of unpaired males suggesting low habitat quality (Gibbs and Faaborg 1990, Bayne and Hobson 2001). Golden-cheeked Warbler pairing success is generally high (often ≥90%) for territorial males at sites considered to be high-quality habitat (Jetté et al. 1998; Becker 2006; Peak 2006; J. L. Reidy, unpubl. data), while lower quality habitat in Austin had low (20–33%) pairing success (Becker 2005, 2006). Pairing success was also lower for second-year males than older males at Fort Hood (Jetté et al. 1998). These observations of differential pairing success are indicative of a population with a lower number of females than males, and we suggest female-biased mortality during the breeding season may be a contributing factor. Better estimates of adult and juvenile survival for males and females, pairing success, and existence and extent of potential non-territorial, or ''floater'' males (Bayne and Hobson 2001) are necessary to examine if predation on adult females during the breeding season affects long-term stability of Golden-cheeked Warbler populations.

Predation of adult females at the nest may partially explain the skewed adult survival rates and sex-ratios exhibited by many songbirds. Wood Thrush (*Hylocichla mustelina*) females had lower survival rates than males during the breeding season (Powell et al. 2000, Coulter 2005). Survival was also lower for Black-throated Blue Warbler (*Dendroica caerulescens*) females than males during the breeding season (Sillett and Holmes 2002) and Ovenbird (*Seiurus aurocapillus*) females had lower annual survival estimates than males (Bayne and Hobson 2002). Many mi-

grant songbird populations exhibit male-biased sex-ratios during the breeding season (Gibbs and Faaborg 1990, Villard et al. 1993, Van Horn et al. 1995). Migrant songbird populations can be more sensitive to changes in adult survival than juvenile or nest survival (Noon and Sauer 1992, Donovan and Thompson 2001). The loss of substantial numbers of breeding females to predators simultaneous to nest failure may be calamitous, especially for an endangered species. Extinction risk for endangered species is greater for populations with male-biased sex-ratios (Donald 2007) and for small, isolated populations experiencing recent habitat fragmentation (Dale 2001).

Songbirds nesting in climates hospitable to snakes, particularly those exhibiting nocturnal foraging patterns such as rat snakes, may be particularly vulnerable to predation while on the nest (Carter et al. 2007). Open-cup nesters may have more opportunity to escape than cavity nesters, but species which nest on sturdy substrates, such as Golden-cheeked Warblers, or on the ground, may not detect a predator in time to escape, especially during the night. We suspect more nesting studies using time-lapse video surveillance in geographic regions with nocturnal snakes will reveal additional predation on incubating and brooding adult songbirds. We believe adult mortality during the breeding season warrants further investigation for other species and ecosystems.

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